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THE HISTORY OF A REMOTE CARIBBEAN CAY, ISLA AVES, AND ITS TERRESTRIAL BIOTA: A REVIEW AND NEW DATA

HAROLD HEATWOLE[1], FRANK TORRES[2], SUSAN K. KING[3], ADOLPHE O. DEBROT[4], AND JAVIER TORRES[5]

ABSTRACT

When discovered in the early 1500s, Isla Aves was a remote guano-covered Caribbean island much larger than it is at present. Gradually over subsequent centuries it became smaller, either leaving behind, or supplanted by, several small cays, now represented by a single coral cay located west of Dominica and south of St. Croix. As it shrank, some of its original biota disappeared, never to return. This island was visited many times over the intervening centuries with explorers recording its dimensions, location, physical features, and notes on various components of its terrestrial biota. Only since 1978 has it been permanently occupied by people. The present paper reviews its history, reports on a previously unpublished survey of its terrestrial biota in 1966, and chronicles what is known about the changes in that biota over time, including recent and ongoing research emanating from an on-site Venezuelan research facility. The various reports over the ages can serve as "time capsules" providing insight into the responses to change under previous conditions, and the present one as a baseline for evaluating those that may result from projected climatic instability and rising sea-level.

Keywords: image classification; island biogeography; remote sensing, seabirds; sea turtles; terrestrial arthropods

INTRODUCTION

Isla Aves is a small, calcareous sandy island (coral cay) in the Caribbean Sea surrounded by a fringing coral reef about 500 km north of Venezuela, the country to which it belongs (Maloney and Schubert 1968) (Fig. 1) and lying somewhat more than 200 km to the west of its nearest island, Dominica. Thus, it is remote, being neither a part of the Greater Antilles, Lesser Antilles, West Indies, or any other Caribbean grouping of islands. At the time of a visit by two of the authors (HH, FT) on 12–13 May 1966, Isla Aves was

> a long, narrow island with the long axis roughly north to south, slightly curved with the northern and southern ends bending toward the west. It has the shape of a slightly curved dumbbell, the two ends being wider than the central strip connecting them...the island is 648 m long with the widest part of the northern end being 107 m wide; the widest part of the southern end is 53 m and the narrowest point in the middle only 14 m. It is surrounded by coral reef. The island's substrate is coral sand with scattered blocks of dead coral. (HH field notes)

[1] Department of Zoology, University of New England, Armidale, NSW 2351, Australia and Department of Biological Science, North Carolina State University, Raleigh, NC 27695-7617, USA.
[2] Department of Biology, University of Puerto Rico, Humacao, PR 00792; present address: 114 Mango Beach, The Village at the Hill, Ceiba, Puerto Rico 00735, USA.
[3] 58 Everett Street, Guyra, NSW 2365, Australia.
[4] Wageningen Marine Research, Wageningen University and Research Centre, P.O. Box 57, 1780 AB, Den Helder, and Marine Animal Ecology, Wageningen University and Research Centre, P.O. Box 3700 AH, Wageningen, The Netherlands.
[5] 36 Camino de Las Azucenas, Sabanera del Rio, Gurabo, Puerto Rico 00778, USA.

Isla Aves was discovered by the Spanish during their era of exploration of the New World. The earliest extant map showing its location was issued in 1529 (Ribeiro 1529; Urbani Patat 2019). In 1865 Queen Isabella II of Spain put Isla Aves under the control of Venezuela (Anonymous 1865), which has maintained sovereignty until the present day.

Over most of its history neither the island, nor its satellite cays, were settled by humans although for a time it was mined for guano, and until recent years it was visited regularly by the inhabitants of various other islands to harvest seabirds' eggs and green turtles. Now there is a permanent research establishment located at the edge of the island**.**

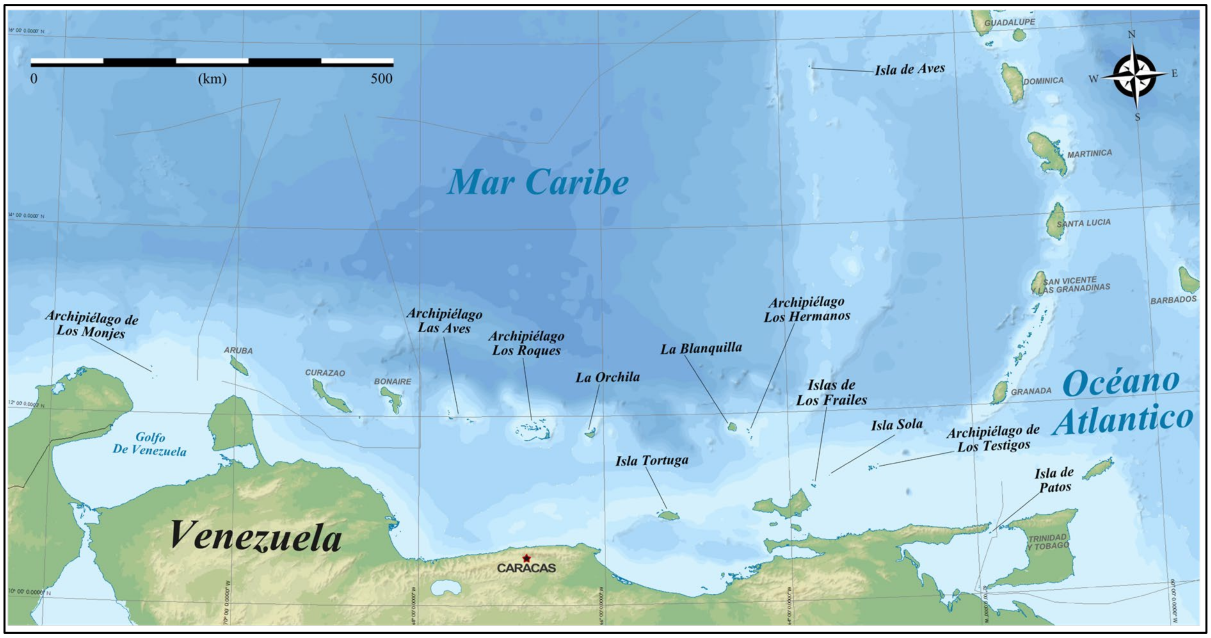

Figure 1. Topographic and political map of the Federal Dependencies of Venezuela, southern Caribbean. From "VE-Dependencias Federales ubicaicion.png," Wikimedia Commons (https://commons.wikimedia.org/wiki/File:VE-Dependencias_Federales_ubicacion.png). Author: Unukalhai (https://commons.wikipedia.org/wiki/User:Unukalhai); created 10 June 2013; CC BY-SA 3.0. Added elements: Scale bar = 500 km; north compass. Created using www.inkscape.org by User: Unukalhai.

Isla Aves lies within the Caribbean hotspot of biodiversity, one of 25 such areas designated for the world (Myers et al. 2000). Various aspects of the marine biota of the reef at Isla Aves have been studied, including the fish fauna (Brownell et al. 1973; Brownell and Guzmán 1974; 87 species in 65 genera and 41 families), corals (Yranzo et al. 2014; 4 hydroid species, 36 species of stony corals, and 13 of octocorals), sponges (Villamizar et al. 2019; 77 species), and plankton (Pereira et al. 2018; 191 species).

There is no sharp line of demarcation between the marine and terrestrial environments. The present paper deals with the terrestrial biota, but its definition is perhaps somewhat broader than usual as many of the species that occupy the land there interact trophically, at least sometime during their life history, with the marine environment, e.g., sea turtles, seabirds, and some isopods and crabs.

Various visitors to Isla Aves over the centuries have reported on its size, topography, geology, fauna, and flora. This body of information is scattered and difficult to access but is of great value as it serves as a benchmark of antecedent conditions against which future events can be evaluated as global instability worsens and fragile ecosystems become increasingly vulnerable. The present paper summarizes and re-interprets the changes chronicled in the literature and adds previously unreported data.

PREVIOUS WORK

Geological History of the Aves Ridge

Isla Aves lies on the arcuate Aves Ridge that stretches from Venezuela toward the Greater Antilles in the eastern Caribbean Sea, west of the Lesser Antilles island arc (Neill et al. 2011) (Fig. 1). It extends from about the latitude of the Lesser Antillean Island of Grenada north approximately to the latitude of Dominica (Zuloaga 1955). The ridge is about 670 km long and up to 100 km wide and is a remnant of the Great Arc of the Caribbean that formed about 80–75 mya (Neill et al. 2011). It rises about 2,000–3,000 m above the ocean floor and, consistent with its shallow submergence over a long time, has no accumulation of sedimentary deposits (Neill et al. 2011). Dredged carbonate samples indicative of active coral growth demonstrate that significant portions of the Aves Ridge were in shallow water during the Eocene and Early Miocene. Later they subsided by 400–14,000 m (Padron et al. 2018) and Isla Aves is the only part that is now above sea level.

Based on seismic interpretation of carbonate platforms the Aves Ridge has been shown to have subsided together with the Grenada Basin since at least the Middle Eocene (Garrocq et al. 2020). It further showed slowing of subsidence or even an uplift during the Late Oligocene, and an accelerated subsidence (0.08–0.12 mm yr^{-1} at positions roughly 400 km south from Aves Island), during the Late Miocene (Garrocq et al. 2020). During that subsidence, major sections of the ridge remained shallow enough to develop reefal carbonate platforms. Schubert and Laredo (1984) estimated the present (slow) rate of subsidence of the Aves Ridge at Aves Island (based on dredge samples) at 0.04–0.06 mm.yr^{-1} since the Early Miocene

Temporal Changes in the Physical Characteristics of Isla Aves

Number of Islands

Early maps and notes by Alonso de Chaves in 1537 indicated Isla Aves to be an islet alone in the sea (Castañeda Delgado et al. 1977). The first report that there were more islands than one was Labat's (1722) indication that in 1705 there was a larger round island with two smaller islets to its west, confirmed by four subsequent maps (Homan 1730; Seutter and Lotter 1739; Haupt 1740; de la Rochette 1784). Later Furlong (1800; 1804), Blunt (1822; 1827), Purdy (1824), and de Genouilly and Chaucheprat (1842) all recorded two islets or barren rocks on the western and northwestern sides joined to Isla Aves by shoals and breakers at low tide. A map published in 1868 by Dirección de Hidrografía (Spain) showed only one island. Thereafter, only one small island has been indicated. Thus, the reduction from one island with two satellites to a single island probably took place sometime after 1842 and before 1868.

The current configuration of Isla Aves is likely to have formed upon the same shallow reef on which the former island rested (Fig. 2). The area of the original large island (about 14 × 13 km) is greater than the reef on which the present Isla Aves is located, indicating that the reef itself may have undergone significant reduction in size since 1705. Mitchell (1957) noted that the reef surrounding Isla Aves underwent drastic reduction in size just over the period of 1939–1954, when many reefs protecting the island on the windward side disappeared.

Location of Isla Aves

The reported location of Isla(s) Aves remained remarkably consistent over more than three centuries (Fig. 2). The coordinates of the satellite islands were never recorded; however, in 1705 they were about 400 m off the west coast of the main island (Mitchell 1957). In 1804 they were joined by shoals to the present Isla Aves. Significant movements of sand cays across their reefs have been observed elsewhere (Flood and Heatwole 1986) but records of latitude remained constant throughout the recorded history of Isla Aves.

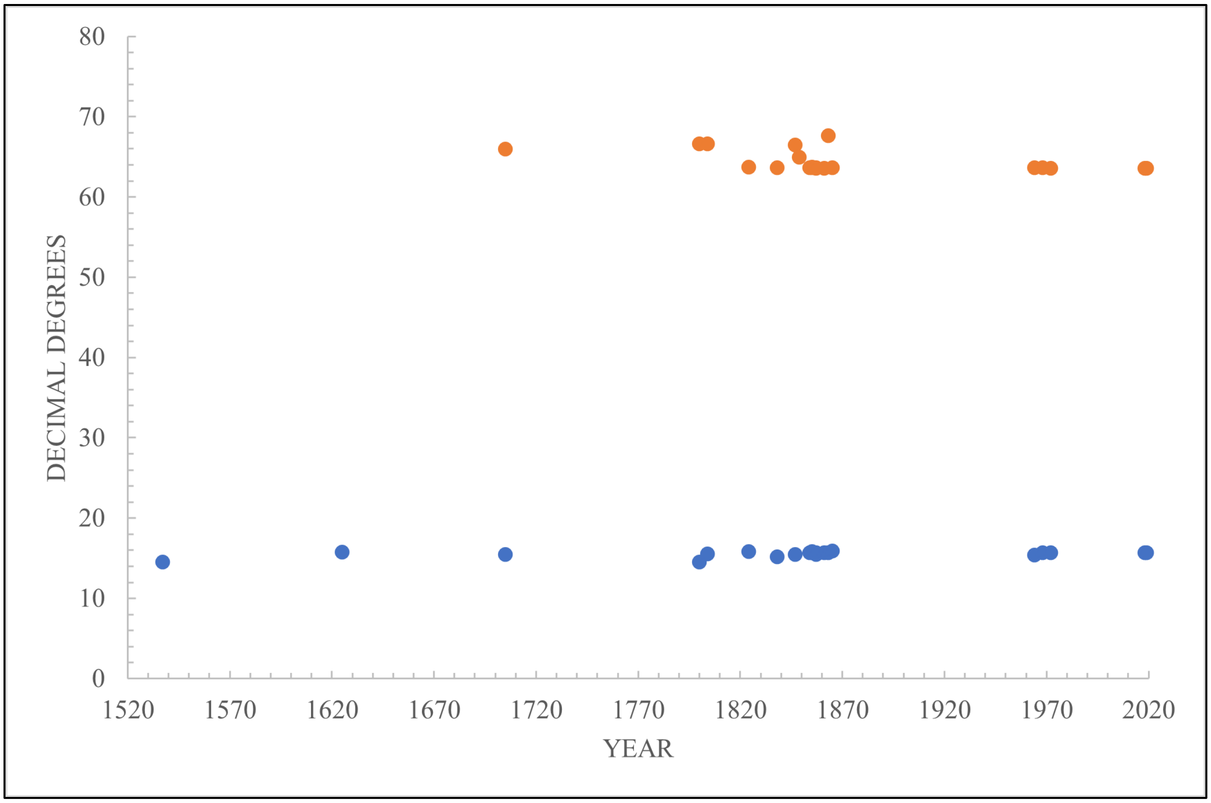

Figure 2. The latitudes (in blue) and longitudes (in orange) of reported locations of Isla Aves Island(s) over about five centuries. Original values were converted to decimal degrees. Data from Blunt (1863); Brownell and Guzman (1974); Buchanan 1861); Casteñeda Delgado et al. (1977); de Laet (1643); Furlong (1800, 1804); Gibbs (1860); Hammelberg (1901); Heatwole et al. (this paper); Hurst (1847); Jones (1857); Labat (1722); Laurance (1849), Maloney and Schubert (1968); Marrero (1964); Pereira et al. (2018); Prieto Torres et al. (2013); Purdy (1824); United States Navy Hydrographic Office (1840–1950); Villamizar et al. (2019); and Whish (1838).

Longitude is much harder to measure accurately and the earliest visitors to Isla Aves reported only latitude, resulting in considerably more scatter of values of longitude until about 1880, after which recorded longitudes were as constant as recorded latitudes. The most recent coordinates of Isla Aves measured *in situ* were latitude 15°40'08"N to 15°40'23.7"N (south tip to north tip) and longitude 63°36'59.9"W to 63°36'59.2"W (east coast to west coast) (Villamizar et al. 2019). Mapping performed in October 2021 with remotely sensed images placed the island's present location at latitude 15°39'58.6"N to 15°40'16.7"N (south tip to north tip) and longitude 63°37'3.93"W to 63°37'11.37"W (east coast to west coast) (SKK: present paper).

Shape of the Island(s)

Maps and notes by anonymous cartographers from 1536 to *ca*. 1540 (Urbani Patat 2019) and by A. de Chaves in 1537 (Castañeda Delgado et al. 1977) indicated that Isla Aves was rounded or ovoid in form. A map by Dudley (1647) shows it that way but somewhat lobulate around the edges; however, some other islands on that map (Fig. 3) that are not now lobulate were also shown that way.

Figure 3. A chart of the eastern Caribbean prepared by Sir Robert Dudley Jr., Earl of Warwick and Leicester, Duke of Northumberland, in 1647. Note that the various islands and shoals are of approximately the correct size, shape, and location as at present, but that Isla Aves (label added) is portrayed as much larger and rounder than at present. Material is in the public domain.

The island was longer than broad in 1705 (Labat 1722). Jeffrey's (1775) map portrays the island as somewhat elongate in a southwest to northeast direction. From 1835 (Anonymous 1835) to the present time the shape consistently has been described as elongate with much variation around wider northern and southern ends and a constricted central section which was at times submerged (Mitchell 1957; Urbani Patat 2019; Lazell 1967). Thus, there may have been periods of two islands (attached at low water), alternating with periods of a single connected island (as at present).

Area of the Island(s)

Estimated areas of Isla Aves declined markedly from historic visits to more recent technologically advanced surveys. Mitchell (1957) reviewed the various estimates of the island's area and reported the following: Year 1647 (115 km^2 or 11,500 hectares); 1705 (500 h); 1840 (19.5 h); 1850 (24 h); 1939 (8.5 h); 1955 (5.2 h). Since then, Bisbal (2008) reported an area of 4.1 ha. Since about 1820, areas based on measured lengths and widths of the island have been consistently under 5 h.

Length and Width of the Island(s)

Zuloaga (1955) noted that by 1954 Isla Aves had shrunk to a much smaller size than that formerly registered by British surveys. Lazo (2015) suggested that the island had decreased greatly from a relatively large island to a much smaller cay over its history. Mitchell (1957), after weeding out records deemed unreliable, concluded that "It seems well enough established that within a period of some 300 odd years at least the essential topographic features of Isla de Aves have undergone change" and "the island has 'migrated' some 75 km eastwards." The latter conclusion, however, does not accord with geological possibility or with the coordinates mentioned above. Coral cays, such as the present Isla Aves, can move short distances over the reef on which they are anchored but none have been observed to migrate so far or off their foundation reefs.

We used reported values of length and width after eliminating records that repeated values from earlier sources. During its recorded history Isla Aves decreased in size from more than 10 kilometers in diameter in the early 1600s to a small island fluctuating in length around a mean of about 625 m and about 167 m in greatest width from the early 1800s onward (Fig. 4). A decrease of that magnitude can be ascribed to ordinary processes of erosion of the island and the supply of sediment but could have been exacerbated by extreme storms as well as a rise in sea level and possible tsunamis generated along the Lesser Antilles.

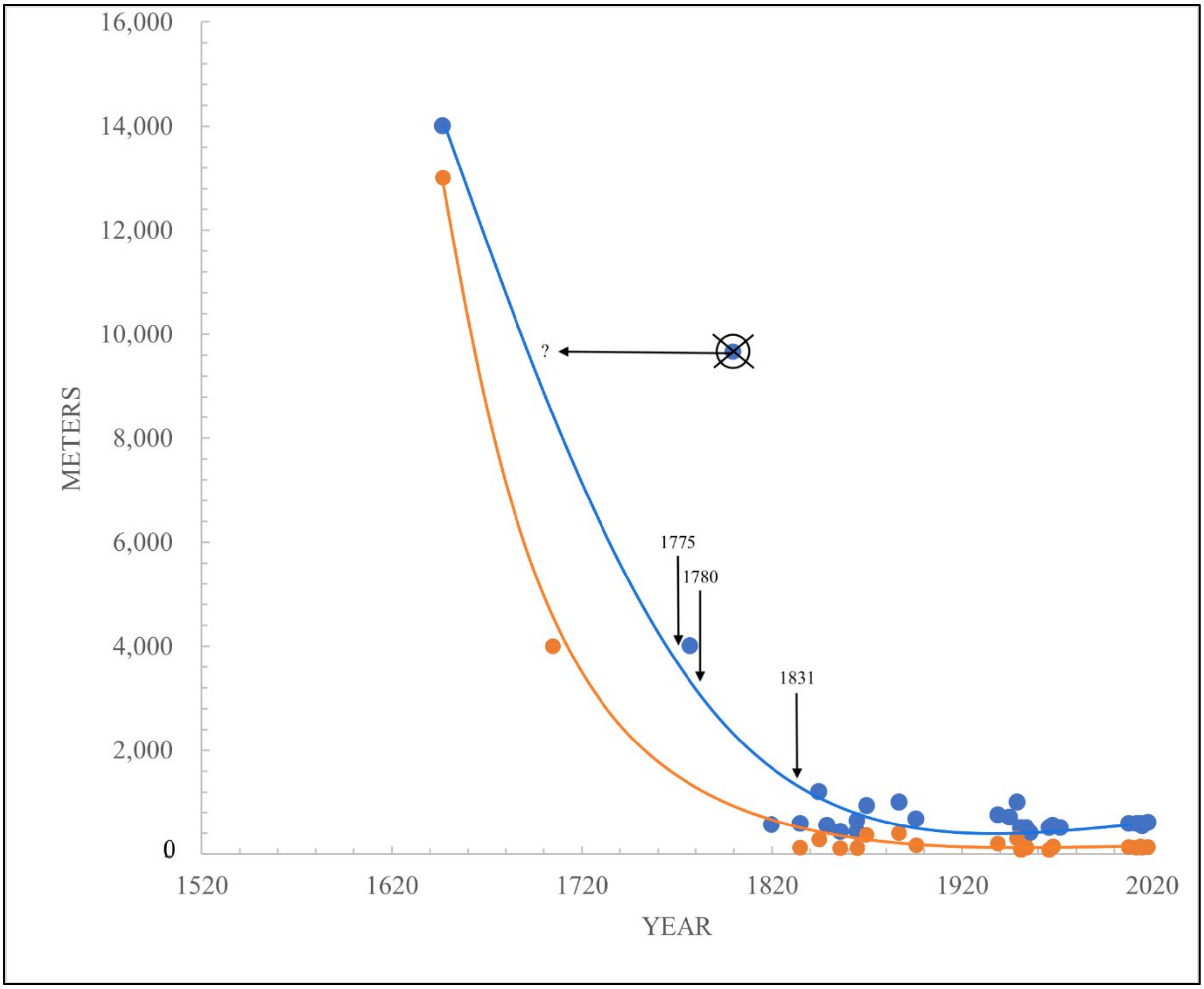

Figure 4. The lengths (or when round, the diameter) (in blue) and widths (in orange) of Isla Aves as reported over about four centuries. The X indicates that its underlying encircled dot probably merely represents an unwarranted repeat of an earlier accurate location and should be deleted; the horizontal arrow with a question mark points in the direction where the proper position probably should be. The vertical arrows indicate the dates of three hurricanes known to pass directly over Isla Aves (see text). Data from Anonymous (1835); Bisbal (2008); Brownell and Guzman (1964); Butterlin (1956); De Vaynes van Brakell (1857, 1879); Dirección de Hydrografía (1820); Dudley (1647); Furlong (1796, 1798, 1800, 1804); Gala et al. (1857); Garcia Cruz et al. (2015); Gibbs (1860); Hadgialy (1945); Hammelberg (1901); Harding (1896); Hummelinck (1952a); Labat (1722); Laurance (1849); Lazo (2015); Maloney and Schubert (1968); Mitchell (1957); Oldendorp (1777); Pereira et al. (2018); Phelps (1953); Pinchon (1952); Urbani Patat (2019); Vera and Buitrago (2012); Yranzo et al. (2014); and Zuloaga (1955); the field study by two of the present authors, HH, FT (1966), and the spatial analysis by another present author, SKK (2021).

Maximum Elevation of the Island(s)

Beginning in 1625 Isla Aves was described as almost at sea level (de Laet 1643), low (de Rochefort 1658; Davies 1666), or flat (Anonymous 1689). The early values of the elevation of Isla Aves were reported to be just above 14 m but from 1810 onward (Dirección de Hidrografía 1820), a series of reports indicated much lower levels (Fig. 5) whose variation may reflect differences in accuracy of the reported values, some being estimates rather than precise measurements. However, other differences may be real and due to overwash and erosion during storms and the migration of dunes due to the action of wind.

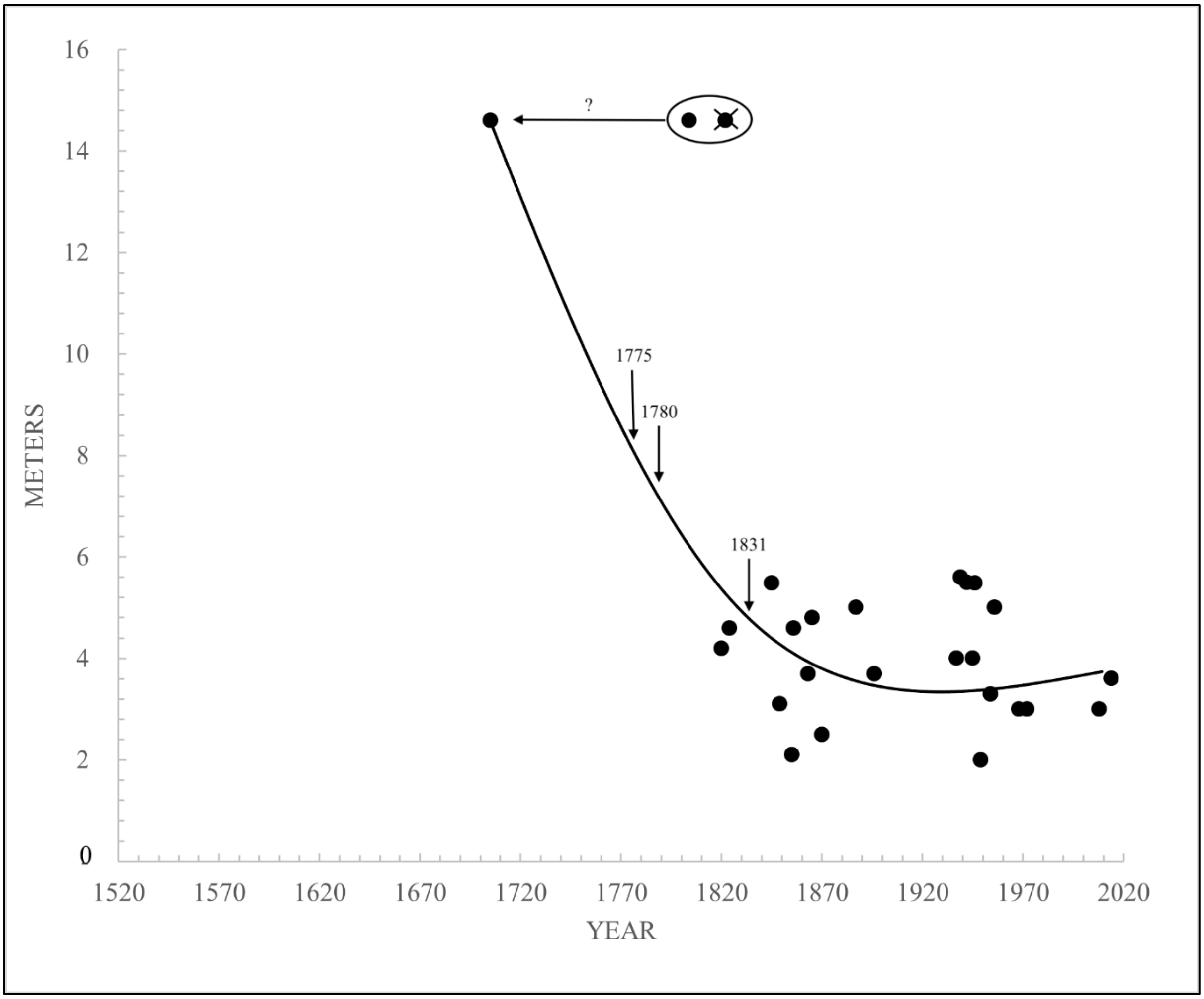

Figure 5. The maximum heights above sea level of Isla Aves as reported over about three centuries. The X indicates that the encircled dots probably represent unwarranted repeats of earlier accurate values that should be deleted; the vertical arrows indicate the dates of three hurricanes known to pass directly over Isla Aves (see text). Data from American Coast Pilot (1863, 1867); Bisbal (2008); Blunt (1827); Brownell and Guzman (1974); Butterlin (1956); De Vaynes van Brakell (1857); Furlong (1800); Gibbs (1860); Hadgialy (1945); Harding (1896); Labat (1722); Laurance (1849); Maloney and Schubert (1968); Mitchell (1957); Phelps (1953); Purdy (1824); West Indies Pilot (1942); Zuloaga (1955); and the field study by two of the present authors (HH, FT 1966).

Stability of the Present Small Island

Maloney and Schubert (1968) inferred that the present-day small cay shifts location on its reef even over short intervals of time driven by erosion on one side and progradation on the opposite side in response to normal oceanic processes. The ends of such cays often move back and forth and lengthen and shorten, with the vegetated core of the island remaining stationary; such movement results in considerable variability in the length of the island. Zuloaga (1955) and Maloney and Schubert (1968) each presented sequential maps of Isla Aves illustrating its successive small changes in shape and location on the reef over time. Mitchell (1957) noted that there was migration of the gravel ramparts on Isla Aves from west to east between 1939 and 1954. Schubert and Laredo (1984) referred to such changes as “normal beach and shore processes” as opposed to those caused by hurricanes. Mitchell’s (1957) observations that (1) all deposits of the modern Isla Aves “are of Recent age and include shell-fragment and reef-detritus limestones…and loose calcareous sands,” (2) “all other minerals were re-worked sediment or chemically precipitated minerals,” and (3) “there are no surface indications of any igneous material” are indicative of a coral cay that likely decreased in size over time, and that the present island is reduced from its original footprint.

Causes of Change

Loss of Protective Coral Reefs

The mortality of corals in the Caribbean is increasing due to the combination of bleaching in response to global rise in sea temperatures, disease, overgrowth of algae, and an influx of wind-born dust from Africa (Shinn et al. 2000; Arnold et al. 2010; Alemu I and Clement 2014; Hughes et al. 2018). The resultant destruction of fringing coral reefs can lead to erosion of islands and even to the complete disappearance of small cays.

Mitchell (1957) noted the decline of protective reefs on the windward (eastern) side of Isla Aves between 1939 and 1954. Brownell and Guzman (1974), however, considered that a general equilibrium existed between the dynamic processes of production and loss of sediment on the reef platform. At that time the island derived invaluable stabilizing protection against waves and tides from dense nearshore ramparts of the branching coral, *Acropora palmata*, at both the northern and southern ends of the elongate island, as well as the common presence of the species along the whole wind-exposed and wave-exposed eastern coast. *Acropora palmata* also has one of the highest rates of growth of all species of coral in the Caribbean (Perry et al. 2013). However, due to the regionwide mass mortalities of *Acropora* that began in the mid-1980s (Aronson and Precht 2001), three decades later Yranzo et al. (2014) documented the virtual disappearance of this large framework-building species from around Isla Aves. Reduced coastal protection by its fringing reef and the consequent decrease in accretion of carbonate due to the loss of *Acropora palmata* and other corals, as well as other marine organisms such as molluscs, foraminifera, echinoids, and coralline algae that also importantly produce essential carbonate sediment, certainly makes the future of Isla Aves much less certain.

Hurricanes and Overwash Events

Storms may have been a major cause of the diminution of Isla Aves. Schubert and Laredo (1984) compared geological maps of 1968 and 1983 and reported that between those dates the prominent southern storm terrace had disappeared, the northern storm terrace had been reduced in area, beach rock had been exposed by removal of covering sand, and shingle beaches reported in 1957 were absent in 1968 but were again present in 1983.

Yranzo et al. (2014) cited a compilation of 113 tropical storms near the island between 1871 and 2008, of which 67 were hurricanes, 36 were storms, and ten were unclassified. It appears that during the period of the greatest decline in size of Isla Aves (late 18th and early 19th centuries), the incidence of catastrophic hurricanes in the Caribbean was higher than in most of the subsequent 20th century prior to 1963 (Table 1). Three hurricanes directly hit Isla Aves between 1775 and 1831 (Table 1; Figs. 4 and 5), all of which occurred *after* the early, drastic reduction in size of the island that had taken place between 1647 and 1705 (Fig. 4). Since there were no direct hits on Isla Aves between 1713 and 1762 (Table 1), the most likely time for a hurricane or hurricanes to have impacted the size of the island would have been between 1647 and 1713. Other hurricanes that passed nearby could have caused significant damage. Because of the paucity of reliable records of the size of Isla Aves during that period, which, if any, hurricane(s) cannot be specified as responsible.

Table 1. Incidence of catastrophic hurricanes in the Caribbean spanning three centuries and the number of direct hits on Isla Aves covering the time that major changes in the size of Isla Aves was taking place. Data directly from, or calculated from, Urbani Patat (2019).

		NUMBER OF HURRICANES		
DATE	INTERVAL (years)	TOTAL	MEAN PER YEAR	DIRECTLY HITTING ISLA AVES
1713–1762	50	10	0.20	0
1763–1812	50	15	0.30	2 (1775; 1780)
1813–1862	50	3	0.06	1 (1831)
1863–1912	50	1	0.02	0
1913–1962	50	8	0.16	0
1963–1970	8	5	0.63	0

The second reduction in reliably reported size of Isla Aves occurred between 1777 and 1820 (Fig. 4) and can be attributed almost certainly to a specific hurricane that directly hit Isla Aves (Table 1). The category 5 El Gran Hurricán of 10–18 October 1780 was the most devastating storm of the 18th, 19th, and 20th centuries and was responsible for the loss of 20,000 lives on various Caribbean islands in its path (Reid 1838; Urbani Patat 2019). This hurricane undoubtedly affected Isla Aves and may have been responsible for its change in configuration.

In 1827 three islands existed before Hurricane Barbados hit Isla Aves directly in 1831 (Urbani Patat 2019). Thereafter the two smaller islands were noted as no longer present. In 1835 the remaining island was described as changed in shape and elevation; both losses were attributed to the impacts of storms and the frequency of hurricanes (Mitchell 1957).

Another possible mechanism for destructive overwash is the tsunamigenic potential in the tectonically active Caribbean basin where active elements such as the Cayman Trough, subduction zones, and submarine slides along the flanks of volcanic islands often result in tsunami (De Buisonjé and Zonneveld 1976; Schwab et al. 1991; Mulcahy 2008; Leslie and Mann 2016), which have been documented since the early history of the island. The decrease in size of Isla Aves could have been accelerated by one or more tsunamigenic events. Schubert and Laredo (1984) concluded that the slow estimated rate of subsidence of 0.04–0.06 $mm.yr^{-1}$ was insufficient to explain the historical changes in the size, shape, and location of Isla Aves on the platform.

We conclude that the configuration of Isla Aves when first reported was a large island lying on, or surrounded by, a much larger reef than the current one. By 1705 the main island had decreased to less than half its previous size (length, width, and height). By the early 1800s, there was only a small sand cay that fluctuated slightly in size and shape around a stable mean. It was flanked by two satellite islets from at least 1705 until 1842. These satellite islands were sand cays that formed *in situ* entirely from reefal material. The original large island disappeared except possibly for a remnant of its beach consisting of reefal materials. This remnant either remains as the present-day Isla Aves, or it coalesced with one or both satellite sand cays to form the present Isla Aves. It is possible that the present Isla Aves represents one of the original satellite cays, or a coalescence of both. Finally it could be that all previous islands disappeared and the present cay formed *de novo* on the reef. These scenarios all are consistent with the stable geographic coordinates reported for Isla Aves throughout its recorded history.

The Modern Reef Surrounding Isla Aves

For details of methods used in mapping, see APPENDIX 1. Our measurements of the digitized outline of the island from an image captured in August 2021 gave Isla Aves a perimeter of 1.342 km (as opposed to 13 km in 1705) and an area of 33,573 m^2 (3.36 h). During its recorded history Isla Aves decreased in size from more than 10 km in diameter in the early 1600s to a small island fluctuating in length around a mean of about 625 m and about 167 m in greatest width from the early 1800s onward (Fig. 6).

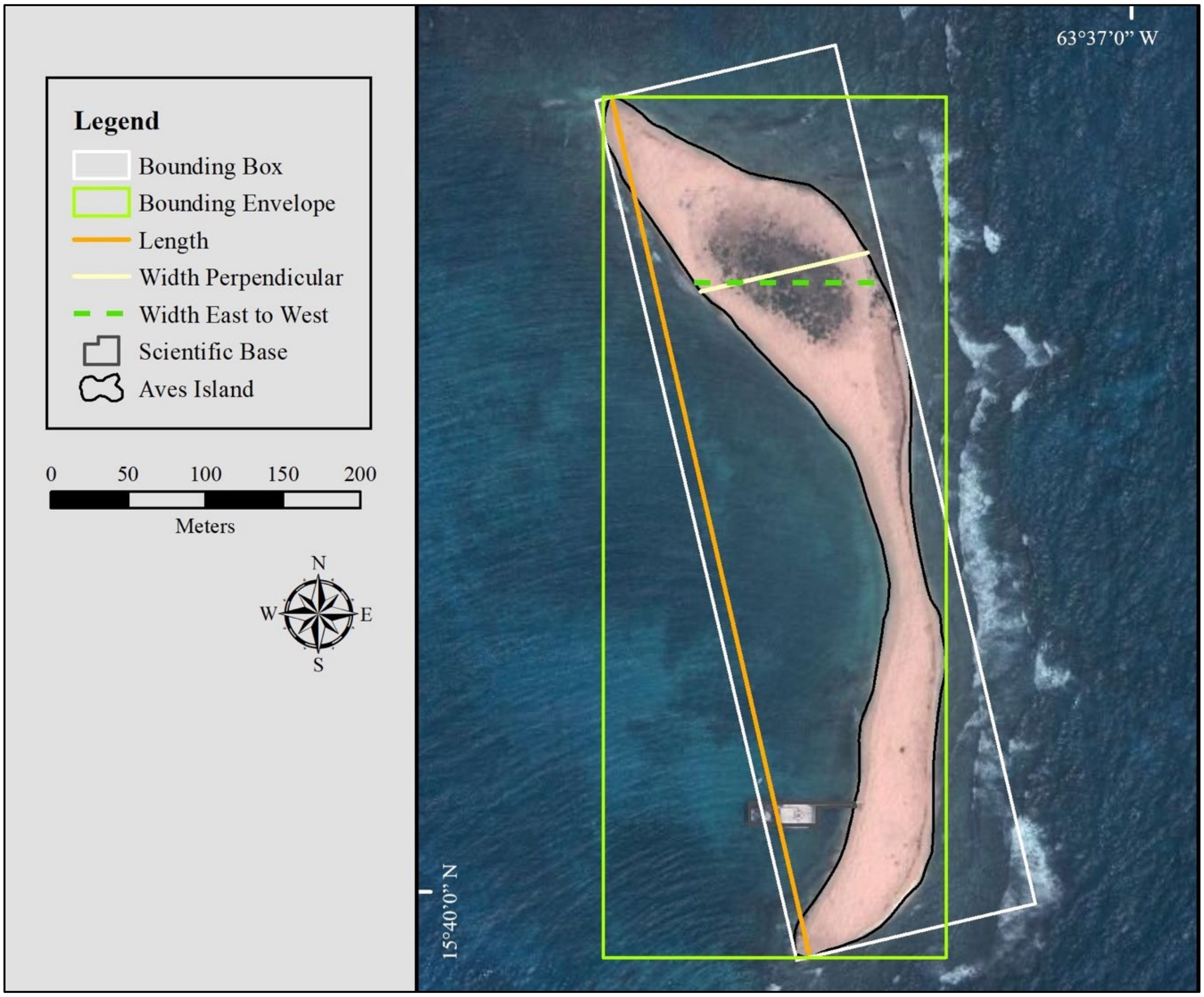

Figure 6. The dimensional measurements of Aves Island can vary depending on the method used to take the measurements.[6] Basemap: World Imagery (Clarity). Source: Esri, DigitalGlobe, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AeroGRID, IGN, and the GIS User Community. Scientific Base refers to Base Cientifico Naval Simón Bolívar. Map by author SKK.

Aves Island appears to be surrounded by a circular area of reef and shallows that is surrounded again by a larger, obovate reef. The island is positioned in the northwestern quadrant of this larger reef, approximately 913 m south, 930 m west, 3,050 m north and 856 m east of the outer reef (Fig. 7).

[6] A complication with these measurements is the irregular shape of the island. For example, an envelope (i.e., a bounding box with the edges aligned to the cardinal directions) indicates that the north-south extent of the island is 555 m and the east-west extent of the island is 221 m. However, the island is not oriented so that its longest axis runs north to south. A bounding box (with the longest edge aligning with the longest axis of the island, bearing 167°) indicates the length of the island to be 569 m and the widest extent to be 158 m, but most of the line that runs between the northern and southern points lies mainly over water, not over the island. Furthermore, the widest extent that lies perpendicular to the line between the northern point and southern point is 111 m, but the widest portion of the island from east to west is 121 m (Fig. 5).

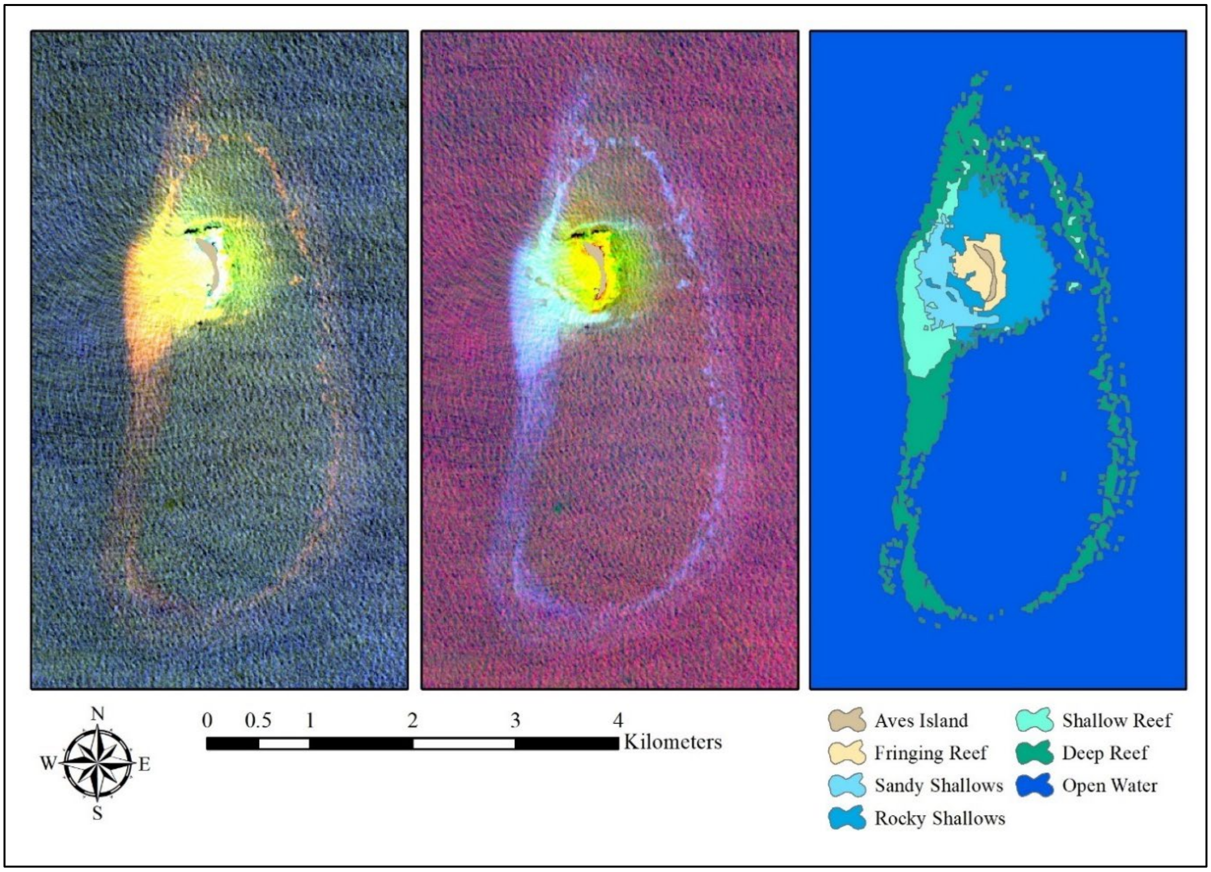

Figure 7. Aves Island and its protective reefs shown as a false-color composite (2,3,4) of Sentinel-2 imagery (left), the image from the principal components analysis of the Sentinel-2 imagery (center), and the final classified image (right). Maps by author SKK.

The image of the Principal Components Analysis (PCA) highlighted differences in the shallows surrounding the island, likely due to the variance in the depth of penetration of the visible bands in water (Fig. 7). Spectral similarities in the very shallow waters off the eastern side of the fringing reef and over the fringing reef appear to have overestimated the extent of the fringing reef on the eastern side of the island compared to Villamizar et al. (2019), who provided a recent map of Isla Aves and its fringing reef, reef platform, and part of the shallow reef around it; our mapping shows a further extent of the shallows and the full extent of the outer protective reef (Fig. 7). Together, their map and ours can serve as a baseline against which future changes can be assessed.

The Vegetation

During the 1966 expedition, the percent cover of plants was estimated by walking along a series of parallel transects, 20 paces apart, each across the width (east to west) of the island. Along each transect the substrate (bare ground or species of plant) at the tip of the right foot was recorded every ten steps. A survey of animals was achieved by searching each habitat on the island, including the intertidal parts of the beach, and preserving examples of each species of invertebrate found. Shells and blocks of dead coral were lifted and a search of the items and the ground beneath them was made. Plants were examined for attendant insects and any litter beneath them spread out and searched. The preserved specimens were sent to various specialists for expert identification. Birds, sea turtles, and plants were identified by sight and no specimens were collected.

In 1966 (the present paper), the vegetation was sparse with bare ground accounting for 87% of the area. *Sesuvium portulacastrum* was the dominant plant and accounted for a coverage of 12% of the terrain with *Portulaca oleracea* only accounting for 0.6%. In some places the *Sesuvium* formed a veritable green sward, but in others it was sparser and mostly withered or dead, possibly because of the action of sea birds. In places *Portulaca* occurred at the border of patches of *Sesuvium* but at others as single plants or in small groups in otherwise bare areas.

A third species of plant found during the visit in 1966 consisted of three sprouting coconuts (*Cocos nucifera*), each a seedling of about 30 cm tall. One of them was about 50% crushed and the other two completely so. It is unknown whether these species reached the island naturally or were planted there by visitors; whatever their origin they did not persist to maturity. Finally, one dead individual of an unidentified plant was found on the island during the 1966 expedition. Other widespread plants common on sand cays pantropically, such as *Sporobolus virginicus*, *Canavalia maritima*, and *Ipomoea pes-caprae* that might be expected to occur on Isla Aves were not present during our visit nor during that of Zuloaga (1955).

The vegetation of the original, large Isla Aves was quite different from that occurring later. Although Anonymous (1689) indicated the island to be "without trees," and notes accompanying a map by an anonymous cartographer provided the same observation (Urbani Patat 2019), Labat (1722) noted that in 1705 there were plenty of bushes and even guavas, soursop, and custard apples but that they were small and stunted. These edible species probably had been planted by previous visitors and Labat himself planted orange trees and lime trees. Subsequently, Laurance (1849) reported that there were "no trees or bushes," and arborescent vegetation was either reported as absent by later visitors, or not mentioned at all. The presence of "grass" was noted by Purdy (1824) and the United States Hydrographic Office (1914), but this may have referred to the succulents (see below).

According to Labat (1722), the soils of Aves Island consisted mostly of sand but with a middle area of shallow, gray, stony earth enriched by guano. He also noted that this early large island lacked standing fresh water but had plenty of brackish marshes and pools inhabited by countless numbers of seabirds. Today, such habitats are lacking and, indeed, the present size of the island is probably incapable of supporting such habitats; a minimum diameter (width) of 350 feet (107 m) is needed for a sandy island to support a lens of fresh-to-brackish water floating atop the water table of seawater that permeates the substrate (Whitehead and Jones 1969). Early records of the diameter of Isla Aves were well above that threshold, but since at least 1835 have hovered near it (75–168 m) (Anonymous 1835). Since that time, it is unlikely that a permanent water table of fresh or brackish water has existed in the soil, with plants probably having to depend on temporary influxes of rain for their sustenance. Consequently, only three species of dry-adapted plants have occurred there in later years.

The succulents *Sesuvium portulacastrum* and *Portulaca oleracea* were stated to be the only two species of plants present on Isla Aves in 1949 by Hummelinck (1952a) and they have been reported as the sole species of mature plants there by all subsequent visitors who made any mention of vegetation at all.

Comparison of Zuloaga's (1955) results with our findings suggests that there had been a change in the relative abundance of these two species during the interval between the two studies. Although Zuloaga did not quantify his observations, one of his photographs shows a higher concentration of *Portulaca* than of *Sesuvium*, the opposite of our findings.

Sea Turtles

Green sea turtles (*Chelonia mydas*) were noted at Isla Aves in 1966 but no assessment of the number present was attempted. One dead carcass was seen on the island then (HH field notes) and Hummelinck (1952b) also reported one.

Most other visitors throughout the recorded history of Isla Aves also have noted the presence of the Green Sea Turtle (Labat 1722); de Verdun De la Crenne et al. (1778); Purdy (1824); Hummelinck (1952a,b); Pinchon (1952); Brownell et al. (1973); Brownell and Guzmán (1974); Clay (1979); Hummelinck (1979). Sea turtles can influence the ecology of the island; during excavation of pits for their eggs they destabilize the upper beach by digging up plants that otherwise protect islands from aeolian movement of sand (Heatwole 2009). In addition to this effect the occasional dead turtle adds organic matter and nutrients to the soil.

The turtles nest on the island (see Phelps and Phelps [2020] for a summary of their reproductive biology there). Hatchlings leave their natal beaches and migrate far afield to forage, even to places where the species does not breed. The importance of the population of green turtles breeding on Isla Aves to the wider occurrence of the species throughout the rest of the Caribbean, and beyond, is beginning to be documented. In a study of mitochondrial DNA, Luke et al. (2004) found that there were eight haplotypes from nine sources of origin for the turtles foraging in Barbadian water (all Barbadian turtles originate elsewhere as that island has no nesting sites). One of those haplotypes was common to Isla Aves and to Suriname and it contributed the second highest number of turtles (23.0%) to the foraging population in the waters of Barbados, exceeded only by the southern-Atlantic island of Ascension. Even the most populous breeding colony of green turtles in the Caribbean, Costa Rica, contributed fewer (19.1%).

Humans have had an impact on the turtle population of Isla Aves at least from 1824 (Purdy 1824) to 1949 (Hummelinck 1952a,b), and probably beyond. Harvesting sea turtles for meat probably took a heavier toll on females as most of those exploited in this way would have been females coming onto land to oviposit. Since 1972, Isla Aves has been a protected wildlife refuge, the *Refugio de Fauna Silvestre Isla de Aves-Venezuela*, and monitoring of the sea turtles began then and became more continuous beginning in 1978 with permanent occupancy by researchers at the Bolivar naval base adjacent to the island (Vera and Buitrago 2012). Accordingly, the threats to the turtle population from humans has diminished. For example, Prieto-Torres and Hernández R. (2014) found no evidence of any human-induced injuries in more than a thousand individuals examined. Also, hematological analyses (red blood cell count, white blood cell count, hematocrit, hemoglobin, mean corpuscular volume, mean corpuscular hemoglobin, and leukocytes' differential count), as well as concentrations of minerals in the blood, indicated a healthy population (Prieto-Torres et al. 2012, 2013).

With protection of the nesting area for more than 30 years, the estimated number of females coming ashore to oviposit showed significant increases from 300 in 1948 (Hummelinck 1952a) to 373 in 2001 to 669 in 2008 (Vera and Buitrago 2012); Isla Aves now is second only to Tortuguero beach in Costa Rica as a nesting site for green turtles in the Caribbean (Vera and Buitrago 2012). Despite the increase in numbers of nesting females, particularly due to recruitment of smaller nesters, Garcia-Cruz et al. (2015) found that their survival was lower than that at some other protected sites. Dangers still do lurk, however, in the marine environment. Prieto-Torres and Hernández R (2014) found that during the breeding season of 2010, of 1,106 female green turtles coming ashore to lay eggs, 30 had healed scars attributed to bites by sharks; two of these bites involved loss of a flipper. There were also low incidences of tumours, abnormalities of the shell, and epibionts.

Birds and Mammals

In 1966 we recorded the presence of four species of birds on Isla Aves, *Anous stolidus*, *Onychoprion anaethetus, Onychoprion fuscatus,* and *Leucophaeus atricilla,* all but the last of which were nesting (Table 2).

Several species of seabirds have nested on Isla Aves in prodigious numbers year after year ever since the island was first discovered—hence its name of Isla Aves (Bird Island). Table 2 provides a list of the species either recorded from the island or seen fishing in its vicinity. Until recently, humans have repeatedly visited the islands to collect their eggs**.**

It is clear from Table 2 that avian biodiversity is lower on the present-day small island compared to the previous large one. Biodiversity increases with larger sizes of islands (MacArthur and Wilson 1963, 1967) and in 1705 eight species of birds were recorded from Isla Aves, more than ever recorded subsequently at any single visit (Table 2). The reason may be that during the spatial decline some habitats required by certain species were lost. For example, coots, pelicans, and flamingos all were present in 1705 and the habitats they require are no longer present on Isla Aves. Two of these taxa were even known to breed on the island in the early days. Labat encountered flamingos and their nests in 1705 but they never have been seen there since and Phelps (1953) suggested that their disappearance was because these birds require "salinas" (saline areas such as salt pans, salt marshes, or salty ponds). When flamingos were nesting on Isla Aves in 1705 it was the only time ponds (brackish) were reported as being present. Poules d'Eau (probably the Caribbean Coot, *Fulica caribaea*) also were present then. This species is found on 15 Caribbean islands where it inhabits wetlands and ponds (Nijman 2010), again a habitat lacking from Isla Aves today. Already by 1822 it was explicitly stated that ponds were not present (Blunt 1822).

Table 2. Species of birds recorded from Isla Aves. + indicates presence, n signifies nesting. Nomenclatural changes are brought up to date. Bisbal (2008; see second column from the right) compiled the data obtained by the Programa Inventario National de Fauna by the Ministerio del Poder Popular para el Ambiente between 1967 and 2003 as well as collective data from various papers published between 1944 and 2003. Padron Lopez et al. (2015; see far right column) portrayed the collective records from 1952 to 2014. Consequently, the last two columns on the right have overlapping data with each other and with some of the previous studies. Authorities are (from left to right): Labat (1722), Pinchon (1952), Hummelinck (1979), Zuloaga (1955), Lazell (1967), the present paper, Clay (1979), Bisbal (2008), and Padron López et al. (2015). The far-right column reflects the continuous occupancy of the research station just offshore Isla Aves in recent years and the consequent ability to detect species stopping off briefly during their migratory flights.

	DATE OF OBSERVATIONS (not date of publication)								
NAME	**1705**	**1951**	**1949**	**1955**	**1966**	**1966**	**1977**	**1944–2003**	**1952–2014**
ANSERIFORMES: ANATIDAE									
Dendrocygna bicolor (Fulvous Whistling Duck)								+	
Unidentified Duck	+								
PHOENICOPTERIFORMES: PHOENICOPTERIDAE									
Phoenicopterus ruber (American Flamingo)	**+n**								
COLUMBIFORMES: COLUMBIDAE									
Patagioenas leucocephala (White Crowned Pigeon)									+
Zenaida auriculata (Eared Dove)									+
CUCULIFORMES: CUCULIDAE									
Coccyzus americanus (Yellow-Billed Cuckoo)									+
GRUIFORMES: RALLIDAE									
Uncertain identification[a]	+								
Porzana carolina (Sora Rail)								+	+
CHARADRIIFORMES: CHARADRIIDAE									
Charadrius alexandrinus (Semipalmated Plover)								+	
Charadrius nivosus (Snowy Plover)									+
Charadrius semipalmatus (Semipalmated Plover)								+	+
Pluvialis dominica (Golden Plover)									+

(Table 2 continued)

NAME	1705	1951	1949	1955	1966	1966	1977	1944–2003	1952–2014
Pluvialis squatarola (Grey Plover)						+			+
Unidentified shorebird						+			
LARIDAE									
Anous minutus (Black Noddy)								+	+
Anous stolidus (Common Noddy)		**+n**	**+n**	**+ n**	**+n**	**+n**	**+n**	+	+
Onychoprion anaethetus (Bridled Tern)					**+n**			+	+
Onychoprion fuscatus (Sooty Tern)		**+n**	**+n**	**+n**	**+n**	**+n**	**+n**	+	+
Larus argentatus (European Herring Gull)								+	+
Leucophaeus atricilla (Laughing Gull)			+	+	+	**+n**		+	+
Sterna dougalli (Roseate Tern)								+	+
Sterna hirundo (Common Tern)								+	+
Unidentified Gull	+								
SCOLOPACIDAE									
Actitis macularius (Spotted Sandpiper)								+	+
Arenaria interpres (Ruddy Turnstone)		+						+	+
Calidris alba (Sanderling)								+	+
Calidris pusilla (Semipalmated Sandpiper)									+
Limnodromus griseus (Short-Billed Dowitcher)									+
Tringa flavipes (Lesser Yellowlegs)								+	+
Tringa semipalmata (Willet)	+						+	+	+
PHAETHONIFORMES: PHAETHONTIDAE									
Phaethon aethereus (Red-Tailed Tropicbird)								+	+
PROCELLARIFORMES: HYDROBATIDAE									
Oceanodroma leucorhoa (Storm Petrel)								+	+
CICONIIFORMES: ARDEIDAE									
Ardea alba (Great Egret)									+
Bubulcus ibis (Cattle Egret)								+	+

(Table 2 continued)

NAME	1705	1951	1949	1955	1966	1966	1977	1944–2003	1952–2014
Egretta caerulea (Little Blue Heron)									+
Egretta thula (Snowy Egret)								+	+
SULIFORMES									
SULIDAE									
Sula dactylatra (Masked Booby)								+	+
Sula leucogaster (Brown Booby)								+	+
Unidentified S*ula* sp.	+								
FRIGATIDAE									
Fregata magnificens (Magnificent Frigate Bird)		+						+	
Unidentified *Fregata* sp.	+			+		+	+		
PHALACROCORACIDAE									
Phalacrocorax brasilianus (Neotropic Cormorant)									+
PELECANIFORMES: PELECANIDAE									
Pelecanus occidentalis (Brown Pelican)								+	+
Unidentified Pelican	+**n**								
ACCIPITRIFORMES: PANDIONIDAE									
Pandion haliaetus (Osprey)								+	
FALCONIFORMES: FALCONIDAE									
Falco columbartus (Merlin)								+	+
Falco peregrinus (Peregrine Falcon)								+	+
PASSERIFORMES:									
CARDINALIDAE									
Pheucticus ludovicianus (Rose-Breasted Grosbeak)									+
Piranga olivacea (Scarlet Tanager)									+
Spiza americana (Dickcissel)									+
HIRUNDINIDAE									
Hirundo rustica (Barn Swallow)									+
Progne subis (Purple Martin)									+
ICTERIDAE									
Icterus galbula (Baltimore Oriole)									+

(Table 2 continued)

NAME	1705	1951	1949	1955	1966	1966	1977	**1944–2003**	**1952–2014**
Icterus mesomelas (Yellow-Tailed Oriole)									+
PARULIDAE									
Parkesia noveboracensis (Northern Waterthrush)									+
Protonotaria citrea (Prothonotary Warbler)									+
Setophaga ruticilla (American Redstart)									+
Setophaga striata (Blackpoll Warbler)									+
Setophaga virens (Black-Throated Green Warbler)									+
TYRANNIDAE									
Tyrannus dominicensis (Gray Kingbird)									+
TOTAL SPECIES	8	4	3	4	4	6	4	**28**	**48**

[a] Identified by Labat (1722) only by its French common name "Poules d'Eau" but probably the Caribbean Coot (*Fulica caribaea*).

Most visitors to the island described the bird populations in superlatives such as "thousands," "multitudes," and "infinite numbers" and most of the many published photographs and drawings show Isla Aves virtually covered by nesting birds (Figs. 8 and 9). This density seems to have persisted over the nearly three centuries that spanned the time the size of island decreased greatly (see Urbani Patat 2019). For example, de Rochefort (1658) and Davies (1666) reported a multitude of birds nesting even on the sand on the beach and Hummelinck (1952a) indicated that, on his visit, the northeastern and middle parts of the island were covered by seabirds lying closely to each other. Zuloaga (1955) recorded the astounding average of 8–10 birds per square meter, not counting the attendant birds' mates who were away fishing, or eggs or chicks to which there was a minimum of one, and sometimes two, to an adult pair. Lazell (1967) calculated the mean density of terns to be 0.67 per square meter and noted that in a few areas as many as four nests could be found in one square meter. Space in suitable habitat for nesting on Isla Aves can be quite scarce!

A few visitors attempted to estimate the total numbers of birds on the island (Table 3). Pinchon (1952) visited Isla Aves in 1951 and assessed the total bird population to be 100,000 individuals. Other investigators have dealt only with the terns, the most abundant group. Lazell (1967) estimated a total of 50,000 terns with the Common Noddy (*Anous stolidus*) being more numerous than the Sooty Terns (*Onychoprion fuscatus*), whereas Clay (1979) found the opposite to be true. In addition to illustrating the prodigious numbers of birds nesting on Isla Aves, these results may indicate some temporal segregation in nesting, and therefore perhaps an adaptation reducing competition for a limited spatial resource. The importance of Isla Aves as a haven for nesting sea birds is exemplified by the fact that the maximum number of nesting pairs of the Common Noddy for the West Indies was estimated to be 10,000–18,000 (Schreiber and Lee 2000) and the number reported from Isla Aves alone reached about that same number (10,000–12,000) (Table 3). Sooty Terns for the entire West Indies was estimated to be 200,000–300,000 whereas 4,000–5,000 (1.7–2.0%) of the total West Indian number) have been recorded for Isla Aves alone. Note, however, that these regional estimates were separated by 34 years.

A food-rich sea that can sustain a large population of birds, but only a tiny speck of land on which they can nest, makes access to nesting sites critical. How do the birds on Isla Aves partition this resource spatially and temporally? Lazell (1967) reviewed literature on the seasonal nesting of terns and found that the two species also nest together elsewhere. On Isla Aves there may be at least slight temporal segregation of their peak nesting period. In March, the number of nesting Common Noddy Terns was double or more the number of nesting Sooty Terns and the former already had a high number of chicks in an advanced stage of development. In April the ratio had changed, with the Sooty Terns being more numerous. By August, the number of Common Noddy Terns was much lower and the increased abundance of Sooty Terns now outnumbered them by sixfold; whereas the remaining Common Noddy Terns had advanced chicks, the Sooty Terns still were incubating many eggs. These observations were made during different years so a direct seasonal comparison cannot be made; indeed, the seasonality and relative overlap may change from year to year, as Sooty Terns may lay eggs at ten-month intervals (Hamer et al. 2002); this sub-annual reproductive cycle is not only characteristic of the population, but of individual birds as well (Reynolds et al. 2014). Consequently, it is unlikely that in any one year a second clutch would occur as soon as only five months after having chicks in the nest.

Even though peak nesting may be somewhat staggered, active competition may occur, although there is disagreement on this point. Zuloaga (1955) indicated that Sooty Terns are territorial and will even kill chicks from neighboring nests if they wander into their territory whereas Clay (1979) stated that these two terns “do not exhibit any hostility toward one another when an occasional straggler lands in the other’s territory.” Perhaps aggressiveness is dependent on the density of birds, a topic meriting further study.

Figure 8. A vegetated part of Isla Aves with a dense population of Common Noddy Terns (*Anous stolidus*). Photograph by Harold Heatwole.

Figure 9. A bare area of Isla Aves with a dense population of Sooty Terns, *Onychoprion fuscatus*. Note the presence of an unidentified dead plant in the foreground. Photograph by Harold Heatwole.

Table 3. Attributes of the breeding populations of terns on Isla Aves. — indicates no data were provided.

NAME Authority	**Date of Visit**	**Birds**	**Nests**	**Eggs**	**Chicks**
Anoüs stolidus					
Common Noddy					
Lazell (1967)	March 1966	—	10,000-12,000	—	Abundant: pulli
Zuloaga (1955)	April 1954	> *O. fuscatus*	—	—	—
Clay (1979)	August 1977	6,000	—	800	—
Onychoprion fuscatus					
Sooty Tern					
Lazell (1967)	March 1966	—	4,000–5,000	—	500 pulli
Zuloaga (1955)	April 1954	> *A. stolidus*	—	—	—
Clay (1979)	August 1977	36,000	—	4,800	—
Onychoprion anaethetus					
Bridled Tern					
Lazell (1967)	March 1966	—	1,000	—	No pulli
Zuloaga (1955)	April 1954	Not present	—	—	—
Clay (1979)	August 1977	—	—	—	—

(Table 3 continued)

Total: terns plus other birds					
Pinchon (1952)	? 1951	100,000	—	—	—
Zuloaga (1955)	April 1954	500,000–1 million	—	—	—
Lazell (1967)	March 1966	About 48,000	—	—	—
Clay (1979)	August 1977	42,000	—	—	—
Martinez (2012)	Feb–June 2011	3,522	—	—	—
Notes					
Zuloaga (1955)		—			
Lazell (1967)		Area occupied by birds: 80% of the island			
Clay (1979)		Area occupied by birds: 60% of the island			

On Isla Aves the two species of terns were partially segregated by choice of different nesting sites (Clay 1979); whereas the Common Noddy mainly chose swards of succulent vegetation (*Sesuvium portulacastrum* and *Portulaca oleracea* (Fig. 10), the Sooty Terns tended to select bare areas (Fig. 11). Nesting was more prevalent on the northern part of the island where the sand was more consolidated.

The total number of species known to nest on Isla Aves over its entire recorded history are six but two of those were recorded only during the period when the island was larger and before habitats suitable for their breeding had disappeared. Thus, the great majority of species recorded for the island are not permanent residents but rather seasonally visiting migratory species, or strays, merely using the island for brief rest-overs. The apparently greater number of species falling into this category in recent years after the island had decreased greatly in size is probably an artifact of sampling. Most of the early reports were based on brief, widely spaced visits that would have missed seasonal migrants or sporadic visitors. From 1705 onward, the total number of species of birds recorded from Isla Aves is 48; of those 43 (90%) were only recorded during the period between 1944–2014 (Table 2), 239 to 309 years later, after the island had already reached its smaller size (Fig. 4). It is highly unlikely that the increase in number of species observed on Isla Aves in later years was because more species actually came there but rather because more people did, more frequently over a greater range of seasons and for longer periods. The island certainly could not sustain a permanent avifauna of 48 resident species of breeding birds. Migratory species inflate the species diversity but otherwise have little sustained ecological impact on the island. The number of migratory species involved may perhaps depend more on such variables as whether or not they are located on flyways of migratory birds, rather than upon the island's size, available resources, or structure of its biotic community. Sorte et al. (2022) in a study covering 690 islands over 21 years found that species-area relationships were weakest for remote islands. Isla Aves is a remote island and is very small. Its functional species-diversity should be assessed in the light of its species of abundant resident breeders as inflated by a few sporadic individuals of seasonal migrants.

The only mammals ever recorded on Isla Aves, other than humans, were unidentified mice (Hummelinck 1952a), and then only observed on one occasion.

Figure 10. Nests of Common Noddy Terns (*Anous stolidus)* on succulent vegetation on Aves Island. Photograph by Harold Heatwole.

Figure 11. Nest of a Sooty Tern (*Onychoprion fuscatus*) on an area devoid of vegetation on Isla Aves. Photograph by Harold Heatwole.

Terrestrial Invertebrates

The total number of terrestrial invertebrates from Isla Aves that have been identified to the species level now reaches 33 (Table 4) of which 20 (61%) were found on the 1966 expedition and have not been reported otherwise. There were 13 additional species identified only to the generic level, of which 12 (92%) arose solely from the 1966 expedition.

Terrestrial invertebrates were not recorded by most of the early visitors to Isla Aves so it cannot be ascertained whether their biodiversity decreased as the area of available terrestrial habitat became smaller, as is the general case for insular faunas (e.g., Levins and Heatwole 1963; MacArthur and Wilson 1963, 1967; Whitehead and Jones 1968). The first records were published by Hummelinck (1952a) who found 20 species of small terrestrial invertebrates, most not identified to species. These included worms, isopods, spiders, and insects including ants, beetles, crickets, flies, and others, as well as some intertidal or upper-beach species (ghost crabs, hermit crabs, and isopods) (Table 4). Brownell and Guzmán (1974) also collected terrestrial invertebrates and although they sent their specimens to specialists for identification, they did not provide the scientific names of species except for the crabs and ectoparasitic ticks; they did, however, provide the higher taxonomic categories for other taxa (Table 4).

The number of species that were identified only to a still higher taxonomic level that was not represented by the two former categories is 29 for a minimum number of species known from Isla Aves over time of 75 species. However, if none of the unidentified species was also represented in the identified group, then the maximum possible species found on the island would be 101. Thus, the number of species found on Isla Aves to date lies between 29 and 101. In any event, since there is repeated immigration and extirpation of species on islands, it is unlikely that all of the species on the accumulated list were represented at any one time and hence the equilibrium number of species (MacArthur and Wilson 1963) would be lower. On the other hand, given the brief time spent by most visitors to the island it is unlikely that all species present were found on those occasions and further investigation should increase not only the total list of species recorded from the island but the equilibrium number as well. In a video describing work currently underway from the research station adjacent to the island, González and Calderón (2020) displayed and narrated the methods they employed in an investigation of the terrestrial invertebrates of Isla Aves. These included looking under blocks of dead coral on the island, conducting sweeps with an insect net both by day and during the night, use of pitfall traps and light traps, extracting specimens from sand and drift algae, sampling deeper into the sand at intervals along a transect line, and inspecting birds for parasites. Their more comprehensive and thorough methods employed over a longer span of time than for any previous study of the insects shows promise of expanding the knowledge of the biodiversity of the terrestrial fauna of this remote island far more comprehensively than the summary presented here, and their results are eagerly awaited. The videos of their specimens, drawings, and notes suggest that they will increase the number of taxa known from the island appreciably.

Table 4. Species of terrestrial invertebrates collected on Isla Aves. Some species may not have become established as breeding populations because only one individual was found.

HABITAT TAXON	**FAMILY/Species**[a]	**AUTHORITY**[b]
INTERTIDAL OR UPPER BEACH		
PHYLUM ARTHROPODA; SUBPHYLUM CRUSTACEA; CLASS MALACOSTRACA		
ORDER ISOPODA	1 unidentified species	HH et al. present paper
	2 unidentified species	Brownell and Guzman (1974)
ORDER DECAPODA	1 unidentified species	HH et al. present paper
	7 unidentified species	Brownell and Guzman (1974)
	OCYPODIDAE	
	Ocypode quadrata	Hummelinck (1952a)
	CENOBITIDAE	
	Coenobita clypeatus	Hummelinck (1952a); Brownell and Guzman (1974)
	GECARCINIDAE	
	Gecarcinus lateralis	Brownell and Guzman (1974)
	GRAPSIDAE	
	Grapsus grapsus	Hummelinck (1952 a)
TERRESTRIAL		
PHYLUM ANNELIDA	1 unidentified species	Brownell and Guzman (1974)
ORDER ARANEAE (Spiders)	5 unidentified species	HH et al. present paper
	3 unidentified species	Brownell and Guzman (1974)
ORDER PSEUDOSCORPIONIDA	1 unidentified species	HH et al. present paper
CLASS CHILOPODA (Centipedes)	1 unidentified species	HH et al. present paper
CLASS INSECTA		
ORDER BLATTODEA; INFRAORDER ISOPTERA	KALOTERMITIDAE *Cryptotermes* sp.	HH et al. present paper
ORDER PSOCODEA	PERIPSOCIDAE	
	Ectopsocus maindroni	HH et al. present paper
ORDER ORTHOPTERA	1 unidentified species	Brownell and Guzman (1974)
	1 unidentified cricket	HH et al. present paper
ORDER DERMAPTERA	1 unidentified species	Brownell and Guzman (1974)
ORDER THYSANOPTERA	1 unidentified species	HH et al. present paper
ORDER HETEROPTERA	1 unidentified species	Brownell and Guzman (1974)
	ANTHOCORIDAE	
	Physopleurella floridana	HH et al. present paper
	MIRIDAE	
	Campylomma cardini	HH et al. present paper.
ORDER HOMOPTERA	1 unidentified species	Brownell and Guzman (1974)
	CICADELLIDAE	
	Cicadulina tortilla	HH et al. present paper
	Empoasca canavalia	HH et al. present paper
	Graminella cognita	HH et al. present paper
ORDER HYMEOPTERA	3 unidentified species	Brownell and Guzman (1974)
	FORMICIDAE	
	Solenopsis globularia	Pacheco and Mackay (2013); HH et al. present paper
	Monomorium salomonis	HH et al. present paper
	Myrmeloclustra ramulorum	HH et al. present paper

(**TERRESTRIAL** continued)

ORDER COLEOPTERA	4 unidentified species	Brownell and Guzman (1974)
	TENEBRIONIDAE	
	Phalera fulva	Marcuzzi (1962); HH et al. present paper
	Blapstinus opacus	Marcuzzi (1962); HH et al. present paper
	ELATERIDAE	
	Conodermus near *lividus*	HH et al. present paper
	LAMPYRIDAE	
	Photinus sp.	HH et al. present paper
	STAPHYLINIDAE	
	1 unidentified species	HH et al. present paper
	SCARABAEIDAE	
	Ligyrus cuniculus	Escalona and Joly (2006)
	SCOLYTIDAE	
	Xyleborus ferrugineus	HH et al. present paper
	Xyleborus near *perforans*	HH et al. present paper
	Pycnarthrum pallidum	HH et al. present paper
	PLATYPODIDAE	
	Platypus rugulosus	HH et al. present paper
	NITIDULIDAE	
	Haptoncus luteolus	HH et al. present paper
ORDER LEPIDOPTERA	2 unidentified species	Brownell and Guzman (1974)
	GELECHIIDAE	
	1 unidentified species	HH et al. present paper
	TINEIDAE	
	1 unidentified species	HH et al. present paper
ORDER DIPTERA	4 unidentified species	Brownell and Guzman (1974)
	CECIDOMYIIDAE	
	1 unidentified species (subfamily Cecidomyiinae)	HH et al. present paper
	Clinodiplosis sp.	HH et al. present paper
	Karschomyia sp.	HH et al. present paper
	Lestodiplosis sp.	HH et al. present paper
	Peromyia photophila	HH et al. present paper
	CERATOPOGONIDAE	
	Dasyhelea sp.	HH et al. present paper
	Foreipomyia sp.	HH et al. present paper
	CHLOROPIDAE	
	Oscinella obscura	HH et al. present paper
	CULICIDAE	HH et al. present paper;
	Aedes aegypti	perhaps brought by the visitors; on ship
	LONCHAEIDAE	
	Lonchaea sp.	HH et al. present paper
	PHORIDAE	
	Megasella sp.	HH et al. present paper
	PSYCHODIDAE	
	Psychoda alternata	HH et al. present paper
	Psychoda alternicula	HH et al. present paper
	Psychoda phaenoides	HH et al. present paper

	Telmatopscopus sp.	HH et al. present paper
	Trichomyia wirthi	HH et al. present paper
	SCIARIDAE	
	Bradysia sp.	HH et al. present paper
	STATOPSIDAE	
	Statopsis fuscipes	HH et al. present paper
PARASITES		
	Unidentified lice and other parasites	Hummelinck (1952a)
PHYLUM ARTHROPODA; CLASS CRUSTACEA; SUBCLASS PENTASTOMIDA		
ORDER CEPHALOBAENIDA	REIGHARDIIDAE	
	1 unidentified species	Holland (1971)
CLASS ARACHNIDA		
ORDER ACARINA (Ticks)	4 unidentified species	Brownell and Guzman (1974)
	ARGASIDAE	
	Alectorobius sp.	Pinchon (1967)
	Ornithodoros capensis	HH et al. present paper; Lazell (1967)
	Orninthodoros rudis	Holland (1971)
ORDER SARCOPTERIFORMES (Mites)	EPIDERMOPTIDAE	
	1 unidentified species	Holland (1971)
ORDER MESOSTIGMATA (Mites)	RHINONYSSIDAE	
	1 unidentified species	Holland (1971)
CLASS INSECTA		
ORDER HYMENOPTERA		
	CYNIPIDAE	
	Pseudeucoila sp.	HH et al. present paper

[a] It is noteworthy that we found two species of marine insects at Isla Aves: a marine water strider, *Halobates micans* (Heteroptera: Gerridae), and an unidentified chironomid fly.
[b] Papers recording the species from Isla Aves; the records arising from Heatwole's expedition in 1966 and reported in the present paper are indicated by "HH et al. present paper."

Mode of Dispersal and Biogeographic Affinities

Drifting objects, such as wood and mats of vegetation, accidentally transport many terrestrial invertebrates, especially insects. Phelps (1953) indicated that there was sufficient wood on Isla Aves to use as firewood. Heatwole and Levins (1972) found that 25% of drift items recovered from the Caribbean Sea contained live terrestrial animals. Eight pieces of drift encountered halfway between Puerto Rico and Isla Aves lacked any terrestrial animals, but these items clearly had been in the sea for an extended time as they had many live barnacles attached and contained marine crabs, shrimp, and polychaete worms. Since driftwood and coconuts occur on the beaches of Isla Aves from time to time (Clay 1979; HH 1966 expedition), it is likely that at least some of its insect fauna was transported by such agents. This conclusion is strengthened by the fact that the known distribution of some of the species on Isla Aves includes those from Lesser Antillean islands upstream from Isla Aves but does not rule out other species being dispersed by wind. Phelps (1953) indicated that the fauna of Isla Aves, unlike that of the other Venezuelan islands, should have a Caribbean affinity rather than a South American one.

The number of species occurring on an island reflects an equilibrium between the dispersal of species new to the island and the extirpation of those already present (Levins and Heatwole 1963; MacArthur and Wilson 1963, 1967) and hence there is a turnover of the actual species present, with the composition of the fauna varying over time as new species immigrate and become established and others disappear. There have been few exhaustive attempts to sample the fauna of Isla Aves, so the turnover of species cannot be calculated at present. However, according to the above model successful dispersal would be expected to be more frequent to large islands close to the source of propagules than to smaller, more distant ones, and extirpation of a species more frequent on small islands than on larger ones. Over the more than half a century of testing, this model has required various modifications, but in general still explains much of the variability in insular biodiversity (Heatwole and Ríos-López, in press). Accordingly, Isla Aves, being remote and small, would be expected to have a relatively low immigration rate and a high rate of extirpation. This expectation is altered by the fact that its remoteness is ameliorated somewhat by lying in a sea current leading directly to it from its nearest neighboring islands in the Lesser Antilles (Gordon 1967). Not surprisingly, therefore, many of the species reported from it are widespread hardy species that can withstand the rigors of oversea dispersal and the paucity of freshwater at their new habitat. For example, all three species of scotylid beetles are widespread, *Xyleborus ferrugineus* and *X. perforans* both being described as pantropical and adapted for colonizing new places (Gohli et al. 2016) and the distribution of *Pycnarthrum pallidum* is "Mexico (Jalisco), Jamaica, and Guadeloupe Island to Venezuela" (Wood 2007). The distribution of *Coenobita clypeatus*, a hermit crab, is variously listed as "from southern Florida and the Bahamas through the West Indies (and doubtfully into southern Brazil)" (de Wilde 1973) and as common in the Windward and Leeward Islands, occurring from coastal regions to several miles inland (Brownell and Guzman 1974). The rock crab, *Grapsus grapsus* occurs in the Pacific Ocean, Western Atlantic Ocean, and in Florida, Bermuda, Gulf of Mexico, the Antilles, and in South America from Colombia to the Brazilian coast; it is found on beaches and rocky shores (de Sá and Câmara de Araújo 2014). A ghost crab, *Ocypode quadrata*, occurs from Rhode Island, USA, to Rio Grande du Sul, Brazil. It burrows in sandy beaches and dunes (Joaquim et al. 2010). Two of the species of ants known from Isla Aves are widespread. According to Pacheco and Mackay (2013) the ant "*Solenopsis globularia* is a widely distributed, highly variable species…consistently found on the coastline on beaches under rocks or most often in logs." Another ant, *Monomorium salomonis*, is an African species introduced into Antigua, Dominican Republic, and St. Croix, and probably is even more widely distributed in the Caribbean (Roy Snelling, personal communication).

The Food Web on Isla Aves

Brownell and Guzmán (1974) are the only investigators to have constructed a food web for Isla Aves. The expected classic pattern of solar radiation powering an autotrophic base of photosynthetic plants with energy then flowing through herbivores to various levels of predators, followed by input from that system into dead organic matter supporting scavengers and their predators was observed but did not constitute the sole pattern (Table 4). The players in this drama were the two species of green plants, with a few species of herbivorous insects feeding on them and in turn preyed upon by spiders, some beetles, and centipedes. The native seabirds are dependent on the sea for their food and consequently they, and their parasites, although mainly terrestrial in habitat are trophically dependent on the marine ecosystem. The transient shorebirds feed mainly in the intertidal zone on marine-derived species. Consequently, the usual terrestrial plant-herbivore-predator-scavenger food web was depauperate of species at all links (Table 4). However, the island's primary food web is based on input from the marine ecosystem by transfer organisms, such as seabirds and sea turtles, and the wash-up of marine carrion, leading to a scavenger-based terrestrial food web culminating in predatory invertebrates and some migratory birds. For example, earthworms feed on decaying eggs of sea turtles (Brownell and Guzman 1974); a number of species of scavenging invertebrates (flies, beetles, crabs) feed on guano, organic detritus, decaying marine carrion, and cadavers of turtles and birds, and nestling birds' food scraps; in turn the smaller species fall prey to predatory insects, spiders and centipedes. Finally, far-distant terrestrial ecosystems provide a third input via driftwood that transport an astonishing variety of invertebrates to the shores of Caribbean islands (Heatwole and Levins 1972), including Isla Aves (e.g., the termite *Cryptotermes* sp., Table 4). There is no native wood consistently on the island and consequently wood-boring species may not become established independently of the vehicle that brought them.

The influence of the marine ecosystem on the trophic structure of biotic communities on small sandy cays is not unusual, but rather is the norm; Isla Aves is not as extreme as some cays. Heatwole (1971) found that some small sandy cays on the Great Barrier Reef of Australia lacked vascular plants entirely, yet had a fauna of terrestrial scavenging mites, collembolans, hermit crabs, flies, and beetles that depended for their food chiefly on the guano, carrion, and food scraps of seabirds nesting on those islands. The scavengers in turn served as food for resident predatory spiders and centipedes.

The amount of vegetation on an island is related to the area of the island and to the amount of food for herbivores, whereas the perimeter of an island is related to the island's interface with the marine environment and hence to the transfer of marine resources from the sea to the terrestrial environment (Hodkinson et al. 2002; Ellis et al. 2006). The smaller the island, the greater is its perimeter-to-surface-area ratio, and consequently small islands have proportionately more species of scavengers relative to herbivores than do larger ones (Heatwole 2018).

The food web on Isla Aves is known only in a general way and the precise links occupied are not adequately known, although all species of some taxa have sufficiently consistent trophic relations that knowing even the family to which they belong can allow placing them in the food web in a general way. For example, in general spiders, pseudoscorpions, centipedes, and lampyrid beetles are predatory; ticks are ectoparasitic.

Some specific links have been identified for Aves Island. For example, sooty terns hosted ticks (*Orninthodoros rudis*) and harbored rhinonyssid mites as parasites in their respiratory tracts and those of the family Epidermoptidae as parasites on their skin, as well as an unidentified species of reighardiid crustacean as a parasite in their buccal cavities (Holland 1971). A ghost crab, *Oxypode quadrata,* feeds on bivalves and some crabs and on organic detritus; its stomach contents indicate its diet contains 10% plant protein but mostly animal protein, including crustaceans, molluscs, and dead fish from the beach, as well as insects, and food discarded by humans (Joaquim et al. 2010). It is an omnivore and its food consists of 90% live intertidal prey (mostly mole crabs and clams) and 10% readily scavenged from any kind of organic matter. At another locality it feeds primarily on terrestrial insects (Wolcott 1978). In turn it is preyed upon by shorebirds and gulls (Joaquim et al. 2010). The rock crab *Grapsus grapsus* is a predator, feeding on hatchling turtles, barnacles, mussels, and boobies, as well as practicing cannibalism (Freire et al. 2011).

Other links are less definite, e.g. the cynipid hymenopteran *Pseudeucoila* sp. may be a parasite of flies (Chabora et al. 1979); sciarid flies are mainly fungivores, phorid flies of the genus *Megasella* mainly eat fungi and decaying vegetal matter; lonchaeid flies of the genus *Lonchaea* mainly feed on damaged plant tissues, fungi, and feces (Wikipedia); psychodid flies sometimes are a pest of sewage-treatment plants (Courtney et al. 2009) and on Isla Aves probably feed on guano (HH field notes); the chloropid fly *Oscinella obscura* is mainly phytophagous; flies of the family Ceratopogonidae mainly feed on the blood of vertebrates; the larvae of those of the family Cecidomyiidae feed mainly within plant tissues and form galls, and chironomids are omnivorous, most genera consuming animal and vegetal detritus as part of their diet but others are predators (Galizzi et al. 2012). The caterpillars of the lepidopteran family Tineidae feed on fungi, lichens, and detritus and those of the family Gelechiidae feed on plants and form galls. Nitidulid beetles of the species *Haptoncus luteolus* feed mainly on vegetal matter, over-ripe fruit, and dead animals (Wikipedia); the platypodid beetle, *Platypus rugulosus,* has been found in wood of coconut palms diseased by the fungus *Ceratocystis paradoxa* in Puerto Rico (Maramorosch et al. 1972) so is probably a fungivore; of the scolytid beetles, both species of *Xyleborus* found on Isla Aves feed on fungi in dead wood (Gohli et al. 2016) and hence must be either restricted to driftwood on Isla Aves, or are able to subsist on other sources of fungi as well.

Eury**troph**ic species (wide food preferences) persist longer than do steno**troph**ic ones (narrow food preferences), because if one source of food is extirpated the eurytrophic ones can opportunistically switch to other sources and thus are better able to become established and persist. Eury**top**ic species (generally wide ecological tolerances) also may be more likely to survive the rigors of dispersal and establishment in an environment devoid of plentiful fresh water than can steno**top**ic ones. This explains why so many of the species on the island are both eury**troph**ic and eury**top**ic. Given the high species-turnover on such very small islands (Heatwole et al. 1981), it is not likely that many species will persist long enough to speciate and become endemic.

Humans' Interaction with Isla Aves

Isla Aves has been the scene of dramatic episodes for humans, including the capsizing of boats in sudden storms, the crash of a small aircraft, and rescues of people stranded on the island. Labat ran aground on the island during a hurricane in 1705 where he encountered an English party that had been stranded previously (Phelps 1953). A more recent rescue occurred in 1973 when a Coast Guard helicopter from Puerto Rico lifted off the participants of a scientific expedition who were threatened by Hurricane Cristina (Brownell and Guzmán 1974).

Humans are responsible for many introductions of non-native species onto Caribbean islands, either purposely or inadvertently (Heatwole and Ríos-López, in press). Over most of Isla Aves' history there was neither sustained occupancy by people, nor permanent houses built. Rather, there were visits by explorers, scientists, and people engaged in harvesting sea turtles and the eggs of birds. Hummelinck (1952a) in a review of the attempts to exploit the guano commercially, cited conflicting views on whether the island was inhabitable by people. Queen Isabela II considered the island to be fit only for collecting birds' eggs, fishing, and catching sea turtles, but not for human habitation (Anonymous 1865). Various visitors have noted the lack of freshwater (de Verdun De La Crenne et al. 1778; Furlong 1800; Blunt 1822; Buchnan 1861). Purdy (1824), however, added the caveat that digging inland might produce water. Some visitors planted various edible plants, none of which persisted indefinitely.

The early activity that had the most potential for long-term occupancy was the mining of guano, but the initial attempts for such an endeavour was not tenable and led to no sustained effort. Clay (1979) pointed out that the territorial right to fishing in the area is of great importance to Venezuela, but that this marine activity had little impact on the island itself, which now is designated as a National Monument. People from the Lesser Antilles have engaged in seasonal fishing and harvesting birds' eggs and sea turtles for food at least since 1824 (Purdy 1824). In 1920 (Hydrographic Department Admiralty 1920), it was reported that during the fishing season a schooner made several trips per week from various neighboring islands to Isla Aves to collect birds' eggs.

A hut was present for a while and a meter-high wall was built by the Dutch. Clay (1979) noted an unmarked wooden cross. A U.S. sailor who died during the war of 1812 was buried on the island (Verrill 1917) and a cross perhaps marked his grave. Clay (1979) was the only person to mention debris discarded by visitors (e.g., a table, an engine shaft, and a boiler). He also noted the modern scourge: anthropogenic flotsam in the beach-drift (e.g., plastic bottles, lumber, a life preserver). However, he did mention that in general the island was exceptionally clean. We (HH, FT) found rubbish on the beach in 1966 (bottles, toilet seat). Until recently, the only structures built on the island seemingly of intent to be permanent fixtures were navigational aids, e.g., three coral cairns (Lazell 1967) a radar reflector (Clay 1979) and some structures built by guano miners.

In June 1978, the Venezuelan Navy set up a scientific naval base named "Base Cientifico Naval Simón Bolívar" (BCNASBO) near the southwestern edge of the island (http://www.shn.mil.ve/hidrografia/base-cientifico-naval-simon-bolivar-bcnasbo). It was constructed as a platform on stilts in the water at the edge of the island. Now it is permanently inhabited by scientists and military personnel. Under the auspices of the Servicio de Hydrografia y Navegación (Hydrographic and Navigational Service) it conducts meteorological, hydrographic, and biological investigations; a new module was constructed in December 2001. Modern technology made possible the construction of facilities immediately offshore, rather than directly on the island, thereby allowing living quarters and scientific equipment to be readily available with minimal impact on the island's natural ecosystem.

Prospectus for the Future

Some small Caribbean islands that lost their protective reefs in recent years have suffered severe erosion as a consequence (Torres 1970, 1972; McKenzie and Benton 1972) and one of them near Puerto Rico, Palominitos, that originally even had a cover of trees and shrubs, as well as low vegetation, disappeared altogether. Isla Aves, because of its small size, low elevation, and sandy rather than rocky substrate, is especially vulnerable to erosive obliteration and Brownell and Guzmán (1974) foreshadowed that its future disappearance might jeopardize the status of Venezuela's zone of marine influence in the area.[7]

As climatic instability, including global warming and bleaching of corals, increases over the coming decades, hurricanes are expected to become a greater menace and the rise in sea level will accelerate (IPCC 2021) due to the melting of glaciers and ice sheets as well as from thermal expansion of seawater, thereby making the existence of the island increasingly precarious. With the deterioration of its fringing reef, Isla Aves is unlikely to survive such assaults and it seems destined to follow the fate of the two other nearby small cays that preceded it. In the meantime, its biota has a semblance of protection by living on an ark that will continue to attract scientists and adventurers, provide a temporary refuge for a miniscule section of the World's biodiversity, and serve as a nursery for multitudes of seabirds—until it exits the terrestrial realm and subsides beneath its final washover. Then, Isla Aves, no longer an island, may become merely a part of history, rather than a hive of avian activity, and for the first time in centuries, the din of birds' cries, once heard by sailors still beyond visual range, will be silenced forever. Or perhaps its remnants will become a focus for renewed life underwater as it becomes the substrate for whatever marine biotic community may supplant the currently extant terrestrial one.

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APPENDIX 1: METHODS FOR MAPPING THE MODERN-DAY ISLA AVES

Earth Explorer (https://earthexplorer.usgs.gov/) was searched for Sentinel-2 images from 01 January 2020 through 13 July 2021 to find the clearest images with the fewest clouds that covered Aves Island and its surrounding reef. The following four multiband raster images were used in the analyses: L1C_T20PMC_A025347_20200429T145728, L1C_T20PMC_A025490_20200509T145730, L1C_T20PMC_A022659_20210708T145727, and L1C_T20PMC_A031639_20210713T145728 (note: the identification encodes the date the image was acquired in the last segment of the identification string; the first image listed was acquired on 29 April 2020. Henceforth the images will be referred to by the four-digit month and date of acquisition; 0429 for this example). All images were in the projected coordinate system WGS 1984 UTM Zone 20N. ArcMap (version 10.8, with the spatial analyst license, Esri 2019) was used to perform analyses of raster images and create the associated map layout(s).

[7] United Nations Convention for the Law of the Sea (UNCLOS) does not consider "rocks, which cannot sustain human habitation or economic life on their own" as entitled to an Exclusive Economic Zone (EEZ), and thus it was contended they are not islands. CARICOM, an organization composed of 20 Caribbean countries as members and Associate Members, argued that Venezuela's base built on stilts partly offshore at Isla Aves did not confer the status of an island. In 2005, Venezuela attempted to resolve the issue through an arrangement (called Petrocaribe) whereby 18 Caribbean states could buy petrol from Venezuela at reduced rates (Haughton 2015). However, the subsequent political upheavals in Venezuela and the death of the president, Hugo Chávez, in 2013 raised uncertainties about the future of Petrocaribe.

To control for the bright reflection from the waves on the surface of the ocean the mosaic to new raster tool was used to combine bands from the four images using several operators to find the best image for each high-resolution (10 m) band. The best image for both the blue bands (band 2; 490 nm) and the green bands (band 3; 560 nm) was created using the mean operator such that the output was a single raster that contained the average of the four input images. The best image for the red band (band 4; 665 nm) was created using the blend operator, which gives more weight to the first image, with the images in the following order: 0429; 0708; 0713; 0509. The best image for the very near infrared (VNIR) band (band 8; 842 nm) was created using the blend operator with the images in the following order: 0713; 0509; 0708; 0429.

Because the VNIR band does not penetrate water a threshold was applied to the blended raster of band 8 to separate the area of the image covered by land from that area covered by water. The result was used to mask the area of water from the best image of the blue, green, and red bands, resulting in rasters containing data only in the area covered by water (the pixels corresponding to the area representing the island contained no data). To highlight the differences between the visible bands (blue, green, and red), which do penetrate water, and the VNIR band, the blended raster of band 8 was subtracted from the water-masked images of the visible bands. The resulting image from each band was then composited into a three-band multispectral image.

A principal components analysis (PCA) using three principal components was run on the three-band multispectral image and the resulting image was used to perform supervised classification using maximum likelihood with the following classes: fringing reef, sandy shallows, rocky shallows, shallow reef, deep reef, and open water. Isolated pixels were removed from the classified image by running the majority filter tool using four neighbors and a majority definition of half until the image stabilized. The boundary clean tool was run with expansion and shrinking once, and zones sorted in descending order. The region group, set null, and nibble tools were used to further remove small, isolated regions of less than 15 pixels per group, resulting in the final, classified image. An accuracy assessment of the final classified image was performed using the three-band multispectral image as the reference data and by generating 402 points in a stratified-random manner to compute a confusion matrix.

Esri's World Imagery (Clarity) base-map was used to digitize the outline of the island at a scale of 1:2,500 and to digitize the outline of the scientific base at a scale of 1:750 (image acquired on 13 August 2021, Esri, DigitalGlobe, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AeroGRID, IGN, and the GIS User Community). Topology was applied to the classified image and the digitized island to ensure that the inner boundary of the fringing reef snapped to the outline of the island and that the entire classified image was free of gaps or overlaps between classes. The area and perimeter of the island were computed with the calculate-geometry tool. An envelope and a bounding box were created to measure the north–south and east–west extent of the island. The distances of the edge of the island to the outer reef and across the island at its narrowest and widest point were measured using the measure tool.

In the PCA of the three-band multispectral image the first component captured 83% of the variance in the data (Table 5). The eigenvector values for band 3 (green) and band 4 (red) were higher than for band 2 (blue) and this may indicate the variance in depths that these bands penetrate water (Table 6). The image of the PCA highlighted differences in the shallows surrounding the island, again likely due to the variance in the depth of penetration of the visible bands in water (Fig. 7).

The overall accuracy of the classified image was 98.5% with a kappa of 0.93. The user's accuracy was lowest (70%) for the class "rocky shallows" and the producer's accuracy was lowest (71.4%) for the class "sandy shallows" (Table 7).

Table 5. Percent and accumulative eigenvalues from the variance-covariance matrix of the 3-band multispectral image of Isla Aves and its surrounding reef.

COMPONENT	EIGENVALUE	PERCENTAGE	CUMULATIVE PERCENTAGE
1	26774.64	82.96	82.96
2	5099.60	15.80	98.76
3	400.47	1.24	100.00

Table 6. Eigenvectors from the variance-covariance matrix of the 3-band multispectral image of Isla Aves and its surrounding reef.

COMPONENT	1	2	3
Band 2	0.17665	0.73394	0.65584
Band 3	0.20988	0.62290	-0.75362
Band 4	0.96164	-0.27077	0.04400

Table 7. Accuracy-assessment report for the final classified image of Isla Aves and the surrounding reef using the 3-band multispectral image as the reference data.

CLASS	1	2	3	4	5	6	TOTAL	USER'S ACCURACY
Open Water	352	0	0	0	0	0	352	1.0
Rocky Shallows	0	7	2	0	1	0	10	0.7
Sandy Shallows	0	0	10	0	0	0	10	1.0
Fringing Reef	0	0	2	8	0	0	10	0.8
Shallow Reef	0	0	0	0	10	0	10	10
Deep Reef	1	0	0	0	0	9	10	0.9
TOTAL	**353**	**7**	**14**	**8**	**11**	**9**	**402**	
Producer's Accuracy	0.997	1	0.714	1	0.909	1		

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