

BIOGEOGRAPHICAL AFFINITIES OF THE BUTTERFLIES OF THE SOUTHWEST CARIBBEAN ISLANDS, SAN ANDRÉS AND PROVIDENCIA

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ABSTRACT. San Andrés and Providencia are small islands east of Nicaragua. N. D. Riley, in his *Field Guide to the Butterflies of the West Indies* (1975), included these islands in his biogeographical definition of the West Indies. Subspecific analyses of butterfly collections made in August 1986, however, show that, of 19 species collected, the 10 that have one or more subspecies in the Antilles are all represented on San Andrés and Providencia by the subspecies occurring on the mainland. Thus, we conclude that this area of the SW Caribbean shows no affinity with Antillean populations, but is clearly an extension of the neighboring populations on the mainland of Central America. Two species are newly recorded for any Caribbean island: *Cymaenes odilia* (Hesperiidae) on San Andrés and *Chlorostymon telea* (Lycaenidae) on Providencia. Based on present, but probably incomplete, sampling, it appears that San Andrés and Providencia maintain discrepant butterfly faunas. These islands are equidistant from a large donor source of immigrants, but differ markedly in geological origin and present vegetation.

Additional key words: island biogeography, subspeciation, dispersal, Nicaragua.

The "West Indies" constitute an area of particular biogeographical interest because they possess components of both the Nearctic (North American) and Neotropical (Central and South American) faunas distributed across a chain of islands, varying greatly in size, topography, and geological history. As a faunistic zone, this region is generally considered to include the Bahamian islands to the north, the Greater Antillean islands of Cuba, Hispaniola, Jamaica (with the small satellite Cayman Islands), and Puerto Rico, and the Lesser Antillean chain from the Virgin Islands east of Puerto Rico south to Grenada, but excluding Trinidad and Tobago, which are insular faunistic extensions of the adjacent continental mainland.

Riley (1975), in the only general account of the butterflies of this area, extended the perimeter to the south and west to include three islands: Swan (in line with the Islas de la Bahía chain off Honduras), Old Providence (Providencia), and St. Andrew (San Andrés). This report is concerned with the biogeographic status of the butterflies of the last

two islands and their supposed affinity with the West Indian (or Antillean) faunistic zone.

San Andrés and Providencia are small isolated islands in the SW Caribbean Sea, situated, respectively, ca. 197 km and 235 km due east of the Central American mainland (Nicaragua) (Fig. 1). Providencia lies ca. 87 km NNE of San Andrés. The latter is situated ca. 365 km due north of the coast of Panamá, while Providencia is ca. 626 km from Jamaica, the nearest neighbor among the Antillean Islands. Despite their proximity, and their relative nearness to the continental landmass, San Andrés and Providencia are thought to have upheaved independently in the early Tertiary and never to have had a land bridge either between them, or between either island and the mainland (Parsons 1956).

The contours of Providencia and San Andrés, with indication of populated areas (and, for Providencia, the altitude of the central peaks) are illustrated in Fig. 1. These maps are based on those in Parsons (1956) and on a Colombian Government publication: "Mapa de la Intendencia Especial de San Andrés y Providencia" (1981). Parsons (1956) has provided a valuable and interesting account of the geology, history, and ecological consequences of colonization, and of the social and cultural geography of San Andrés and Providencia. The following summary is abstracted from that work, with some details obtained from Emmel's (1975) account.

Neither island has a known history of pre-Columbian settlement. Following initial colonization in the early 17th century, much of the islands' original forests were removed for ship building and repair, notably during the 18th century. The two islands differ strikingly in terrain and in their present pattern of vegetation. Providencia is steeply mountainous with igneous peaks (to 360 m) in the interior of the island. Originally, Providencia was densely forested (Parsons 1956); today, the island supports lowland agriculture, the higher areas being dominated by grass and cattle grazing, extending much of the way to the peaks where, in a few areas, the vegetation is described by Proctor (in Parsons 1956) as showing "distinctly Central American" affinities. San Andrés is a slender N-S oriented block of limestone (thought to overlie an igneous base) with a single cliff-bound hill rising to ca. 100 m. Destruction of original forest occurred as on Providencia; a period of cotton planting followed, and in the 1850's the island was thickly planted with coconut palms, a virtual monoculture that dominates much of the island today, although the ancient palm stands are untended and of little economic importance. Abandoned fields and paths through these plantations provide the most ready access to the interior of San Andrés.

Commercial development, primarily for the tourist industry, was

virtually non-existent on either island when Parsons wrote, but was more extensive when Emmel visited the islands (in 1967–68) and clearly continues. On San Andrés (Fig. 1) development is centered primarily around the town. On Providencia, however, other than expansion of the main settlement and some development along the perimeter road, little change has occurred since Parsons' visit in 1953, and little encroachment into the interior has taken place.

BUTTERFLY FAUNAS OF THE ISLANDS

The only published records of the butterflies of these small islands are those of Emmel (1975) who, with coworkers, collected on San Andrés during five visits, and on Providencia during two brief visits, in 1967 and 1968. Work on the former was in February–March and June–July, while Providencia was sampled on one day in June, and two days in July, 1968. Emmel documented 17 species from the two islands. Although of considerable value, these records generally did not include subspecific determinations, and thus afford little information on the affinities of these island faunas to continental America and the Antilles, where subspeciation has been a conspicuous factor (Riley 1975).

The present account is based on an intensive collecting visit by one of us (DSS) to these two islands between 7–23 August 1986, apportioned between San Andrés (9 collecting days) and Providencia (5 collecting days). Several species recorded by Emmel were not found in 1986 and, conversely, a number of species were newly recorded (Table 1). The extent of the discrepancy is noteworthy, and contributory factors may include differing habitat sampling (even on small islands), seasonal fluctuation in adult populations, presence or absence of occasional vagrant species, and recent extinction and/or colonization.

All species collected were determined where appropriate to subspecies, primarily to establish the southwestern limits of the Antillean faunal area and to evaluate the appropriateness of Riley's SW-directed extension of this zone. Taxonomic determination of material collected in 1986 was facilitated by comparison with often extensive series in the Allyn Museum of Entomology, Sarasota, Florida, the Hope Entomological Collections, University of Oxford, and the British Museum (Natural History), London. The sequence of taxa follows that of Miller and Brown (1981). All specimens collected in 1986 are deposited in the Hope Entomological Collections, the University Museum, Oxford, England.

The following list of species includes both Emmel's published records and our records from August 1986; those species recorded by Emmel but not seen during this study are enclosed in parentheses. A compar-

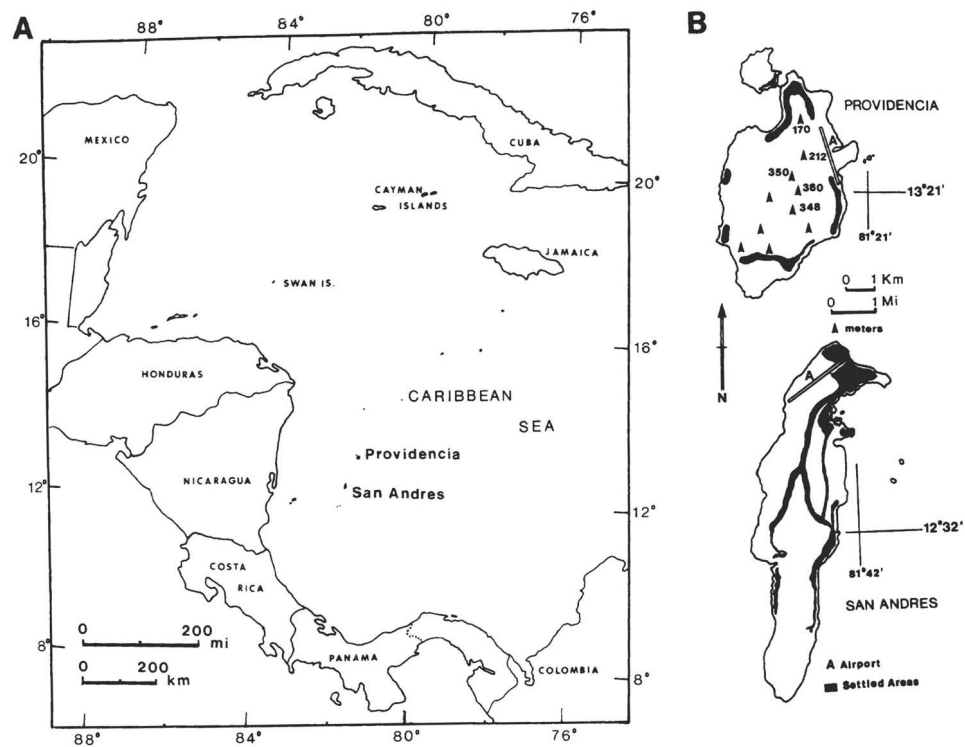


FIG. 1. A. Position of San Andrés and Providencia Islands, in the SW Caribbean Sea. B. Outline maps of Providencia and San Andrés, indicating the main "settled areas" and (Providencia) the principal hills of the interior. A coastal road around each island is not indicated.

TABLE 1. Butterflies collected in 1986 (this study) and in 1967-68 (Emmel 1975).

San Andrés	Providencia
Hesperiidae	Hesperiidae
++ <i>Urbanus d. dorantes</i> **	++ <i>Urbanus d. dorantes</i> **
++ <i>Urbanus p. proteus</i>	++ <i>Urbanus p. proteus</i> **
++ <i>Cymaenes odilia trebius</i> **	(<i>Hylephila phyleus</i>)
-- <i>Hylephila phyleus</i>	
-- <i>Panoquina sylvicola</i> **	
Papilionidae	
++ <i>Battus p. polydamas</i> **	
Pieridae	Pieridae
++ <i>Ascia m. monuste</i> **	<i>Phoebis sennae</i>
<i>Phoebis sennae</i>	++ <i>P. p. philea</i> **
++ <i>P. p. philea</i> **	-- <i>Abaeis nicippe</i> **
++ <i>Eurema venusta limbia</i> **	(<i>Phoebis statira</i>)
(<i>Eurema daira</i>)	
(<i>E. lisa</i>)	
Lycaenidae	Lycaenidae
++ <i>Leptotes cassius striata</i>	<i>Chlorostrymon telea</i> **
	++ <i>Leptotes cassius striata</i>
	++ <i>Hemiargus hanno zachaeina</i> **
Heliconiidae	Heliconiidae
++ <i>Agraulis v. vanillae</i>	++ <i>Agraulis v. vanillae</i>
(<i>Dryas iulia</i>)	(<i>Dryas iulia</i>)
Nymphalidae	Nymphalidae
-- <i>Vanessa cardui</i> **	++ <i>Anartia jatrophae luteipicta</i> **
-- <i>Junonia genoveva</i> **	(<i>Historis odius</i>)
++ <i>Anartia jatrophae luteipicta</i>	
<i>Historis odius</i>	
(<i>Junonia evarete</i>)	
(<i>Siproeta stelenes</i>)	
Danaidae	Danaidae
(<i>Danaus plexippus</i>)	(<i>Danaus plexippus</i>)

++ Subspecies shared with Central America.

-- Species invariant in the area.

** Newly recorded in 1986.

() Recorded by Emmel (1975) but not seen in 1986.

ative summary of species recorded from both islands is given in Table 1.

Hesperiidae

Urbanus p. proteus Linnaeus (n = 12). Emmel recorded this skipper as common on San Andrés, as it was during the 1986 survey, when a single specimen was also recorded from Providencia. A recent revision of the *proteus* group (Steinhauser 1981) stresses the external similarity of a number of related species occurring in Central and South America, reliably separated only by genitalic characters. All specimens collected in 1986 were dissected and confirmed as *U. p. proteus*: the generally large size of the forewing maculations shows the San Andrés and Providencia populations to represent the Continental

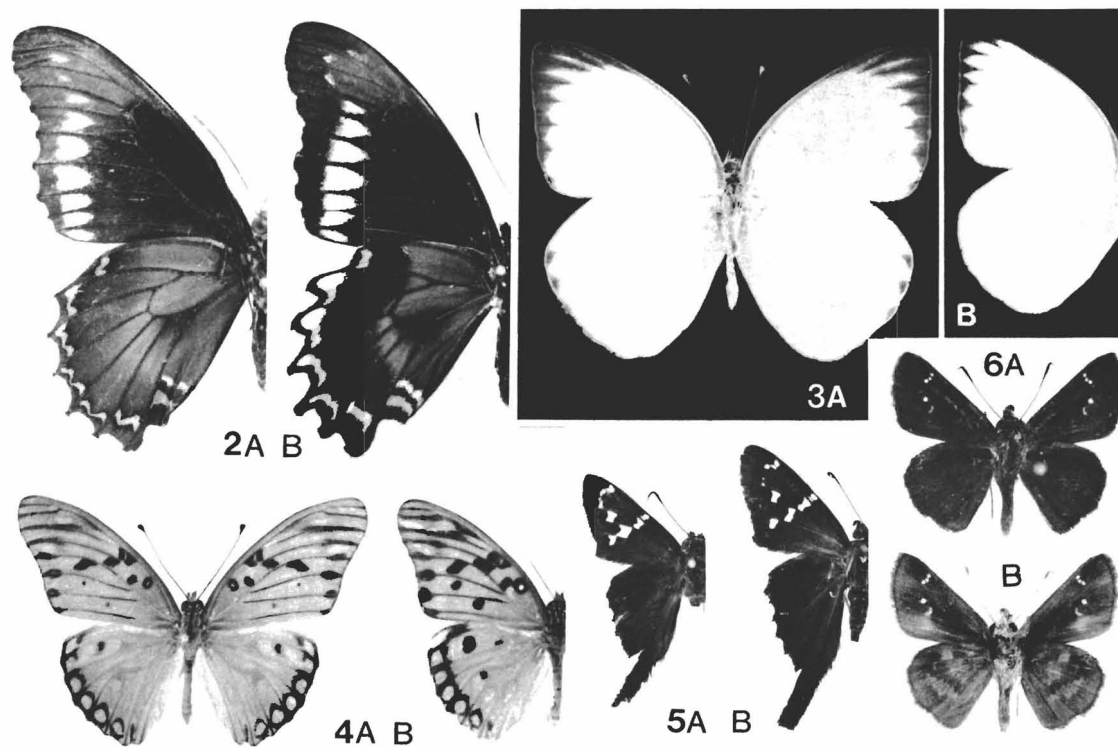


FIG. 2. *Battus polydamas* males, undersides. A: *B. p. polydamas*, San Andrés, August 1986. B: *B. p. polycrates*, Jarabacoa, Dominican Republic, January 1985. ($\times 1.0$). FIG. 3. *Ascia monuste* males, uppersides. A: *A. m. monuste*, San Andrés, August 1986. B: *A. m. eubotea*, Mona Island (Puerto Rico), July 1986. ($\times 1.0$). FIG. 4. *Agraaulis vanillae* males, uppersides. A: *A. v. vanillae*, San Andrés, August 1986. B: *A. v. insularis*, Culebra Is. (Puerto Rico), September 1986. ($\times 0.8$). FIG. 5. *Urbanus proteus* males, uppersides. A: *U. p. proteus*, San Andrés, August 1986. B: *U. p. domingo*, Luquillo, Puerto Rico, June 1980. ($\times 0.7$). FIG. 6. *Cymaenes odilia trebius*, male. A: upperside, B: underside. San Andrés, August 1986. ($\times 1.3$)

nominate subspecies (Fig. 5A), rather than the Antillean *U. proteus domingo* Scudder (Fig. 5B).

U. d. dorantes Stoll (n = 6). This species, absent from Emmel's list, is newly recorded from San Andrés and Providencia, occurring frequently on both islands. All male specimens collected were determined as *U. dorantes*, by comparison with Evans (1952). All are clearly referable to the nominate subspecies occurring on the mainland of the Americas rather than to either of the Antillean subspecies (*U. d. cramptoni* Comstock and *U. d. santiago* Lucas), which differ, respectively, in reduction of forewing maculation (Comstock 1944) and underside markings (Riley 1975).

(*Pyrgus oileus* Linnaeus). This widely distributed skipper, recorded by Emmel as sporadic around Big Pond (San Andrés) in February 1968, was seen on neither island in August 1986.

Cymaenes odilia trebius Mabille (n = 10). This skipper, in flight much resembling *C. tripunctus*, was found commonly, but very locally on San Andrés in August 1986 with a pronounced mid-morning flight period, nectaring at *Stachytarpheta* flowers on an E-W track crossing the island near the southern point. This subspecies (Fig. 6) is recognized primarily by the extent of grey scaling on the forewing underside and by uniformity of the ground color and the distribution and size of the pale spots on the hindwing beneath (Evans 1955). It extends from southern Texas (Howe 1975) through Central America into northern Colombia [Type locality Bogotá]. This species has not previously been recorded from any Caribbean island.

Hylephila phyleus Drury (n = 2). Perhaps the most widely distributed of New World skippers, ranging from Canada to Argentina, *H. phyleus* was noted by Emmel as possibly present on San Andrés, but occurring commonly on Providencia. It was rare on San Andrés in August 1986, and not recorded from Providencia. This skipper has no described insular subspecies in the West Indian region.

Panoquina sylvicola Herrich-Schaeffer (n = 1). Another widely ranging species (from the southern U.S. south to Argentina and through the Antilles), *P. sylvicola* is newly recorded from San Andrés by a single specimen (August 1986).

Papilionidae

Battus p. polydamas Linnaeus (n = 7). This swallowtail is newly recorded from San Andrés, where it was seen, but never common, in August 1986 in scrubby beachside areas, where *Aristolochia* was present. Riley (1975) lists 13 insular subspecific taxa sometimes differentiated on island pairs separated by remarkably short distances. The San Andrés population represents the nominate subspecies (Fig. 2A), which Riley (1975) considered confined to the mainland of Central and South America and not now present on any Antillean island, "... though it seems to have been present earlier on the island of Barbados." A representative Antillean subspecies (*B. polydamas polycrates* Hopffer from Hispaniola and Puerto Rico) is illustrated in Fig. 2B. The island forms are distinguished, one from another, by variations in a number of characters, including the shape, size and tint of the pale upperside spots, and, on the underside, by the uniformity (or otherwise) of the brown ground color of the fore- and hind wings, the size, shape and brightness of the submarginal red markings on the hindwing and, where present, the size and shape of the accompanying silver wedges and distal cream spots (Riley 1975). Each described subspecies is distinctive and the extremes are dramatically different. The nominate subspecies, ranging through Central and much of South America with little variation, cannot be confused with any of the island races. The generally pale brown-grey color of the hindwing beneath, the absence of submarginal pale spots and silver patches associated with the submarginal red markings, and the reduction of the last two pairs of narrow lunules, are diagnostic.

Pieridae

Ascia m. monuste Linnaeus (n = 7). This butterfly was first recorded from San Andrés in August 1986, when it was locally frequent in disturbed coastal waste land and abandoned

fields. Males (all collected) are large, white beneath, with prominent marginal markings (Fig. 3A), and are referable to the continental nominate subspecies which, according to Riley (1975), elsewhere enters the Antillean area from South America *via* Trinidad into the southern Lesser Antilles, possibly occurring further North as an occasional vagrant (Comstock 1944). Despite its migratory proclivity, *A. monuste* has evolved two subspecies in the West Indies: *A. m. eubotea* Latreille (*evonima* Boisduval; see Comstock 1944) is less heavily marked, pale yellow-ochreous on the hindwing beneath, and occurs from Florida and the Bahamas through the Greater Antilles, and *A. m. virginia* Godart, very lightly marked on the upperside, occupying the area between the Virgin Islands and St. Vincent. For comparison with *A. m. monuste*, subspecies *eubotea* is illustrated in Fig. 3B.

***Phoebis sennae* Linnaeus** (n = 35). This widely distributed sulfur was noted by Emmel on each visit to San Andrés and Providencia; in August 1986 it was common on the former and occasional on the latter. Antillean and southern U.S. populations are usually regarded as referable to the nominate subspecies, intergrading with the more northern *P. s. eubule* Linnaeus. The mainland tropical subspecies, *marcellina* Cramer, is described (Howe 1975) as showing a more orange and heavily patterned underside (male) and conspicuous patterning and a ground color of pinkish orange (female) beneath. Klots (1960) regarded this last subspecies as "of dubious worth." Specimens collected in 1986 from San Andrés and Providencia are quite variable and fall within the range of variation of very extensive series examined from the Antilles and the mainland of Central and South America. They do not, therefore, yield reliable information about the affinities of the San Andrés and Providencia populations.

***Phoebis p. philea* Johansson**. This large and (in the male) conspicuously colored species is newly reported from both San Andrés and Providencia (August 1986). Although no specimens were collected, close sightings of males established the identity of the nominate subspecies, which occurs from southern Florida through the mainland south to Brazil (Riley 1975). The two Antillean subspecies, *P. p. huebneri* Fruhstorfer (Cuba) and *P. p. thalestris* Illiger (Hispaniola) are readily distinguished from *p. philea* by a conspicuous large black spot at the end of the forewing cell—certainly absent in specimens seen on San Andrés and Providencia.

***Aphrissa statira* Cramer**. This sulfur was reported by Emmel from two reliable sightings on Providencia in July 1968. The nominate subspecies occurs on the mainland and according to Klots (1960) migrates annually *via* Trinidad into the Lesser Antilles. Two Antillean subspecies have been described, from Cuba and Hispaniola, but until specimens from San Andrés and/or Providencia are examined, the affinity of *statira* in these islands cannot be assessed.

***Eurema daira* Godart**. Emmel recorded this species as "relatively rare" on San Andrés in July, but absent in February, noting that it is widely distributed in the Antilles and the mainland of Central America (and indeed ranges from the SE U.S. to Brazil). It was not found on San Andrés or Providencia in August 1986.

***Eurema venusta limbia* Felder & Felder** (n = 32). Very surprisingly, this "southern" *Eurema* was not encountered by Emmel, yet was one of the most common butterflies on San Andrés in August 1986, notably in abandoned fields and neglected coconut plantations in the southern part of the island. It was not found on Providencia. *Eurema v. emanoma* Dillon, the Antillean subspecies (Fig. 9B), is found in the Lesser Antilles, from Grenada north to Guadeloupe (Pinchon & Enrico 1969, Riley 1975). Specimens collected on San Andrés represent the more heavily marked continental subspecies *E. v. limbia* occurring in Central America (Fig. 9A). The reported food plant, *Mimosa* (Riley 1975), is present on San Andrés, and the discrepancy between the 1968 and 1986 records may reflect a recent successful colonization of the island from Central America.

***Eurema (Pyrritia) lisa* Boisduval & Leconte**. As with *E. daira*, this small sulfur was recorded by Emmel as relatively rare on San Andrés in July and absent in February. It was not found on either in August 1986.

***Abaeis (Eurema) nicippe* Cramer** (n = 16). This species was not found on San Andrés in August 1986, yet was one of the most common butterflies on Providencia at a time when few adult butterflies were seen. On Providencia, *nicippe* was generally distributed along the road around the perimeter of the island. No subspecies have been described.

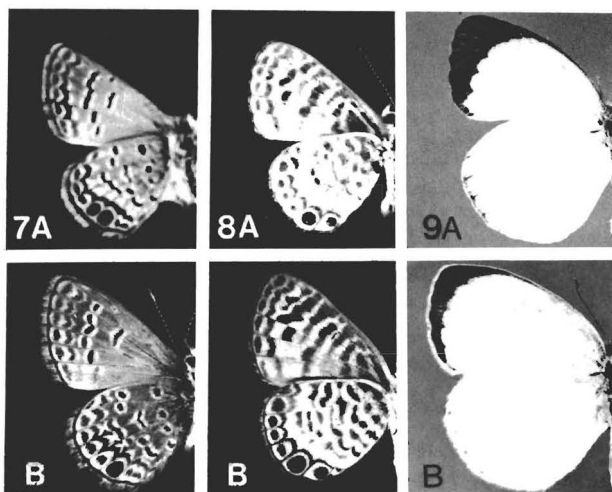


FIG. 7. *Hemiargus hanno* males, undersides. A: *H. h. zachaeina*, Providencia, August 1986. B: *H. h. filenus*, New Providence Is. (Bahamas), July 1980. ($\times 2.0$)

FIG. 8. *Leptotes cassius* males, undersides. A: *L. c. striata*, Providencia, August 1986. B: *L. c. theonus*, Big Pine Key, Florida, September 1984. ($\times 2.0$)

FIG. 9. *Eurema venusta* males, uppersides. A: *E. v. limbica*, San Andrés, August 1986. B: *E. v. emanoma*, Bequia Is. (St. Vincent Grenadines), August 1987. ($\times 1.4$)

Lycaenidae

Hemiargus hanno zachaeina Butler & H. Druce ($n = 10$). This lycaenid was newly recorded for Providencia in August 1986, where it occurred in the same localities and in comparable numbers with *Leptotes cassius*, discussed below. Comparison between the Providencia material and extensive series in the British Museum (Natural History) establishes the former's grouping with the continental subspecies *H. h. zachaeina* [Type locality Costa Rica]. *Hemiargus h. zachaeina* (Fig. 7A) is readily distinguished from the three described island races (Fig. 7B) by the presence of two well demarcated eye-spots near the anal angle of the hindwing beneath, rather than one.

Leptotes cassius striata W. H. Edwards ($n = 12$). Emmel noted *L. cassius* as present on Providencia and distinctly colonial on San Andrés. During the 1986 survey, it was widespread and generally common on San Andrés, while on Providencia, at a time when adult butterflies were very scarce, it was the species seen most frequently. Three Caribbean sub-species have been described: *theonus* Lucas from Florida, the Bahamas, and Greater Antilles; and two subspecies from the Lesser Antilles (Riley). Reference to extensive material in the British Museum (Natural History) clearly associates both San Andrés and Providencia specimens with the mainland subspecies *L. c. striata* [Type locality Bogotá], which ranges throughout Central America. Populations of *L. cassius* show considerable variation, but *L. c. striata* (Fig. 8A) is distinguishable from other forms (Fig. 8B) by reduction of the blue suffusion in the upper surface of the female and, in both sexes, in the generally paler brown underside markings, and in the reduced size and more circular shape of the hindwing eye-spots.

Chlorostrymon telea Hewitson ($n = 1$). A single worn female of this continental hairstreak was collected on Providencia (17 August 1986), representing a new record for a Caribbean island.

Heliconiidae

Agraulis v. vanillae Linnaeus (n = 33). Emmel recorded this species as locally abundant on San Andrés and noted it from Providencia. In August 1986 it was locally common on San Andrés and generally distributed in lowland disturbed areas on Providencia. Emmel described it as resembling "... typical Florida *A. v. nigrrior* Michener, although the black forewing spots often form a bar-like continuous row." Material collected in August 1986 does not conform to this description: specimens are much more lightly marked than *nigrrior* or the widespread Antillean subspecies *A. v. insularis* Maynard, and correspond to the nominate subspecies, which according to Riley (1975) enters the southern Lesser Antilles from the mainland (Fig. 4).

(*Dryas iulia* Fabricius). Emmel found this widespread species (of which numerous Antillean subspecies have been described) commonly on San Andrés "throughout the year" and also recorded it from Providencia. Surprisingly, *D. iulia* was not seen on either island in August 1986.

Nymphalidae

(*Junonia evarete* Cramer). Emmel reported this species, as *Precis evarete zonalis* (C. & R. Felder), to be relatively rare on San Andrés, from one locality in February and July, and did not report it from Providencia. The proposed reinstatement (Turner and Parnell 1985) of *Junonia evarete* is adopted here for this species, which ranges widely from S Texas and Florida through the West Indies and Central America into South America. It was not seen on San Andrés or Providencia in August 1986.

Junonia genoveva Stoll (n = 25). As for the preceding species, the terminology proposed by Turner and Parnell (1985) is adopted here. It was not recorded by Emmel, but in 1986 it occurred in beach areas and abandoned fields on San Andrés, but was not found on Providencia. Specimens collected correspond well with Turner and Parnell's figures of Jamaican *genoveva*; this species shows considerable general and seasonal variation, but the San Andrés material falls within the range shown by series examined from Hispaniola, Puerto Rico, Trinidad, Guatemala, Costa Rica, and Panama.

Anartia jatrophae luteipicta Fruhstorfer (n = 15). This is another nymphalid exhibiting incompletely documented general and seasonal variation. According to Riley (1975) the nominate subspecies is primarily South American, extending into the Lesser Antilles north to St. Kitts. A number of Antillean subspecies have been described (Munroe 1942, Riley 1975), generally darker than populations on the mainland. Emmel found this species to be fairly common on San Andrés in July, though rare in February. In August 1986, it was locally quite common on San Andrés, especially around ornamental flowers in the town and at the airport, and a single specimen was collected on Providencia. These specimens correspond most closely (particularly in their generally light markings and in displaying a conspicuously yellow distal margin of the hindwing) to the Central American subspecies *A. j. luteipicta* [Type locality Honduras], noted by Munroe (1942) as ranging south from Mexico and merging with the nominate subspecies in Panama.

Vanessa cardui Linnaeus (n = 1). Howe (1975) suggests that this cosmopolitan and invariant species is largely nonresident over much of its range in North and Central America, dispersing widely from a few breeding areas. It has been recorded occasionally from many of the Antillean islands (Riley 1975) and is newly recorded from San Andrés from a single worn specimen collected in August 1986.

(*Siproeta stelenes* Linnaeus). This conspicuous and widely ranging nymphalid was regularly recorded by Emmel at one locality on San Andrés during February 1968, and more rarely in other months, but was not found on either island in August 1986.

Historius odius Fabricius. This species was noted by Emmel from both islands, but rarely on San Andrés (July). In August 1986, it was seen on several occasions, along E-W tracks crossing the southern part of San Andrés, but was not recorded from Providencia. Emmel suggested that the few specimens encountered on San Andrés may have been vagrants from the sister island "or even the mainland," but *Cecropia*, the larval food plant, occurs on San Andrés, and this insect may well be resident there. Because no

specimens were collected in 1986, it was not possible to determine whether the San Andrés population belongs to the nominate subspecies, which occupies the Greater Antilles, or to *H. odius orion* Kaye, which ranges through tropical America to Argentina and (Riley 1975) enters the Lesser Antilles from the mainland.

Danaidae

(*Danaus plexippus* Linnaeus). Emmel recorded "scattered and relatively worn" specimens on all visits to San Andrés (February, March, June, July), and also on Providencia. It was not seen on either island in August 1986, and its resident status is unknown. Emmel found no Asclepiadaceae on San Andrés, but potential larval food plants could be present in the shrubby untended coconut plantation understorey of that island, or in the grasslands and disturbed areas of Providencia.

DISCUSSION

An island's observed fauna and flora may be regarded as the result of a balance between addition by successful colonization from outside and, potentially (in long established populations), by evolution of new species and/or races, countered by extinctions (Munroe 1953, 1957, 1984, MacArthur & Wilson 1967, Williamson 1981). In the West Indian-Caribbean region, evolution of butterfly species and subspecies, frequently endemic to a single island, is a conspicuous feature (Riley 1975), particularly on the large islands of the Greater Antilles (Cuba, Jamaica, Hispaniola, and Puerto Rico). The present butterfly faunas of these islands, together with the Bahamian chain, appear to have drawn primarily from a Central American species pool, while the small islands of the Lesser Antilles show more South American donor input (Fox 1963, Scott 1972, Riley 1975, Munroe 1984).

Scott (1972) has provided a survey of the affinities of Antillean butterflies with respect to individual islands and island groups, and the continental land masses of North, Central, and South America. His analysis makes use of an "index of faunal resemblance" (see also Munroe 1957) defined as "the percentage of species found on the island with the smaller fauna which are the same as those on the island [or continental land mass] with the larger fauna." Although providing a valuable basis for analyzing faunal affinities across the entire West Indian region, Scott's index is of limited value when employed at the specific level to assess short-range affinities, especially between an island pair of greatly disparate area, or between a small island and a nearby continental land mass. In the context of San Andrés and Providencia Islands, Emmel (1975) cites Scott's recognition of the great dispersal ability of many species found in the Antilles, and (of the 17 species he recorded) notes that "All . . . are also found on the adjacent Nicaraguan mainland area, and all represent species that are migratory or are known to be frequent colonisers."

At the level employed, this view is substantially accurate, with only

Chlorostrymon telea (Providencia) and *Cymaenes odilia* (San Andrés) representing new Caribbean island records of continental species without obvious dispersal potential. However, if the "higher resolution" data provided by analysis of subspecies are taken into account, the biogeographical status of Providencia and San Andrés takes on a very different aspect.

In the following discussion, only the 19 species recorded during the 1986 survey are considered, although Emmel's records of species not seen during the present field work raise the total species count for these two islands substantially. Except where noted, the species records from the two islands may be pooled for purposes of discussion of their affinities. The two species noted above (*Chlorostrymon telea* and *Cymaenes odilia*) are clearly derived from continental Central or South America; Scott's index would remain at 1.0 with respect to continental America, and the addition of 2 species (of 19) not present in the Antillean islands would reduce the index with respect to the Caribbean area from 1.0 (as implied by Emmel) to 0.89.

Several species recorded from San Andrés and Providencia (*Hylephila phyleus*, *Panoquina sylvicola*, *Abaeis nicippe*, *Phoebis sennae*, *Vanessa cardui* and *Junonia genoveva*) are considered to be invariant in the area (Antilles and the adjacent tropical American mainland) and thus provide no information on biogeographical origins of the islands' populations. To this group must be added *Historius odius*, given the absence of subspecifically determined material. The remaining 10 taxa, determined to the subspecific level (*Urbanus d. dorantes*, *U. p. proteus*, *Battus p. polydamas*, *Ascia m. monuste*, *Phoebis p. philea*, *Eurema venusta limbia*, *Leptotes cassius striata*, *Hemiargus hanno zachaeina*, *Agraulis v. vanillae*, and *Anartia jatrophae luteipicta*), in each instance possessing one or more Antillean subspecies, are represented on San Andrés and/or Providencia by a subspecies in common with continental tropical America. Thus, while the San Andrés-Providencia butterfly populations remain at 1.0 (Scott index) with respect to Central and South America, this index drops to a *maximum* of 0.39 (7 of 19) with respect to the Antillean islands; the balance being largely accounted for by wide-ranging species that afford no affinity data.

It is now clear that the butterfly faunas of these islands, although presumably much affected by destruction of native habitats, considerable on Providencia and virtually complete on San Andrés, represent extensions of the adjacent Central American mainland with no documented Antillean component.

This not unexpected conclusion exemplifies the value of using subspecific information in approaching the question of affinity determination in island groups such as the Antilles, an approach for comparing

closely related faunas first proposed by Munroe (1957). Another recent application of this approach documented the Puerto Rican, rather than Hispaniolan, contribution to the present butterfly fauna of Mona Island (Smith et al. 1988). In the case of San Andrés and Providencia, their proximity to the continental mainland evidently outweighs potential wind-borne dispersal from the Antilles by predominantly easterly winds (Fox 1963, Calvesbert 1973). In considering records for the two islands, Emmel suggests that "Every species found on San Andrés must occur on Providencia, and with the greatly increased diversity of vegetation [on the latter], one would presume that several additional species of butterflies should occur," a forecast that has received some confirmation here. However, we do not feel that one of a pair of small islands, of approximately equal area and similarly positioned with respect to a large and faunistically rich area, should *necessarily* support a butterfly fauna fully represented on the other.

Even if islands in such a pair are ecologically similar, chance variation in the distribution of incoming vagrant species, reaching one and not the other, could well lead to discrepant faunas. Where the islands differ substantially, as do San Andrés and Providencia, the probability of differences between the two faunas may well be enhanced by different environmental spectra that engender differing probabilities of successful colonization.

Present documentation of the butterfly faunas of San Andrés and Providencia is undoubtedly very incomplete, relying only on brief periods of sampling in 1967–68 and 1986. However, of the nine species recorded in August 1986 on Providencia, three were not seen on San Andrés, of which *Abaeis nicippe* is widely ranging, while *Chlorostymon telea* is not obviously dispersive. *Hemiargus hanno*, at the specific level, is one of the widest-ranging lycaenids in the American tropics, yet a continental subspecies is noted on only one island (Providencia). Of the 16 species found during the same period on San Andrés, eight were not noted on Providencia (although sampling followed a prolonged rainless period on that island). Of these, *Vanessa cardui* is a well known wanderer, occasionally recorded as a vagrant on many Caribbean islands: *Panoquina sylvicola* and *Junonia genoveva* are widely dispersed residents in the area and beyond, as is *Hylephila phyleus*, found by Emmel on both islands in 1967–68, but only on San Andrés in 1986. The remaining four butterflies (*Cymaenes odilia trebius*, *Eurema venusta limbia*, *Battus p. polydamas*, *Ascia m. monuste*), at the subspecific level noted, show either limited or no dispersive colonization of the Antillean islands. Yet the last three, at the specific level, are amongst the most widely distributed of the Antillean butterflies. While it is, of course, possible that their absence from the Providencia list merely

reflects our incomplete documentation, it seems as possible that this reflects a real disparity between the butterfly faunas of Providencia and San Andrés.

The position of these ecologically dissimilar islands—about 87 km apart, separated by long distances from a windward potential source of immigrants (the Antilles), but approximately equidistant from a much closer continental land mass—may be regarded as a “natural experiment” from which further data pertinent to questions of general biogeographical interest may be expected. Further field work on these islands would be of great value, not only adding to our knowledge of their butterflies, but in providing data which may refute, modify, or substantiate the biogeographical hypotheses outlined above.

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