GUANA

1999

The Conservation Agency
Exploration, Education, and Research

President
James D. Lazell, Ph.D.
401-423-2652

6 Swinburne Street
Conanicut Island
R.I. 02835 U.S.A.

5/22/00

Dr. Henry Jarecki
10 Timber Trail
Rye, NY 10580

Dear Henry:

The century's closeout was no doubt our best month ever in terms of data collected, and we have also amassed a large number of peer-reviewed publications -- some going back to 1997 but only recently discovered, some already in 2000.

We started off last October by locating young-of-the-year white-crowned pigeons -- identified by their gray crowns -- the very first day in the field, and went right on spotting white-crowns through the month, including adults (with snow-white crowns) clearly paired.

Next, we got on Carval Rock and collected three more (for a total now of five) specimens of what appears to be a new, nameless species of Sphaerodactylus gecko. Padre Sanchez climbed up to get them (Lianna and I collected welks at the edge). He is working on writing the description, but if he bogs down I may have to get involved.

Then, several of us popped over to Little St. James, as reported. In my report, I made a huge blunder: close examination of the photos proves the hatchling sea turtles are ordinary greens, not amazing loggerheads. Dumb mistake on my part, but it in no way detracts from our desire to return to LSJ.

Lizard work went extraordinarily well. We electronically documented parameters of niche space like temperature and humidity, and visually quantified perch height, insulation, activity periods, and relative densities for all three species of *Anolis* at three very different sites: Guana, Sage Mountain, and Beef Island. We marked 10 iguanas right around the hotel and steadily built our point estimator of the population there to 13 ± 2. In 1992 we also marked 10. The point estimator then was an insignificantly different 12 ± 2, but in 1992 six were young-of-the-year, whereas in 1999 only three were. They seem to be growing up in place. Numi and her crew believe they documented an island-wide doubling to tripling of the iguana population, using radio-tracking and GPS transect censusing. Those data have yet to be fully processed.

Dr. Barry and Buena Valentine, both superb general biologists, synergized the entomological efforts on site (see below); we can expect publications soon. Dr. Scott Miller did not attend, but he has returned from two years in Africa to be Chairman at the Entomology Department of the Smithsonian, and has tracked down several papers I would not have found. He will become more involved again, he says.

On all other fronts things went very well, as the participants attest in their reports and publications that follow. I have illuminated some texts and lists with illustrations and brief descriptions of the organisms, whenever I could (some will have to wait until next year).

I have annotated material directly in what follows.

A large lot of people are very disappointed by the 2000-2001 reductions. I have had to turn down a lot of excellent proposals. Everyone hopes this is truly temporary and we will be back up to speed again in 2002.

See you in October, if not sooner. Meantime, email will be the best way to stay in touch.

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All the best, Skip

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COVER STORY:

RETURN OF THE NATIVE

The native resident yellow warbler, Dendroica petechia cruziana, was formerly a nesting species on Guana, often noted by the Island's first ornithologist, Erma J. (Jonnie) Fiske, in the 1950's. Jonnie and her husband Bradley built "Fiske House," today Camanoe. She came back to Guana in her 80's in 1988. By then, however, our mangroves had been severely cut and our yellow warblers -- strict mangrove nesters -- were gone.

There have been some sightings in more recent years, as the mangroves have recovered. However, North American migrant yellow warblers may have accounted for these: one cannot tell the birds apart in the field. The critical distinction is the length of the primary wing feathers: the first is the longest in the strong-flying migrant, but short -- shorter than the second primary feather -- in the resident.

The Virgin Island yellow warbler is not today a common bird except on Anegada. (It is very conspicuous on Necker too, but there are probably only two or three pairs there.) Because it is a weak flier, we suspect it recolonizes regrown habitats with difficulty and rarely. Years went by without proof of them again on Guana.

On 12 October 1999, Fred Sibley and his crew got this one photographed by Kris Ovaska: apparently and adult male in breeding plumage.

We hope they are back to stay.

United States Department of Agriculure
Forest Service
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Dr. James D. Lazelle
The Conservation Agency
6 Swainburne Street
Jamestown, RI 02835

13 May 2000

Dear Dr. Lazelle:

The basidiomycete fungal collecting on Guana and Tortola islands in October of 1999 was very fruitful, despite being cut short by the hurricane. I managed to describe and dry all the collections just as the storm struck. I brought back 97 collections from that trip.

The results of the 1999 collecting on Guana are particularly exciting because this was the first time we were able to collect fruiting bodies of beneficial symbionts associated with the roots of *Pisonia*. We found *Inocybe xerophytica* associated with *Pisonia* in the White Bay Beach area – the first report of this species outside the Lesser Antilles. Previous collecting trips had yeilded ectomycorrhizal symbionts of the sea grape, *Coccoloba uvifera*, but not symbionts of *Pisonia*. What is especially interesting is that these two host plants, belonging to different families, appear to have different ectomycorrhizal symbionts. While host differences have been observed before among some temperate ectomycorrhizal fungi, such studies are rare in tropical broad leaved forests. Based on our results, *Coccoloba* and *Pisonia* each have a different species of *Scleroderma* associated with their roots. Similarly, *Russula littoralis* is associated with *Coccoloba*, while another one or two species of *Russula* are associated with *Pisonia*. Such host differences can greatly increase species diversity among ectomycorrhizal fungi.

Other exciting finds from the 1999 Guana collections include a new species that is being described from Panama and now Guana island (*Rhodocybe luteocinnamomea* Baroni & Ovrebo, sp. nov., in prep.) It was found in the old Tamarind orchard at the base of Quail Dove Ghut. I found a new species of *Mycena* I am describing (*M. vitellina* Lodge, sp. nov., in prep.) which I have previously found in Puerto Rico and Trinidad. *Cuphophyllus buccinulus*, *Hygrocybe conica* var. *brevispora*, *Leucopaxillus gracillimus*, and *Mycena delica* (all neotropical species) and *Leptonia cerrusatum* (an eastern N.Am. species) are new records for Guana Island.

The most startling results are from the breif collecting forays outside Sage Mtn. National Park on Tortola. In 1999, I found a drab, fan-shaped fungus growing from soil that is related to some other species we have found in Puerto Rico. The DNA sequences show that this group of fungi is not closely related to any of the major groups of basidiomycetes. It undoubtedly belongs to a new family, and possibly a new order. I went through all the collections from previous years to see if there are others in this group, and found instead another odd fungus from Sage Mtn. in Tortola. I sent part of the specimen up to Dr. Joey Spatafora for

DNA analysis, and it turns out to be ancestral to the Gomphaceae. Further comparisons are underway with sequences from the genus *Gloeocantharellus*, but that genus has true lamellae whereas the fungus from Tortola has only forked wrinkles on the fertile surface. It is certainly an important and interesting piece of the puzzle in the evolution of the Gomphales.

I want to thank you, The Conservation Agency, and the Falconwood Foundation for making the collection of these fungi possible. I understand that in October 2000much repair work is being done on Guana Island, and you want to minimize the number of scientists working there. I do not need to return to Guana this October. I know that some of the other scientists would like to work in the Caribbean National Forest, and if they did that for part of their normal stay on Guana, it would further decrease the number of number of scientist-days on Guana. The Virgin Islands are part of the Puerto Rico Bank, and the whole land mass was united above water during the past ice age, 10,000 years ago. Many of the unique species in the Virgin Islands have arisen since the ice sheets melted, so it is natural that biologists, especially the herpetologists, would want to compare populations on Guana with those on the main island of Puerto Rico. We have two field stations in the forest, one where I am at Sabana near Luquillo, and the other at El Verde. The Sabana Station is run by the US Forest Service, and the cost per person is only about $3.60 per night to stay in the dormitory. The El Verde Research Station is run by the University of Puerto Rico, where it costs $10.00 per night per person. Although neither station provides food, there are kitchens available, and catering could probably be arranged. The cost would be about $30/person/day. The overall costs of $35-40per person per day are quite reasonable, and undoubtedly less than on Guana Island.

If this suggestion is agreeable, we would need to clear permits far in advance.

Sincerely,

D. Jean Lodge

D. Jean Lodge
Center for Forest Mycology Research

P.S. The publication of <u>Amanita</u> <u>arenicola</u> with it's type locality on Guana Island, will appear in print soon. I'll send a reprint when it arrives.

MUSEUM OF COMPARATIVE ZOOLOGY
The Agassiz Museum

HARVARD UNIVERSITY
26 OXFORD STREET
CAMBRIDGE, MASSACHUSETTS 02138

4 January 2000

Dr. James D. Lazell
The Conservation Agency
6 Swinburne Street
Conanicut Island, RI 02835

Dear Skip,

I suspect you need documentation of my accomplishments while on Guana Island. Thus, enclosed are reports from my 1998 and 1999 collecting expeditions. Although, specific guidelines were never given to me, I hope you'll find them useful.

I continue my studies on the molluscan biodiversity of Guana Island here at the MCZ. In December, I traveled to the Florida Museum of Natural History to meet Fred Thompson and use their collections. In addition we discussed the species identifications of the terrestrial mollusks of Guana and other Virgin Islands. I have nearly completed a species list of Guana with a comparison to others Virgin Islands that will be published in the Occasional Papers on Mollusks. However, I have run into some difficult taxonomic problems. Most of these can and should be resolved by return visits to Guana Island. In addition, I would like to continue to photograph terrestrial mollusks such that my work on a web based interactive pictorial key can be completed. The internet address of this prototype can be found in either one of the enclosed reports.

Please do not hesitate to contact me with any questions. I look forward to seeing you again on Guana Island in October.

Sincerely,

Adam J. Baldinger

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The Mollusca of Guana Island, B.V.I. - Results of a recent collecting expedition and a proposal for future research

The following details the results of a recent collecting expedition (27-30 October 1998) to Guana Island, British Virgin Islands by Adam Baldinger [Museum of Comparative Zoology (MCZ), Harvard University] and Eric Lazo-Wasem [Peabody Museum of Natural History (YPM), Yale University]. Although I assisted Eric Lazo-Wasem in collecting marine amphipods for future study, this report will focus specifically on the Mollusca and outline a proposal for future research.

Summary of collecting expedition

Twelve intertidal and terrestrial collection sites were surveyed for conspicuous (visible by eye) mollusks. Any mollusks collected were fixed and preserved prior to leaving Guana. Upon return the Mollusca were sorted and identified. The collection consisted 35 species in 73 specimen lots of marine and terrestrial mollusks. These samples will be divided and incorporated into both the MCZ and YPM collections. A list of the taxa collected are summarized in Table 1.

Prior to this expedition the MCZ mollusk collection contained approximately 60 lots of mainly marine and some terrestrial species collected during three separate visits to Guana Island in 1937-1938 by Mr. and Mrs. George T. Dewey. The Dewey's who lived in the Boston area donated their entire collection to the Museum of Comparative Zoology. Many of the taxa collected by them are represented in the collection by one dry preserved lot with only one or few specimens available for study. Of the material collected by the Dewey's none contained alcohol preserved animals.

It was our intention to augment the MCZ and YPM collections and hopefully collect specimens currently not represented at both institutions. In addition, we hoped to begin to document any potential population changes of the molluscan taxa on Guana Island over the past sixty years utilizing the Dewey collection as a reference collection. Also, most specimens we collected were preserved in alcohol (except those collected already dead; i.e. empty shells) such that future molecular and other taxonomic studies can potentially be accomplished using not only the shells, but the animals (bodies) too.

Of primary interest to us was the terrestrial mollusk species diversity on Guana Island. Only two papers (to our knowledge) on the terrestrial mollusks of Guana Island have been published. The first written by W.J. Clench (1939) provided a list of 11 terrestrial species found on Guana Island. This list was developed directly from the Dewey collection currently housed in the MCZ. Of the three terrestrial species collected by us, only one of the species appears on the list provided by Clench. More recently, J.D. Lazell (1983) published a paper on the rediscovery of the Palm Snail [*Hemitrochus nemoralinus intensus* (Pilsbry, 1889)] that he collected on Guana Island. This species was not listed by Clench (1939). Lazell (1983) also mentioned that the above species was described by Pilsbry and apparently without a type locality. Recently, the syntypic lot of this species was obtained on loan from the Academy of Natural Sciences in Philadelphia (ANSP). The labels with specimens appear to indicate that the type locality is San Juan, Puerto Rico. Also, the taxonomic name assigned to this species by the ANSP is *Cepolis* (*Leviceoplis*) *nemoralina intensa* (Pilsbry, 1889). Interestingly, *Hemitrochus nemoralinus* Petit, also described from Puerto Rico, was listed as occurring on Guana Island by Clench (1939). Further investigation into the type status, taxonomy, nomenclature and distribution of this *Hemitrochus* species and sub-species complex is in preparation. However, for further research to continue more sampling for specimens for comparative studies from Guana Island are needed.

Proposal for future collecting and research

A return visit to Guana Island would focus primarily on the terrestrial molluscan diversity. Vigorous sampling of terrestrial habitats are needed for accurate comparisons of "modern" day species to those provided by Clench (1939) sixty years ago. In addition, photographs of living specimens would be taken, and then the animals preserved in ethyl alcohol for future descriptive and molecular research. The photographs along with habitat information would then be downloaded onto a web page providing an interactive key to all that are interested in identifying species and investigating the diversity of the terrestrial mollusks of Guana Island. A prototype of this web page has been developed using the three common marine littorinid species found on Guana Island. The information (i.e. photographs, distribution data, etc.) of the species on this web page has resulted from the data acquired from our recent collecting expedition. This interactive and pictorial key is maintained on the MCZ Department of Mollusks web page at the following address:

http://www.mcz.harvard.edu/Departments/Mollusks/guanalittorinidae.htm.

Guana Island is a ideal site to carry out molluscan biodiversity studies. Knowing the species diversity particularly of the terrestrial mollusks can provide valuable taxonomic and baseline distributional data for all the Islands of the British Virgin Islands.

Literature Cited

Clench, W.J. 1939. Land shells of Guana Island, Virgin Islands, West Indies. Mem. Soc. Cubana Nat. Hist. 13: 287-288.

Lazell, J.D. 1983. Rediscovery of the palm snail, *Hemitrochus nemoralinus intensus* Pilsbry (Cepolinae). The Nautilus 97(3): 91-92.

Table 1. Mollusks collected by A.J. Baldinger and E.A. Lazo-Wasem during a recent collection expedition to Guana Island (27-30 Oct 1998)

Acmaeidae:	*Acmaea lecuopleura* (Gmelin, 1791)
	Acmaea antillarum (Sowerby, 1831)
Annulariidae:	*Chondropoma totolense* Pfeiffer
Arcidae:	*Barbatia cancellaria* (Lamarck, 1819)
Buccinidae:	*Engina turbinella* (Kiener, 1835)
Bulimulidae:	*Bulimulus guadalupensis* (Bruguiere, 1789)
Camaenidae:	*Granodomus incertus* Ferussac
Cardiidae:	*Americardia media* (Linnaeus, 1758)
Chitonidae:	*Acanthopleura granulata* (Gmelin, 1791)
	Chiton marmoratus Gmelin, 1791
	Chiton squamosus Linnaeus, 1758
	Chiton tuberculatus Linnaeus, 1758
Fissurellidae:	*Diodora dysoni* (Reeve, 1850)
	Diodora listeri (Orbigny, 1842)
	Fissurella barbadensis (Gmelin, 1791)
	Hemitoma octoradiata (Gmelin, 1791)

Ischnochitonidae: *Ceratozona squalida* (C.B. Adams, 1845)

Littorindae: *Littorina angulifera* (Lamarck, 1842)
Littorina meleagris (Potiez & Michaud, 1838)
Littorina ziczac (Gmelin, 1791)
Tectarius muricatus (Linnaeus, 1758)

Lucinidae: *Codakia orbicularis* (Linnaeus, 1758)
Linga pensylvanica (Linnaeus, 1758)

Muricidae: *Purpura patula* (Linnaeus, 1758)
Thais sp.

Neritidae: *Nerita peloronta* Linnaeus, 1758
Nerita tessellata Gmelin, 1791
Nerita versicolor Gmelin, 1791

Olividae: *Oliva reticularis* Lamarck, 1810

Planaxidae: *Planaxis nucleus* (Bruguiere, 1789)

Pteriidae: *Pinctada imbricata* Rodin, 1798
Pteria colymbus (Roding, 1798)

Tonnidae: *Tonna maculosa* (Dillwyn, 1817)

Trochidae: *Cittarium pica* (Linnaeus, 1758)

Xanthonycidae: *Hemitrochus* sp.

The Terrestrial and Freshwater Mollusca of Guana Island, B.V.I.

The following outlines the results of a recent collecting expedition (13-16 October 1999) to Guana Island, British Virgin Islands by Adam Baldinger, Museum of Comparative Zoology (MCZ), Harvard University. This report will focus specifically on the terrestrial and freshwater mollusks obtained this year and a comparison to the taxa listed by William Clench in his 1939 paper on the land snail of Guana Island. In addition I assisted Eric Lazo-Wasem, Peabody Museum of Natural History (YPM), Yale University in collecting marine amphipods for future study.

Introduction

Many 19th and 20th century malacologists were generally considered conchologists studying only the shell morphology and excluding any anatomical characters. Most malacologists also agreed that populations on Islands, like those of the West Indies, that were separated by geographical barriers, must be distinct and separated species. Thus, every new population sampled from different Islands were considered new to science. This practice gave rise to a substantial number of land snail species, some 30,000 names in about 85 families. Modern day malacologists are conchologists too, but also utilize anatomical characters such as radular teeth or those found in the digestive and reproductive systems in species descriptions.

Very few biogeographical studies have been published on the land snails of the British Virgin Islands and most of these papers are either descriptions of new species or new locality records of a given species. Only two papers on the terrestrial mollusks of Guana Island have been published. The first written by W.J. Clench in 1939 was essentially a species list based on a rather extensive collection of land mollusks taken from Guana Island in 1937 and 1938 by Mr. & Mrs. George Dewey. The second by J.D. Lazell published in 1983 was on the rediscovery of the Palm Snail, *Hemitrochus nemoralinus intensus* (Pilsbry, 1889). Although these two publications contain valuable historical and distributional data, both contain erroneous species identifications and reveal taxonomic problems.

Specific Islands that are devoid of development and industrialization are ideal starting points for biogeographical studies. Identifying the terrestrial molluscan species diversity of Guana Island can provide valuable taxonomic and baseline distributional data for all the Islands of the British Virgin Islands.

This years visit was to begin a study to document the terrestrial and freshwater molluscan diversity on Guana Island. And complete a comparison to those species first reported on Guana Island by William Clench sixty years prior and then to species known from nearby Islands like Tortola (from MCZ collections) and St. John, U.S.V.I. (from a species list provided by Muchmore, 1993). In addition, an attempt was made to photograph living specimens for development of a interactive and pictorial key to be utilized by both scientists and lay persons visiting Guana Island. A prototype of this interactive key has been developed using the three common high intertidal marine littorinid species from Guana Island. It is maintained on the MCZ Department of Mollusks web page (http://www.mcz.harvard.edu/Departments/Mollusks/). Lastly the animals were preserved in ethyl alcohol for future anatomical or molecular research.

Terrestrial and freshwater sites were surveyed for conspicuous (visible by eye) mollusks. Any live mollusks collected were drowned in fresh water for 24 hours, fixed and then preserved in alcohol prior to leaving Guana. The samples were then later sorted and identified. This year's collection consisted of 35 specimen lots of terrestrial mollusks. No freshwater mollusks were found. Eleven species (Table 1) were identified although the taxonomic status of each of these species is currently being researched.

In addition, the terrestrial mollusks collected by Fred Kraus who visited Guana Island in 1991 will be analyzed. This includes a visit in early December (1999) to the collections at the Florida Museum of Natural History (FMNH) where Fred deposited much of his material. A preliminary species list for Guana Island that includes Baldinger's 1998 and 1999 collections and those of Fred Kraus who deposited them in the FMNH are also presented in Table 1.

Conclusions and future research

Although the species status of some of the taxa presented in Tables 1-3 are questionable, the land and fresh water species diversity on Guana differs from the known taxa on Tortola, Anegada and St. John. Also, five of the twenty-six taxa listed in Table 1 were either collected by Baldinger or published in Clench (1939) and not collected by Kraus (1991). Conversely, ten of the twenty-six taxa were collected by Kraus (1991) and not by Baldinger or reported by Clench (1939). Additional sampling of specific habitats are needed for comparative studies and for accurate identifications that would allow one to generate a reliable hypothesis of the terrestrial and freshwater molluscan diversity on Guana Island. Thus by determining the land and fresh water mollusks of Guana Island would greatly enhance further research on the biodiversity or biogeographical patterns of the Virgin Islands.

Literature Cited

Clench, W.J. 1939. Land shells of Guana Island, Virgin Islands, West Indies. Mem. Soc. Cubana Nat. Hist. 13: 287-288.

Lazell, J.D. 1983. Rediscovery of the palm snail, *Hemitrochus nemoralinus intensus* Pilsbry (Cepolinae). The Nautilus 97(3): 91-92.

Muchmore, W.B. 1993. List of terrestrial invertebrates of St. John, U.S. Virgin Islands (Exclusive of Acarina and Insecta), with some records of freshwater species. Carib. J Sci. 29(1-2): 30-38.

Table 1 Terrestrial and fresh water mollusks found on Guana Island based on MCZ, FMNH and Baldinger 1998, 1999 collections.

SUBCLASS PROSOBRANCHIA
ORDER NERITOPSINA (ARCHAEOGASTROPODA)
HELICINIDAE
[1,2,3]Alcadia foveata Pfeiffer

ORDER NEOTAIENIOGLOSSA (CAENOGASTROPODA)
CHONDROPOMATIDAE (=ANNULARIDAE)
[1,2,3]Chondropoma tortolensis Pfeiffer, 1857

ORDER NERITOPSINA
NERITIDAE (=NERTINIDAE)
[2]Neritina virginea (Linnaeus, 1758) (Estuarine)

ORDER MESOGASTROPODA =? NEOTAENIOGLOSSA)
HYDROBIIDAE
[3]Pyrgophorus sp.(FW/Estuarine)

SUBCLASS PULUMONATA
ORDER STYLOMMATOPHORA
PUPILLIDAE (=VERTIGINIDAE)
[3]Gastrocopta servilis (Gould, 1843)
[3]Gastrocopta pellucida (Pfeiffer, 1841)

STREPTAXIDAE
[3]Gulella bicolor Hutton, 1834

FERUSSACHIIDAE
[3]Cecilioides consobrina Orbigny, 1855

HELICARIONIDAE
[3]Guppya gundlachi (Pfeiffer, 1839)

BULIMULIDAE
[1,3]Bulimulus guadalupensis (Bruguiere, 1789)
[1,3]Drymaeus elongatus (Roding, 1798)

CAMAENIDAE
[1,3]Zachrysia provisoria (Pfeiffer, 1858)

SUBCLASS PULUMONATA (Cont.)

ORDER STYLOMMATOPHORA

SUBULINDAE
[1,2,3]Subulina octona (Bruguiere, 1792)
[1,2,3]Lamellaxis micra (d'Orbigny, 1835)
[2]Obeliscus swiftianus Pfeiffer
[3]Beckianum beckianum (Pfeiffer, 1846)
[3]Opeas pumilum (Pfeiffer, 1840)
[3]Opeas pyrgula Schmacker & Boettger, 1891

XANTHONYCHIDAE
[1,2,3]Hemitrochus nemorlinus (Petit, 1836)
[3]Hemitrochus nermolinus intensus (Pilsbry, 1889)
[1,2]Plagiotycha euclasta (Shuttleworth, 1854)
[3]Plagiotycha musicola euclasta Shuttleworth, 1854
[3]Plagiotycha musicola musicola Shuttleworth, 1854

SAGDIDAE
[2]Hojeda subaquila (Shuttleworth, 1854)
[3]Hojeda inaguensis Weinland

ORDER BASOMMATOPHORA

PHYSIDAE
[2]Physa cubensis (FW) - Identified as "Aplexa" harryi D.W. Taylor, 4-1992

[1] = species collected by Baldinger in 1998, 1999
[2] = from Clench 1939 (MCZ collection)
[3] = from FMNH collections

Table 2. Land and freshwater molluscan species known to occur on Tortola and Anegada based upon MCZ collections.

Tortola	Anegada
Bulimulus guadeloupensis	*Bulimulus diaphanus* Pfeiffer
Chrondropoma tortolense Pfeiffer	*Chrondropoma newcombiana* C.B. Adams
Megalomastoma brunneum Swainson	*Drymaeus elongatus* Bolt
Drymaeus elongatus Bolt	*Glycymeris urdata* Linne
D. ludouicus "Rang" Pfeiffer	*Granodomus incertus* Ferussac
Granodomus incertus Ferussac	*Maeroceramus signatus* Guild
Hojeda subaquila Shutt	*M. microdou* Pfeiffer
Maeroceramus signatus Guild	*Melampus coffeus* Linne
Melampus flavus Gmel	*Succinea ochracina* Pfeiffer
Obeliscus swiftianus Pfeiffer	*Cerion striotellum* Guerin
Opeas micra Orbigny	
Polydontes incerta For	
Potamopyrgas anthraeina Migh.	
Subulina octona Brug	
Succinea approximans Schutt	
Alcadia foreata	
A. subfusca Mke	

Table 3. Land and freshwater molluscan species known to occur on St. John (after Muchmore, 1993).

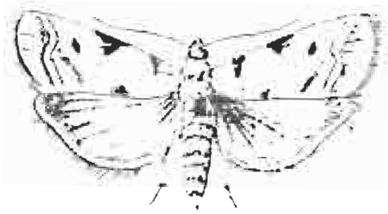
Phylum Mollusca
Class Gastropoda

- Subclass Prosobranchia
  - Order Archaeogastropoda
    - Family Helicinidae
      - *Alcadia foveata* (Pfeiffer 1853) (6)
      - *Alcadia striata* (Lamarck 1822)
  - Order Mesogastropoda
    - Family Littorinidae
      - *Littorina angulifera* (Lamarck 1822)
      - *Littorina ziczac* (Gmelin 1791)
      - *Nodilittorina tuberculata* (Menke 1828)
      - *Tectarius muricatus* (Linnaeus 1758)
    - Family Annularidae
      - *Chondropoma newcombiana* (C. B. Adams 1849) (6)
    - Family Cyclophoridae
      - *Megalomastoma petiti* Bartsch 1942
    - Family Truncatellidae
      - *Truncatella scalaris* Michaud 1830
- Subclass Pulmonata
  - Order Basommatophora
    - Family Ellobiidae
      - *Melampus coffeus* (Linnaeus 1758)

  - Order Systellommatophora
    - Family Veronicellidae
      - *Leidyula kraussi* (Fèrussac 1825)
      - *Leidyula floridana* (Leidy 1851)
  - Order Stylommatophora
    - Family Ariophantidae
      - *Guppya gundlachi* (Pfeiffer 1840)
    - Family Bulimulidae
      - *Bulimulus guadalupensis* (Bruguière 1792) (6)
      - *Bulimulus diaphanus* (Pfeiffer 1854)
      - *Drymaeus virgulatus* (Fèrussac 1822) (6)
    - Family Camaenidae
      - *Polydontes incertus* (Férussac 1823) (6, 71)
    - Family Ferussacidae
      - *Caecilioides gundlachi* (Pfeiffer 1850)
      - *Caecilioides consobrinus* (Orbigny 1855)
    - Family Helminthoglyptidae
      - – *Hemitrochus nemoralinus* (Petit 1836) (6, 71)
      - – *Plagioptycha euclasta* (Shuttleworth 1854)
    - Family Oleacinidae
      - *Varicella terebraeformis* (Shuttleworth 1854)
    - Family Pupillidae
      - *Gastrocopta pellucida* (Pfeiffer 1841)
    - Family Sagdidae
      - *Hyalosagda subaquila* (Shuttleworth 1854)
      - *Lacteoluna selenina* (Gould 1848)
    - Family Streptaxidae
      - *Streptaxis glaber* Pfeiffer 1850
      - *Gulella bicolor* (Hutton 1834)
    - Family Subulinidae
      - *Beckianum beckianum* (Pfeiffer 1846)
      - *Lamellaxis gracilis* (Hutton 1834)
      - – *Lamellaxis micra* (Orbigny 1835)
      - *Opeas pumilum* (Pfeiffer 1840)
      - – *Subulina octona* (Bruguière 1789)

- Subclass Prosobranchia
  - Family Thiaridae
    - *Thiara tuberculata* (Muller 1774)
      - pools in Fish Bay Gut (lower)
  - Family Hydrobiidae
    - *Pyrgophorus parvulus* (Guilding 1828)
      - pools in Fish Bay Gut (upper) and Great Lameshur Bay Gut
- Subclass Pulmonata
  - Family Physidae
    - *Physa marmorata* (Guilding 1828)
      - Petroglyph pools in Living Gut

  - Family Planorbidae
    - *Drepanotrema lucidum* (Pfeiffer 1839)
      - pools in Great Lameshur Bay Gut
  - Family Ancylidae
    - *Ferrissia irrorata* (Guilding 1828)
      - pools in Fish Bay Gut (upper)



Subj: **Guana Island moth manuscript**
Date: 05/12/2000 1:11:44 PM Eastern Daylight Time
From: miller.scott@nmnh.si.edu (Scott Miller)
To: jcinjtown@aol.com

Dr. James Lazell
The Conservation Agency

Dear Skip:

I am sorry that I did not have a chance to unpack the illustrations, so that I could send you the manuscript and illustrations, before I departed on the present trip. Therefore, I am appending below the title and abstract of the manuscript, which treats 148 species of moths from Guana Island, including color illustrations of all and detailed morphological illustrations of some. I must further apologize that my two year sabbatical in Africa, and then my move to Washington, have prevented me from finishing this manuscript for the last three years. Vitor Becker will be visiting Washington during the summer, and we intend to finish the manuscript then and submit it for publication to the series "Supplements to Tropical Lepidoptera."

After finishing this manuscript, we will turn our attention to several other manuscripts on Guana moths, including one nearing completion on the superfamily Pyraloidea.

In the meantime, we have made material available for studies by other systematists, as evidenced by the publications by Don Davis* and others.

Again, we are grateful for the opportunity to undertake these studies and I am sorry that my other duties have slowed progress on finishing the manuscripts.

* only "in press" now: next year.... Skip

THE LARGE MOTHS OF GUANA ISLAND, BRITISH VIRGIN ISLANDS: A SURVEY OF EFFICIENT COLONIZERS

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ABSTRACT. An illustrated and commented list of large moths of Guana, a 297 ha island located on the north shore of the Caribbean island of Tortola, British West Indies, is presented for the first time. Of the 148 species listed, 98 have distribution throughout the neotropics, 41 throughout the Antilles, with some ranging into Florida, and 9 endemic to the Puerto Rican Bank, two of them described here: Catabenoides lazelli sp. n., and Perigea gloria sp. n. The following synonyms and combinations were also found in this study: Leucania solita Walker, syn. n. [=L. humidicola Guenée], L. dorsalis Walker, sp. rev. , L. extenuata Guenée, sp. rev.], Kakopoda cincta Smith, syn. n. [=K. progenies (Guenée)], Drepanopalpia polycyma Hampson, syn. n. [=D. lunifera (Butler), comb. n.], Sphacelodes fusilineatus Walker, stat. rev., Ptychopoda monata Forbes, syn. n. and Sterrha insulensis Rindge, syn. n. [=Lobocleta nataria (Walker)], Ptychopoda curtaria Warren, syn. n. [=Idaea minuta (Schaus)]. A new genus, Catabenoides Poole, gen. n., type-species: Laphygma vitrina Walker, is also described. The palatability to birds of two species: Diphthera festiva and Calidota strigosa, were tested and showed distasteful.

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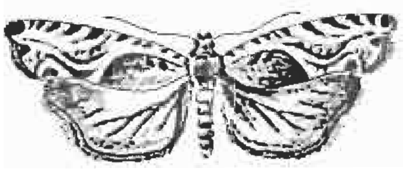

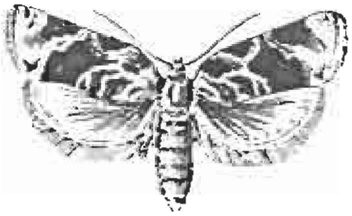

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Annotated Checklist of Puerto Rican Cockroaches

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ABSTRACT

We present type localities, type depository of endemic species, distributions of nonendemic species, taxonomic references, notes and some comments for 58 species of cockroaches recorded from Puerto Rico. Two previously known species, *Eurycotis decipiens* from Trinidad and *Symploce pararuficollis* from Guana Island, and seven undescribed species in the genera *Colapteroblatta, Euthlastoblatta, Henicotyle, Nelipophygus* and *Nyctibora* are here reported (but not described or named) from Puerto Rico. Corrections to Wolcott's 1948 cockroaches scientific names are given in a table. Drawings are included for *Eurycotis decipiens* and *Neoblattella adusta*, two species from Puerto Rico, previously known only from the original verbal descriptions.

RESUMEN

Las localidades tipo, el depositorio de los tipos de las especies endémicas, la distribución de las no endémicas, referencias taxonómicas, notas y algunos comentarios son presentados para 58 especies de cucarachas reportadas de Puerto Rico. Se citan por primera vez para Puerto Rico, *Eurycotis decipiens* conocida previamente de Trinidad y *Symploce pararuficollis* conocida de Guana Island, así como siete especies aún por describir de los géneros *Colapteroblatta, Euthlastoblatta, Henicotyle, Nelipophygus* y *Nyctibora* y. Se brinda en una tabla los nombres científicos corregidos de las especies tratadas en Wolcott 1948. Se incluyen dibujos de *Eurycotis decipiens* y *Neoblattella adusta*, las únicas dos especies sin ilustrar presentes en la isla y conocidas solo a partir de sus descripciones originales.

INTRODUCTION

This paper is a second contribution to the knowledge of the Antillean fauna following the "Annotated Checklist of Cuban Cockroaches" (Gutiérrez 1995). It includes a list all known cockroach species from Puerto Rico. This checklist serves as a starting point for researchers interested in Puerto Rican cockroaches, and as a useful tool for the inventory of the poorly known Puerto Rican cockroach diversity.

Many authors have studied Puerto Rican cockroaches. The first endemic species was described by Burmeister in 1838 (*Plectoptera dorsalis*). In this century 20 endemic taxa were published by the following authors: Rehn (1903), Caudell (1905), Rehn (1910), Hebard (1916), Rehn & Hebard (1927), Rehn (1930, 1945), J. W. H. Rehn (1951)

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Subfamily **PANCHLORINAE**

1. Genus **PANCHLORA** Burmeister

Panchlora, Burmeister 1838: 506. Type species: *Panchlora pulchella* Burmeister, selected by Rehn 1903.

1. **nivea** (Linné) 1758: 424 [*Blatta*]; figs. in: De Geer (1773): pl. 44, fig. 10; Roth & Willis (1957): pl. 22, figs. 1-3, 9, 10.

Distribution.—Antilles, Central and South America[7], Puerto Rico[16], Bahamas, Southeastern USA[1], Canada[15].

2. **sagax** Rehn & Hebard 1927: 251, pl. 19, figs. 1-4.

Distribution.—Puerto Rico, Dominica, Colombia[7], Guadeloupe[2], Guana Island (British Virgin Is.)[14].

Subfamily **PYCNOSCELINAE**

1. Genus **PYCNOSCELUS** Scudder

Pycnoscelus, Scudder 1862: 421. Type species: *Pycnoscelus surinamensis* (Linné) =*Blatta surinamensis* Linné =*P. obscurus* Scudder, by monotypy.

1. **surinamensis** (Linné) 1758: 242 [*Blatta*]

Distribution.—Circumtropical[7,10].

Note.—This interesting species is parthenogenetic (Roth & Willis 1961; Roth 1967; Roth 1974).

Family **BLATTELLIDAE**
Subfamily **ANAPLECTINAE**

1. Genus **ANAPLECTA** Burmeister

Anaplecta, Burmeister 1838: 494. Type species: *Anaplecta lateralis* Burmeister, selected by Kirby 1904.

1. **sp.**

Note.—Peck (1974) records: "*Anaplecta* or near, A. B. Gurney det. Aguas Buenas Cave, 1 male, 1female, in river passage, Fenton collection. The species is new, with entirely vestigial hind wings which is an unusual condition for the genus.". We have not seen this specimen.

Comments.—The genus *Anaplecta* is not included in previous Puerto Rican lists (Gundlach 1887, Rehn 1903, and Wolcott 1923, 1936, 1948).

1. **sp.**

Note.—Fisk (1977) writes: "Another species of *Nesomylacris* with tegmina lateral and wings lacking has been taken in Puerto Rico and is the subject of a paper in preparation (FISK and GURNEY b)." That paper was not published, but 9 specimens (4 males, 1 female and 4 nymphs) from Parguera, Cabo Rojo and Guánica are deposited at NMNH.

Comments.—The genus *Nesomylacris* was not included in previous Puerto Rican lists (Gundlach 1887, Rehn 1903, and Wolcott 1923, 1936, 1948).

5. Genus **SYMPLOCE** Hebard

Symploce, Hebard 1916b: 355-356. Type species: *Symploce hebardi* Princis 1969.

1. **bicolor** (Beauvois) 1805: 183 [*Blatta*], pl. 1b; additional figs. in: Roth (1984): 5A-H.

Distribution.—Gonave, Mona, Dominican Republic [11].

Note.—Wolcott (1948) writes: "The Hispaniolan *Symploce bicolor*..., has repeatedly been collected on Mona Island." Roth (1984) studied material from Las Caobas, Mona Island in litter, and in houses in the same island, deposited at NMNH.

2. **flagellata** Hebard 1916b: 367, pl. 18, figs. 14-17; additional figs. in: Roth (1984): 6A-H, 13I.

Distribution.—Saona, Desecheo, Mona [11].

Note.—Wolcott (1948) wrote: " . . . according to Rehn & Hebard (1927-136), this species "does not occur on the island of Porto Rico itself . . . ." García Tudurí et al (1974) list this species from Desecheo. Roth (1984) studied material from Desecheo and Mona.

3. **jamaicana** (Rehn) 1903: 264 [*Ischnoptera*]; figs. in: Hebard (1916b): pl. 18, figs. 5-7; Roth (1984): figs. 8A-G, 9A-E, 10A-I, 11A-H.

Distribution.—Caiman Islands, Jamaica, Puerto Rico [11], Haiti, Bahamas Islands[13].

Note.—Roth (1984) studied material from Ensenada, Puerto Rico at AMNH.

4. **pallens** (Stephens) 1829: 304 [*Blatta*]; figs. in: Hebard (1916b): pl. 17, fig. 8, pl. 18, figs. 1-4 [as *S. lita*]; Hebard (1917): pl. 2, figs. 16-20; Roth (1984): figs. 15A-I, 16A-E, 17A-E, 18A-E. 19A-F, 20A-E, 21A-E, 22A-F, 23A-I.

Distribution.—Circumtropical[1].

Note.—Princis (1969) listed this species from Puerto Rico.

5. **pararuficollis** Roth 1994: 45, figs. 1A-D, 2.

Distribution.—Guana Is. (British Virgin Is.) [14] and Puerto Rico.

Note.—There are two specimens (1 male and 1 female) determined as *S. pararuficollis* by E. Gutiérrez at MNHNC from "Cabezas de San Juan, Puerto Rico, XII-1993, bajo cocos secos en el suelo, Cols. R. Thomas, E. Gutiérrez, A. Pérez-Asso". This is the first record for Puerto Rico.

6. **ruficollis** (Fabricius) 1787: 226 [*Blatta*]; figs. in: Rehn & Hebard (1927): pl. 10, figs. 6-9 [as *S. bilabiata*]; Roth (1984): figs. 13A-H, 14A-H; Roth (1994): figs. 1E, 1F, 2.

Distribution.—Puerto Rico, Culebra, St. Thomas, St. John [11], Guana Island[14].

Note.—Roth 1994 provides excellent comments and drawings useful for distinguishing *Symploce ruficollis* from *Symploce pararuficollis*.

Subfamily **NYCTIBORINAE**

1. Genus **NYCTIBORA** Burmeister

Nyctibora, Burmeister 1838: 501. Type species: *Nyctibora sericea* Burmeister, selected by Kirby 1904.

1. **lutzi** Rehn & Hebard 1927: 193, pl. 16, figs. 1, 2.

Type Locality.—Ensenada, near Guanica, Department of Aguadilla, Puerto Rico. /Type F3473d male (AMNH), allotype (NMNH).

Note.—The allotype of this endemic species comes from "Utuado, Department of Arecibo, Puerto Rico" (Rehn & Hebard 1927). Wolcott 1948 writes: " . . . possibly to be found most often in the highest mountains, in rotten tree trunks. Some found at San Sebastián were in a large rotten stump which they shared with "comején" termites, yellow wood-ants and rhinoceros beetle grubs."

2. **sp.**

Note.—Specimen number 256 deposited at NMNH from Puerto Rico, represents an undescribed species of this genus, and it is determined as "*Nyctibora* n.sp. Y". This information was provided by Dr. Louis M. Roth (MCZ) who worked with Dr. A. B. Gurney on an unpublished revision of the genus *Nyctibora* (Roth pers.com.). This taxon is here recorded for the first time from Puerto Rico.

Subfamily **PSEUDOPHYLLODROMIINAE**

1. Genus **AMAZONINA**

Amazonina, Hebard 1929: 353. Type species: *Phyllodromia conspersa* Brunner, selected by Hebard 1929.

1. **conspersa** (Brunner) 1865: 106 [*Phyllodromia*]; figs. in: Hebard (1921): pl. 9, fig. 20 [*Neoblattella*].

Distribution.—Venezuela, Trinidad, British Guiana, Surinam, French Guiana, Brazil, Peru, Paraguay, Argentina [11], Puerto Rico[12].

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4. **sp.**

Note.—There is one specimen male from "El Yunque, P. R., 753 m., VI-8-'70, R. Lavigne collector" at NMNH which is determined as *Aglaopteryx* n.sp. by A. B. Gurney in 1970. This undescribed species of *Euthlastoblatta* is reported here for the first time from Puerto Rico.

5. **sp.**

Note.—There is one male of an undescribed species of *Euthlastoblatta* at NMNH from "Camp Cofresi, Mona Is., P. R., 27 Oct. 1955, W. H. Cross collector." The present taxon is the first record for the island.

5. Genus **NEOBLATTELLA** Shelford

Neoblattella, Shelford 1911: 155. Type species: *Blatta adspersicollis* Stål 1858, by monotypy.

1. **adusta** (Caudell) 1905 : 237 [*Ischnoptera*]. (Not illustrated).

Type Locality.—Arroyo, Puerto Rico. /Type male 8400 (NMNH).

Note.—There is a female from "El Yunque, N. Este, bajo piedra, 23-VIII-1995, Cols. G. Alayón-R. Arencibia," at MNHNC, determined as *Neoblattella adusta* by E. Gutiérrez. The species is known only from a male which is not illustrated. We here provide the first illustrations of this endemic taxon useful for its identification (Figs. 6-10).

2. **borinquenensis** Rehn & Hebard 1927: 80, pl. 5, figs. 11-13.

Type Locality.—El Yunque, Department of Humacao, Puerto Rico (800 feet). /Type male (NMNH).

Note.—Wolcott 1948 writes: "The type of *Neoblattella borinquenensis* Rehn & Hebard (1927-80 to 83) is from El Yunque, but others are from San Juan, Caguas, Manatí and Utuado..."

3. **vomer** Rehn & Hebard 1927: 83, pl. 5, figs. 14-18.

Type Locality.—Mayaguez, Department of Mayaguez, Puerto Rico. /Type male 3725 and allotype F3968d (AMNH).

Note.—*Neoblattella vomer* has been frequently collected in bracts of *Bambusa* sp. that had fallen on the floor from Carretera P. R. 511, km 10, Real Anón, Ponce, during December 1993 January 1994, by E. Gutiérrez and A. Pérez-Asso. This material is deposited at MNHNC.

6. Genus **PLECTOPTERA** Saussure

Plectoptera, Saussure 1864b: 173. Type species: *Blatta porcellana* Saussure 1862, selected by Rehn 1903.

1. **dorsalis** (Burmeister) 1838: 494 [*Anaplecta*]; figs. in: Rehn & Hebard (1927): pl. 21, fig. 5, pl. 22, figs. 7, 13-14, pl. 23, figs. 4, 5.

Type Locality.—Puerto Rico. / Syntypes 411 (ZMB).

Note.—There are 2 syntypes with the catalog number ZMB Orth. 411, which bear a green handwritten label "Portorico / Moritz". At

See Next Page

least one of them seems to be a female and the other one is covered by fungus and the sex cannot be determined (M. Ohl, pers. com.). Rehn & Hebard 1927 studied specimens of this endemic taxon from Mayaguez, Maricao, Arecibo, Cayey and Aibonito.

2. **infulata** Rehn & Hebard 1927: 314, pl. 23, fig. 11.
Type Locality.—Mayaguez, Department of Mayaguez, Puerto Rico. /Type male 3725 and allotype 3710 (AMNH).
Note.—Princis 1965 lists this endemic species from Puerto Rico and Vieques Island.

3. **rhabdota** Rehn & Hebard 1927: 305, pl. 21, figs. 8, 9, pl. 22, fig. 9, pl. 23, fig. 7.
Distribution.—Puerto Rico, St. Thomas[8], Guadeloupe, Marie Galante, Dominica, Vieques Island[2], Guana Is. (British Virgin Is.)[14].
Note.—This species originally was described from San Juan and Aibonito, Puerto Rico, and Rehn & Hebard (1927) note: "The species is, apparently, one of fairly wide distribution in Porto Rico."

7. Genus PSEUDOSYMPLOCE Rehn & Hebard

Pseudosymploce, Rehn & Hebard 1927: 103. Type species: *Pseudosymploce schistopyga* Rehn & Hebard, by original designation.

1. **personata** Rehn 1930: 22, pl. 1, fig. 3, pl. 5, fig. 2.
Type Locality.—Luquillo National Forest, Puerto Rico (1500 feet). / Type female F5111 unique (AMNH).
Note.—This endemic species is known only from a male. There are one male and two females at ANSP from "El Yunque c. 3000 ft., May 1938, Darlington collector" and two female specimens at MNHNC from "El Yunque, N. Este, bajo piedras, 23-VIII-1995, G. Alayón-R. Arencibia collectors" determined by E. Gutiérrez.

2. **sp.**
Note.—Peck (1974) records one undescribed species of "*Pseudosymploce* sp., A. B. Gurney det.". About this taxon Peck notes: "...is already known from El Verde Field Station, Luquillo Forest, Puerto Rico.". The senior author has examined a male specimen from Aguas Buenas cave ("Aguas Buenas, Aguas Buenas cave. River passage, 14-II-1968, M. B. Fenton collection (Thru S. B. Peck)") deposited in NMNH. There are two additional specimens (one male and one female) of this species at ANSP from "El Yunque c. 3000 ft., May 1938, Darlington collector".

8. Genus SUPELLA Shelford

Supella, Shelford 1911: Type species: *Blatta longipalpa* Fabricius 1798 = *Blatta/ Phyllodromia supellectilium* Serville 1839, by monotypy.

1. **longipalpa** (Fabricius) 1798: 185 [*Blatta*].
Distribution.—Circumtropical[11].

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West Indian species of *Beameromyia* Martin (Diptera: Asilidae)

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Abstract: The West Indian species of *Beameromyia* Martin are reviewed. Four new species are described, and *Beameromyia insulara* Martin and *B. cubensis* (Bigot) are redescribed. Illustrations of the genitalia and a key to the known West Indian species are included.

Key Words: Diptera, Asilidae, robber flies, *Beameromyia* Martin, West Indies, New Species

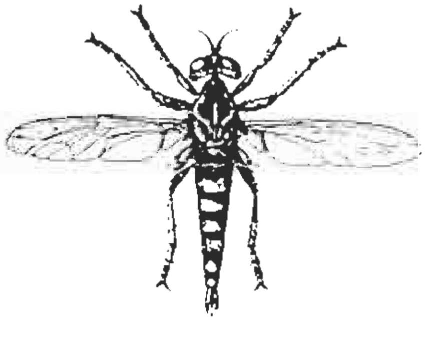
Introduction

Martin (1957a) proposed the genus *Beameromyia* Martin to include small (4.5-8 mm) leptogastrine flies in the United States. Species included in this genus are all very similar, having only slight differences in the structures of the male genitalia. They also have weak postocular setae, usually a band of fine, erect setae across the middle of the second abdominal tergum, the first and second sterna are narrow or obsolete, vein M2 is sharply angular, and the apex of the epandrium is tapered to a point or it has a shallow apical notch. Furthermore, the apical one-third of the hind femur and most of the length of the hind tibia are unusually swollen. The hind tibia and most of the hind femur are otherwise contrastingly narrow.

Members of this genus are common in the United States with at least sixteen valid species (Martin 1957a). Though specimens are common in museum collections, only a few species are known from other parts of the New World, i. e. *B. chrysops* Martin (Martin 1957a), *B. insulara* Martin (Martin 1957b) from the Bahamas, and *B. graminicola* Farr (Farr 1963) from Jamaica. *Beameromyia floridensis* (Johnson) (Johnson 1894, Martin 1957a) from Florida may also occur in nearby continental islands. Of the confirmed West Indian species, the male of *B. insulara* is unknown, and its genitalia is neither described nor illustrated. The epandrium of *B. chrysops* (Martin 1957a) and dorsal and lateral views of the intact male genitalia of *B. graminicola* (Farr 1963) are illustrated. The purpose of this paper is to describe four new West Indian species, redescribe *B. cubensis* (Bigot) and the female of *B. insulara*, provide illustrations of the genitalia of these species and a key to the known species from the West Indies. Type specimens are deposited in the collections of the United States National Museum (USNM) and Museum of Comparative Zoology (MCZC). The codens AMNH and MNHN in the text refer to the American Museum of Natural History, New York, USA, and the Museum National d'Historie Naturelle, Paris, France, respectively.

Beameromyia Martin

Of the known West Indian fauna, the species may be divided into two discrete groups: 1) with a long, slender, acutely pointed epandrium; aedeagus long, thin, and curved behind the base of the genitalia; and the lateral spermatheca with a single, elongate, apical bulbous capsule; crossvein cu-m is present; and veins CuA1 and M3 are not fused; and 2) with a shallow apically notched epandrium; aedeagus short, slightly arched; each lateral spermatheca with a median and an apical swollen bulbous capsule; crossvein cu-m absent; and veins CuA1 and M3 are fused.



Family **Asilidae**—Robber Flies: This is a large group, with about 850 North American species, and many species are quite common. The adults are found in a variety of habitats, but each species usually occurs in a characteristic type of habitat. The adults are predaceous and attack a variety of insects, including wasps, bees, dragonflies, grasshoppers, and other flies, which they usually capture on the wing; they often attack an insect as large as or larger than themselves. Some of the larger robber flies can inflict a painful bite if carelessly handled.

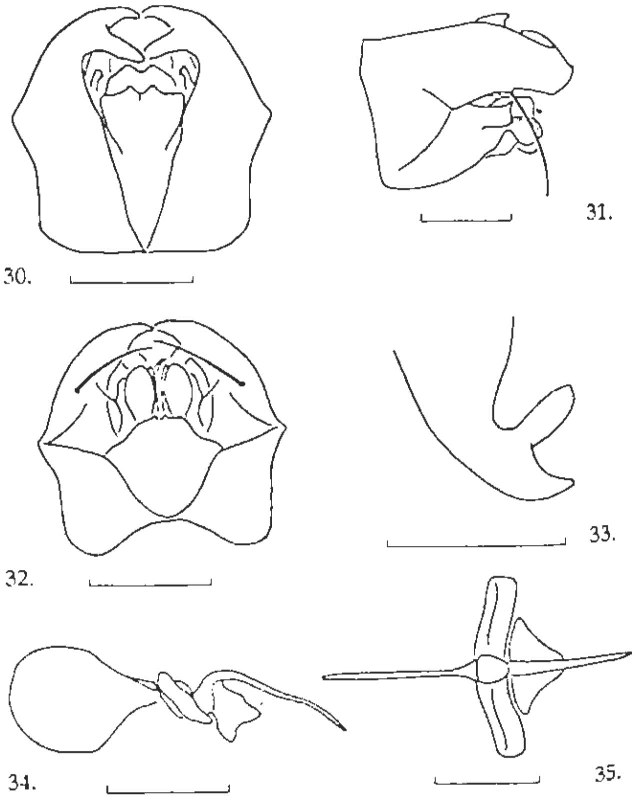
Robber flies have the top of the head hollowed out between the eyes (Figure 492 D), the face more or less bearded, and they have a stout thorax with long, strong legs. Most of them are elongate, with the abdomen tapering (Figure 492 B, C), but some are stout-bodied and very hairy, and strongly resemble bumble bees or other Hymenóptera (Figure 492 A). The larvae live in soil, decaying wood, and similar places, and feed chiefly on the larvae of other insects.

Beameromyia virginensis, new species

Figs. 30-37

Male. Body largely yellowish brown or blond. Length: body 6.9-9.1 mm; wing 5.0-7.0. Face largely yellowish tomentose grading to whitish ventrally, mystax with 8 long, pale yellow setae. Proboscis brown apically to yellowish brown basally, Palpus yellowish brown with pale yellow vestiture. Frons light to dark yellow-brown tomentose. Basal 2 antennomeres yellow, clearly shorter than flagellum; brown flagellum and style of equal Length: flagellum 2½ x as long as wide. Occiput brownish gray or brownish yellow tomentose dorsally grading to whitish ventrally, vestiture pale yellow.

Mesonotum largely brown, yellow-brown anterolaterally and laterally, postalar callus yellow; dorsum brown tomentose with median stripe bordered by narrow yellow-brown stripe of tomentum, mesonotum laterally and posteriorly yellow to grayish tomentose; middle stripe anteriorly divided



Figs. 30-35. *Beameromyia virginensis*, new species. ♂ 30-32: Genitalia, dorsal, lateral and ventral views. 33: Apex of epandrium 34-35: Aedeagus, lateral and dorsal views. Scales: 30-35 = 3 mm

with faint line of light yellowish brown tomentum. Dorsum with sparse vestiture, largely brown, consisting mostly of long row of dorsocentral setae and two bristles on each side; posterior dorsocentral setae longer than crossvein r-m. Scutellum and mesopleuron pale yellow to whitish tomentose with largely or entirely pale yellow vestiture. Margin of scutellum with several short, brown and yellow setae, none as long as r-m crossvein. Halter yellow, with knob brownish.

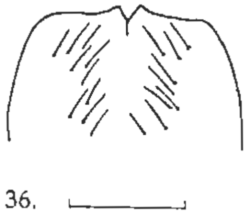
Wing with abundant, brown microtrichia. Vein CuA1+M3 short, less than length of crossvein r-m; crossvein r-m well before middle of cell d; base of cell r4 just beyond apex of cell d.

Coxae yellow with pale yellow or whitish tomentum and vestiture. Trochanter yellow. Fore and mid femora yellow basally, yellowish brown to brown otherwise, brown band or anterior spot often present on apical ⅔; both femora slightly lighter in color posteriorly. Hind femur with apical ½ greatly swollen; basal ½ of hind femur usually yellow, sometimes with narrow, brown, anterior stripe; apical ½ with brown band or spot grading into yellow-brown apically. Fore and mid tibiae brownish anteriorly, yellowish posteriorly, bristles yellow. Hind tibia gradually swollen apically, apex 3-4x basal width, brown with subapical, yellowish band. Tarsi with tarsomeres yellowish basally, apices light to dark brown; basal tarsomere lightest, often pale yellow, and apical tarsomere darkest; all bristles dark brown. Claw and empodium black, empodium of hind tarsus short, ¼-½ as long as claw.

Abdomen mostly brown, yellow as follows: narrow sides, wide band at apical ¼ and narrow, subapical band of tergum 2; narrow sides, and narrow basal and subapical bands of terga 3-5; and narrow sides and subapical band of tergum 7. Tomentum of abdomen mostly brown, gray to yellowish gray in yellow areas of basal 2 segments, tomentum grading to yellowish gray to brown-yellow in yellow areas of each successive segment. Pale tomentose areas with abundant, pale yellow setae, tomentum elsewhere brown.

Genitalia (Figs. 30-35). Dorsal lobe of epandrium thick, posterior branch pointed, shorter with wide base. Secondary penal valve subrectangular with short, dorsolateral point, tertiary valve spatulate. Aedeagus (Figs. 34-35) slightly angled downward, without distinct undulation.

Female. As male except as follows: Length: body 7.3-9.7 mm; wing 6.1-6.2. Basal antennomeres light to dark yellowish brown. Legs darker brown than in males, light apex of hind femur and yellow band of hind tibia less contrasting than in males. Sternum 8 (Fig. 36) with apical margin, subtruncate, membranous, numerous bristly setae present beside middle; shorter, thicker setae present just behind membranous apical margin. Lateral spermatheca (Fig. 37) with large, apical capsule, and slighter larger, longer, intermediate capsule; spermathecal ducts with numerous, weak tentacles, especially between basal valves and median capsules, sparse tentacles present before valves. Median spermatheca, narrow, tube-like with abundant tentacles beyond valves.



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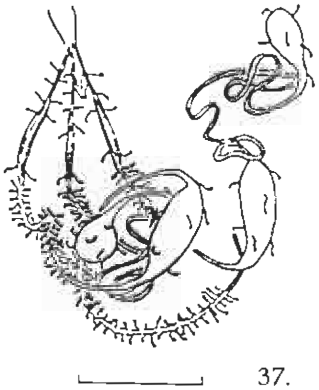

37.

Figs. 36-37. *Beameromyia virginensis*, new species ♀. 36. Sternum 8. 37. Spermathecae. Scale: Fig. 36 = .3 mm; Fig. 37 = .2 mm

Holotype ♂ **& allotype** ♀, British Virgin Islands: Guana Island, 1-14.vii.1984, S. E. & P. M. Miller. (USNM). Paratypes: 10 ♂ & 3 ♀, same data as types; 1 ♀, St. Thomas Island, Frenchman Bay Estates, 25 May, 1978, 750 ft., M. A. Ivie. (USNM).

Etymology. Latin, *virginensis*, refers to the type locality of this species, British and the U. S. Virgin Islands.

Remarks. *Beameromyia virginensis* is similar to *B. graminicola* Farr and *B. quaterna* but differs by the color of the cuticle, with *B. virginensis* being blond, *B. quaterna* red, and *B. graminicola* brown. In addition, *B. virginensis* differs in the yellow tomentose face, brown-yellow front, the median tomentose stripe and brown-yellow tomentum of the mesonotum; the legs are also much darker, yellow-brown to light brown anteriorly, and lack distinct bands. Furthermore, the style is longer than that in *B. graminicola*, being as long as the flagellum, and the empodium of the hind tarsus is short, less than ½ as long as the claws. The yellow bands of terga 2-5, the abundant yellowish to yel-

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low-brown tomentum of the abdomen, and the combined characters of the genitalia separate the species. In addition to the blond color of the body, the yellow bands of the abdomen, the shape of the epandrium, and the penal valve, and 6 facial setae separate it from *B. quaterna*.

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A REVISION OF THE *ANASTREPHA DACIFORMIS* SPECIES GROUP (DIPTERA: TEPHRITIDAE)

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Abstract.—The *Anastrepha daciformis* species group is revised. Thirteen species are recognized: ***A. antilliensis,* n. sp.** (Puerto Rico, Dominican Republic); ***A. aquila,* n. sp.** (Costa Rica); ***A. avispa,* n. sp.** (Costa Rica); *A. bicolor* (Stone) (s. Texas to Costa Rica); ***A. castanea,* n. sp.** (Argentina and Brazil (Mato Grosso do Sul)); *A. daciformis* Bezzi (s. Brazil, Paraguay, Argentina); ***A. katiyari,* n. sp.** (Venezuela); *A. macrura* Hendel (w. Venezuela, Ecuador, Paraguay, Brazil (Bahia, Rio Grande do Norte)); ***A. maculata,* n. sp.** (Virgin Is., Mona I.); ***A. murrayi,* n. sp.** (Jamaica); *A. pallens* Coquillett (s. Texas to Honduras and El Salvador); *A. stonei* Steyskal (Florida, Bahamas, Dominican Republic); ***A. zucchii,* n. sp.** (Brazil (Roraima)). A key to the species and an analysis of their phylogenetic relationships is presented and a diagnosis, description and illustrations of each species are provided.

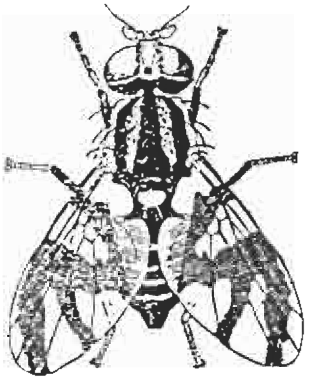
Key Words: *Anastrepha, daciformis,* species group, key, Neotropical, phylogeny

Resumen.—Se revisan las especies de *Anastrepha* del grupo *daciformis* en el cual se reconocen trece especies: ***A. antilliensis,* n. sp.** (Puerto Rico, Dominican Republic); ***A. aquila,* n. sp.** (Costa Rica); ***A. avispa,* n. sp.** (Costa Rica); *A. bicolor* (Stone) (sur de Texas a Costa Rica); ***A. castanea,* n. sp.** (Argentina y Brasil (Mato Grosso do Sul)); *A. daciformis* Bezzi (sur de Brasil, Paraguay, Argentina); ***A. katiyari,* n. sp.** (Venezuela); *A. macrura* Hendel (oeste de Venezuela, Ecuador, Paraguay, Brazil (Bahia, Rio Grande do Norte)); ***A. maculata,* n. sp.** (Virgin Is., Mona I.); ***A. murrayi,* n. sp.** (Jamaica); *A. pallens* Coquillett (sur de Texas a Honduras y El Salvador); *A. stonei* Steyskal (Florida, Bahamas, Republica Dominicana); ***A. zucchii,* n. sp.** (Brasil (Roraima)). Se presenta además una clave para la separación de las especies y un análisis de sus relaciones filogenéticas, y se proporcionan diagnosis, descripciones e ilustraciones de cada una de las especies estudiadas.

The *daciformis* species group includes some of the most distinctive species of *Anastrepha*, the largest New World genus of Tephritidae, with almost 200 species. The *daciformis* group includes 13 species, eight of which are described in this paper. Together these species range from the West Indies and southern Texas to Argentina. All 13 species have dark brown markings of some type, and all but three have uninterrupted marginal wing bands, presumably for mimicry of vespid or other wasps.

Family **Tephritidae** – Fruit Flies. The members of this group are small to medium-sized flies that usually have spotted or banded wings, the spotting often forming complicated and attractive patterns (Figures 505 and 506). They can be recognized by the structure of the subcosta, which apically bends forward at almost a right angle and then fades out; in most species the anal cell has an acute distal projection posteriorly (Figure 460 B). The adults are found on flowers or vegetation. Some species have the habit of slowly moving their wings up and down while resting on vegetation, and are often called peacock flies. This group is a large one (239 North American species), and many species are quite common.

The larvae of most tephritids feed on plants, and some are rather serious pests. The larva of *Rhagóletis pomonélla* (Walsh), usually called the apple maggot, tunnels in the fruit of apple and other orchard trees (Figure 505); other species in this genus attack cherries. The Mediterranean fruit fly, *Cerátitis capitàta* (Wiedemann), attacks citrus and other fruits, and some years ago threatened to become a serious pest in the South; this species is now eradicated from the South. Species of the genus *Eurósta* form stem galls on goldenrod (Figure 507); the galls are rounded and thick-walled, with a single larva in the center. In the fall, the larva cuts a tunnel to the surface, overwinters as a larva in the gall, and pupates in the spring. A few of the tephritids are leaf miners in the larval stage.



Anastrepha maculata Norrbom, new species

(Figs. 2C–E, 6B, 7I)

Diagnosis.—This species differs from other species of the *daciformis* group except *stonei* in having the distal arm of the V-band present. It differs from *stonei* as indicated in the key and in the diagnosis for *stonei*, and by the following characters: Scutum entirely microtrichose (nonmicrotrichose except lateral margin in *ston*
posterior half of anatergite dark brown (white except posteroventral corner in *stonei*); and subscutellum and mediotergite entirely dark brown, or latter sometimes dark orange with 3 dark brown stripes (in *stonei*,

subscutellum orange, often with medial dark brown spot; mediotergite entirely orange). The female terminalia are relatively short compared to the other 3 Antillean species of the group (see Table 2).

Description.—Body predominantly yellow to orange. *Head:* Yellow except ocellar tubercle usually brown. Posterior orbital seta usually absent (weakly present on one side in 1♂). *Thorax* (Fig. 7I): Scutum usually with dark brown spot above postalar seta, sometimes with dark brown spot mesal to intra-alar seta and/or unpaired dark brown spot posterior to acrostichal setae. Medial pale stripe bilobed posteriorly, lobes stout, with distinct anterolateral corner, extended to dorsocentral seta. Presutural dorsocentral pale stripe connected anteriorly to pale area on postpronotal lobe and connected to or narrowly separated from pale lateral stripe. Presutural lateral pale stripe poorly differentiated, appears to be complete, including posterior part of notopleuron. Scutellum with 3 dark brown spots, one medial and pair on margin between yellow basal and white apical areas. Pleuron with following dark brown spots: two dorsal spots on anepisternum; anterodorsal and posteromedial spots on katepisternum; medial spot on anepimeron; and posterior half of laterotergite. Subscutellum and mediotergite entirely dark brown, or latter sometimes dark orange with 3 dark brown stripes. Scutum and notopleuron entirely microtrichose; scutellum microtrichose basally, nonmicrotrichose on dark brown spots and apical white area. *Wing* (Fig. 6B): Bands yellow, orange and brown. C- and S-bands completely fused along costa, forming uninterrupted marginal band; cell R_1 without hyaline marginal area. C-band covering cell r_{2+3} to beyond level of r-m. S-band interrupted in medial cells and along vein Cu_1; basally with broad extension across vein Cu_2+A_1 almost to posterior wing margin; middle part not extended anteriorly beyond vein M, but often narrowly connected to V-band; subapically relatively broad, with large hyaline area in cell r_{2+3} but well separated from vein R_{2+3}; apically of medium breadth, extended to or almost to apex of vein M. V-band complete, not connected to S-band along vein R_{4+5}. Vein M strongly curved apically; M ratio 1.21–1.53. *Abdomen:* Tergites entirely yellow or orange, without dark brown marks. *Female terminalia:* Syntergosternite 7 length 2.58–2.85 mm, 1.03–1.15 times as long as mesonotum. Aculeus length 2.33 mm; tip with a few fine apical serrations, length 0.10 mm, width 0.025 mm.

Remarks.—The name of this species refers to the spots on its mesopleuron and scutellum.

Distribution.—Virgin Islands, Mona Island (between Puerto Rico and Hispaniola). This species presumably also occurs on Puerto Rico, which is between the Virgin Islands and Mona Island.

Types.—Holotype: ♀ (USNM), BRITISH VIRGIN ISLANDS: Guana Island, 0–80 m., 13–26.VII.1986, S.E. Miller & M.G. Pogue. Paratypes. BRITISH VIRGIN ISLANDS: Great Camanoe Isld., ⅓ mi. ESE Cam Bay, 20.III.1974, C.L. Remington, 1♂ (MCZ); Guana Island, 0–80 m., 13–26.VII.1986, S.E. Miller & M.G. Pogue, 1♂3♀ (USNM). PUERTO RICO: Mona Isld., Uvero, 19.X.1955, W.H. Cross, 1♂ (USNM).

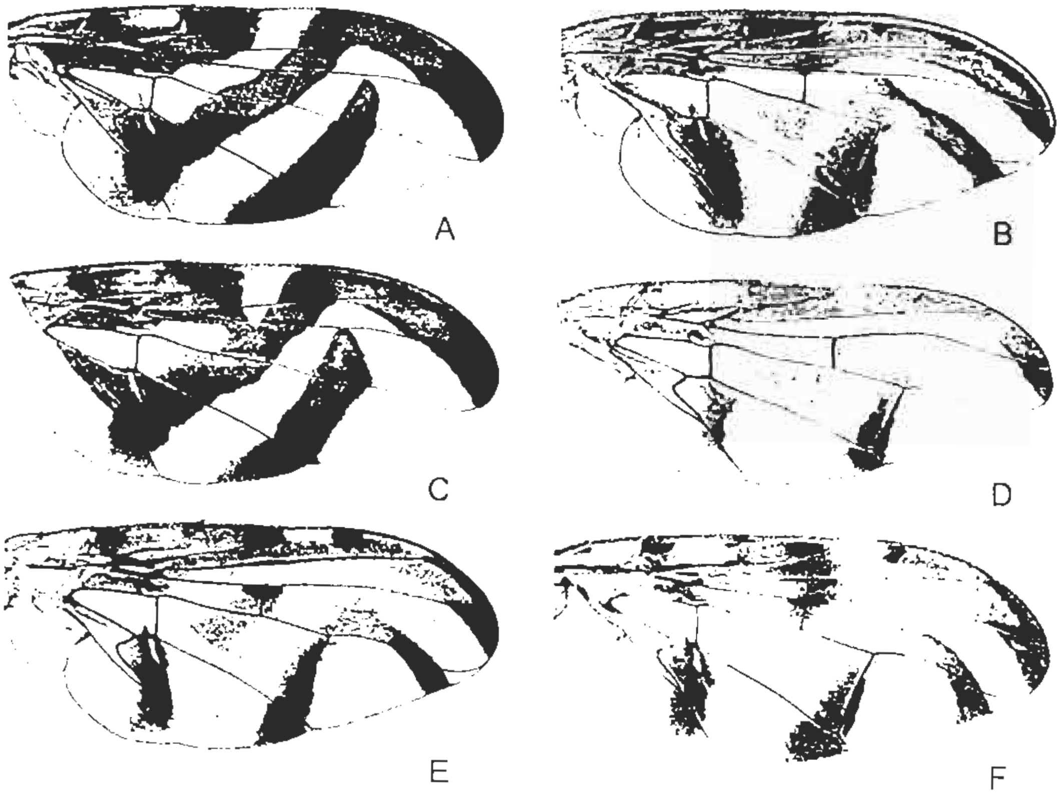


Fig. 6. Wings. A, *A. antilliensis* (37 km N Cabo Rojo, Dominican Republic). B, *A. maculata* (Guana Island, British Virgin Islands). C, *A. murrayi* (holotype). D, *A. pallens* (Pharr, Texas, USA). E, *A. stonei* (Nassau, Bahamas). F, *A. stonei* (Santo Domingo, Dominican Republic).

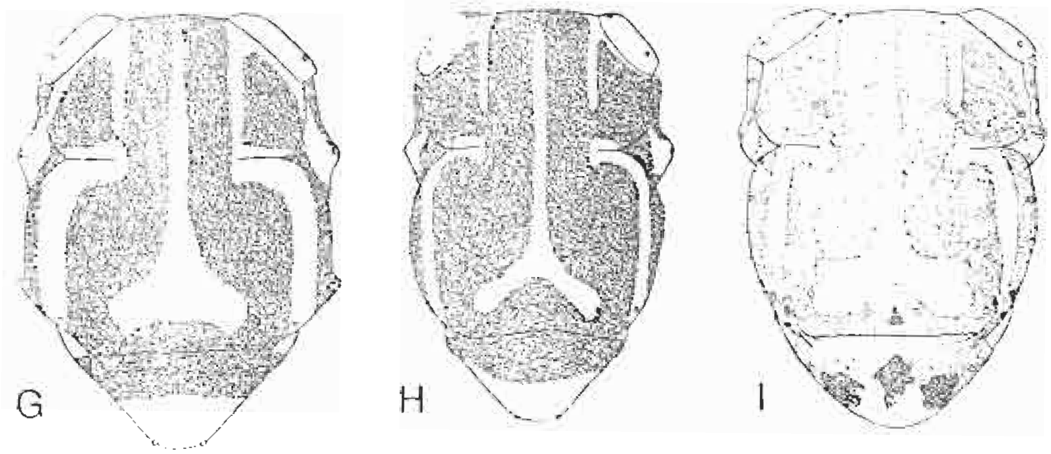


Fig. 7. Mesonotum, dorsal view (setae not shown). A, *A. antilliensis* (Puerta de Tierra, Puerto Rico). B, *A. aquila* (Las Pailas, Costa Rica). C, *A. avispa* (20 km S Upala, Costa Rica). D, *A. bicolor* (Harlingen, Texas). E, *A. castanea* (Bella Vista, Argentina). F, *A. dactiformis* (São Paulo, Brazil). G, *A. katiyari* (Pugamora, Venezuela). H, *A. macrura* (Bahia, Brazil). I, *A. maculata* (Great Camanoe I., British Virgin Islands). Abbreviations: d = dorsocentral stripe; l = lateral presutural stripe; m = medial stripe; s = sublateral stripe.

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A MOLECULAR PHYLOGENY OF THE *DROSOPHILA WILLISTONI* GROUP: CONFLICTS BETWEEN SPECIES CONCEPTS?

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Abstract.—The six sibling species of the Neotropical *Drosophila willistoni* group have a long history in studies of evolutionary biology, yet to date only one molecular study, which used allozymes, has been published on the phylogeny of the group. Here we present a phylogeny of the siblings based on the sequences of two nuclear genes, *period* (*per*) and *Alcohol dehydrogenase* (*Adh*), as well as the mitochondrial gene Cytochrome oxidase I (COI). Taken individually, only *per* has a strong phylogenetic signal supporting a well-resolved phylogeny of the group, and this phylogeny is different from that obtained using allozymes. The COI dataset by itself produces trees that disagree with *per*, and neither that data nor the *Adh* data have a strong phylogenetic signal, as indicated by low bootstrap values for all analyses. Combining the *Adh* and COI datasets results in the same tree as *per* alone. Combining all three genes results in the same topology, which is strongly supported. Two problematic taxa, *D. pavlovskiana* and a "Carmody strain," which were identified as potentially separate species based on reproductive isolation, clearly cluster in the phylogenetic analyses within *D. paulistorum* and *D. equinoxialis*, respectively. Thus, there appears to be a conflict between the biological species concept and the phylogenetic species concept.

Key words.—*Adh*, COI, *Drosophila willistoni*, *period*, phylogenetics, species concepts.

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The *Drosophila willistoni* group has been extensively studied since the 1940s. Research on the group has contributed significantly to evolutionary theory. Studying the chromosomes of *D. willistoni* led Dobzhansky and coworkers to propose hypotheses on why there is more variation in central than in marginal populations (e.g., Dobzhansky 1950; da Cunha et al. 1959). The group was also one of the first studied for allozymes (e.g., Ayala et al. 1970, 1974a). Ehrman (1961, 1965) has examined asymmetrical reproductive isolation in one species of the group, *D. paulistorum*, such that it is now a classical example of reproductive character displacement. More recently it has been discovered that the *D. melanogaster P* element was probably transferred horizontally from *D. willistoni* (Daniels et al. 1990; Clark et al. 1994; Powell and Gleason 1996).

The group comprises 25 Neotropical species of the subgenus *Sophophora* (Throckmorton 1975). Within the group, the six *willistoni* sibling species include *D. willistoni*, *D. equinoxialis*, *D. tropicalis*, *D. insularis*, *D. pavlovskiana*, and *D. paulistorum*. These species are morphologically indistinguishable, yet they exhibit varying degrees of premating isolation and fail to cross-hybridize (reviewed in Ehrman and Powell 1982). This group also exhibits great variability in geographical ranges including both widespread species and narrowly distributed, insular and mainland endemics. In addition to the species designations, subspecies have been described for *D. tropicalis*, *D. equinoxialis*, and *D. willistoni*. *Drosophila paulistorum* is composed of six semispecies as defined by ability to produce fertile hybrids. There is also an anomalous category termed the "Carmody strains" (Carmody 1965). These strains originated from two localities, Girardot, Colombia, and Belem, Brazil; the latter is included in this study. These two strains are completely interfertile with one another and do not display any premating isolation. The Belem strain was interfertile with six strains of *D. equinoxialis* (of 16 tested) and one semispecies (of six) of *D. paulistorum*. Both Carmody strains display high premating isolation with both *D. paulistorum* and *D. equinoxialis*. Thus the *willistoni* group is a complex of various taxonomic levels.

To date, only two studies have been published on the phylogenetic relationships of the *willistoni* siblings. Spassky et al. (1971) developed a schematic diagram of the evolutionary relationships based on available biogeographical, genetic, cytological, and biochemical evidence (Fig. 1a). In the second study, Ayala et al. (1974a) based a phylogeny on the genetic differentiation of the species at 36 allozyme loci. Nei's *D* (Nei 1972) and Wagner's distance method (Farris 1972) were used to construct a dendrogram of the relationships (Fig. 1b).

There are several reasons why knowledge of the evolutionary relationships of the *D. willistoni* group is important. A phylogeny provides opportunities to better understand the processes of speciation in the group, for example, it will allow more detailed examination of the evolution of premating and postmating isolation of the species. Courtship song differences have recently been investigated and have been found to be widely divergent (Ritchie and Gleason 1995), but the patterns of evolution of song cannot be assessed without a phylogeny.

In addition, a phylogeny of the group provides an opportunity to compare and contrast two species concepts. All of the species of the *D. willistoni* group were originally defined by the biological species concept; that is, species are groups of reproductively compatible populations that are reproductively incompatible with other species (Dobzhansky 1937; Mayr 1963). In contrast, a phylogenetic species is a diagnosably distinct cluster with a common ancestry and descent (Cracraft 1989). By definition, a phylogenetic species is monophyletic. The biological species concept does not imply

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TABLE 1. Species and strains with GenBank accession numbers for sequences.

Species/strain	Abbreviation[a]	Location	Source	*per*[b]	*Adh*	COI
D. willistoni						
0.811.0	wil0	Santa Maria, Nicaragua	Bowling Green[c]	U51056	U95251	
0811.4	wil4	Cuernavaca, Mexico	Bowling Green	U51057	U95252	U51589
Atlixco	wilA	Atlixco, Mexico	F. Ayala	U51055	U95255	
A57	wilA5	Aguas do los Rios, Brazil	J. Powell		U95254	
W3L	wil3L	Aguas do los Rios, Brazil	J. Powell		U95253	
W4L	wil4L	Aguas do los Rios, Brazil	J. Powell		L08648	
Belize II	wilB2	Belize	F. Ayala	U51058	U95256	
Belize VI	wilB6	Belize	F. Ayala	U51059	U95257	
Caño Mora	wilC	Costa Rica	F. Ayala	U51060	U95258	
Guadeloupe	wilG1	Guadeloupe	P. Chabora	U51061		
Guana	wilG2	Guana Island	P. Chabora	U51062	U95259	
L'Habitatué	wilH	L'Habitatué	P. Chabora	U51063		
Lima B	wilL	Lima, Peru	F. Ayala	U51064	U95260	U51590
M1	wilM1	Manaus, Brazil	V. Valente	U51065	U95261	
M2	wilM2	Manaus, Brazil	V. Valente	U51066	U95262	
M3	wilM3	Manaus, Brazil	V. Valente	U51067	U95263	
M4	wilM4	Manaus, Brazil	V. Valente	U51068	U95264	
PA1	wilPA1	Pôrto Alegre, Brazil	V. Valente	U51069		
PA2	wilPA2	Pôrto Alegre, Brazil	V. Valente	U51070	U95265	
PA3	wilPA3	Pôrto Alegre, Brazil	V. Valente	U51071	U95266	
PA4	wilPA4	Pôrto Alegre, Brazil	V. Valente	U51072	U95267	
D. equinoxialis						
0741.0	equ0	La Hina, Honduras	Bowling Green	U51073	U95268	U51591
0741.1	equ1	Tefe, Brazil	Bowling Green	U51074		
B33	equB	Brazil	V. Valente	U51075		
La Maya	equC	La Maya, Cuba	P. Chabora	U51076		U51592
Lee's A	equL	Aguas de los Rios, Brazil	L. Ehrman	U51077		
Puerto Rico	equP	Puerto Rico	P. Chabora	U51078	U95269	
Carmody[d]						
K2	Car	Brazil	L. Ehrman	U51079		U51593
D. paulistorum[e]						
Amazonian, A28	pauA	Belem, Brazil	L. Ehrman	U51080		U51594
Andean-Brazilian, ABM	pauAB	Mesitas, Colombia	L. Ehrman	U51081	U95271	U51595
Centroamerican, C2	pauC	Lancetilla, Honduras	L. Ehrman	U51082		U51596
Interior, I1	pauI	Llanos, Colombia	L. Ehrman	U51083		U51597
Orinocan, O11	pauO	Georgetown, Guyana	L. Ehrman	U51084		U51598
Transitional, T1	pauT	Santa Marta, Colombia	L. Ehrman	U51085		U51599
Tame	pauTM	Tame, Colombia	F. Ayala		U95272	
0771.4	pau4	Llanos, Colombia	Bowling Green		U95270	
D. pavlovskiana						
P1	pav	Georgetown, Guyana	L. Ehrman	U51086		U51600
D. tropicalis						
0801.0	tro	San Salvador, El Salvador	Bowling Green	U51087	U95274	U51601
D. insularis						
FA	insF	Lesser Antilles	L. Strausbaugh	U51088	U95273	U51602
WE2	insW	Lesser Antilles	L. Strausbaugh	U51089		
D. nebulosa						
0761.0	neb	Palmira, Colombia	Bowling Green	U51090	U95275	
0761.1	neb	San Jose, Costa Rica	Bowling Green			U51603
D. sucinea						
0791.3	suc	Tezintlan, Mexico	Bowling Green	U51091		
D. capricorni						
0721.0	cap	Palmira, Colombia	Bowling Green	U51092		

[a] Abbreviations as used in the text.

[b] Accession numbers for GenBank.

[c] National *Drosophila* Species Resource Center, Bowling Green State University, Bowling Green, Ohio.

[d] The Carmody strain is a strain of unknown taxonomic status. See text for details.

[e] *D. paulistorum* is a cluster of six semispecies. Semispecies designations are given when known.

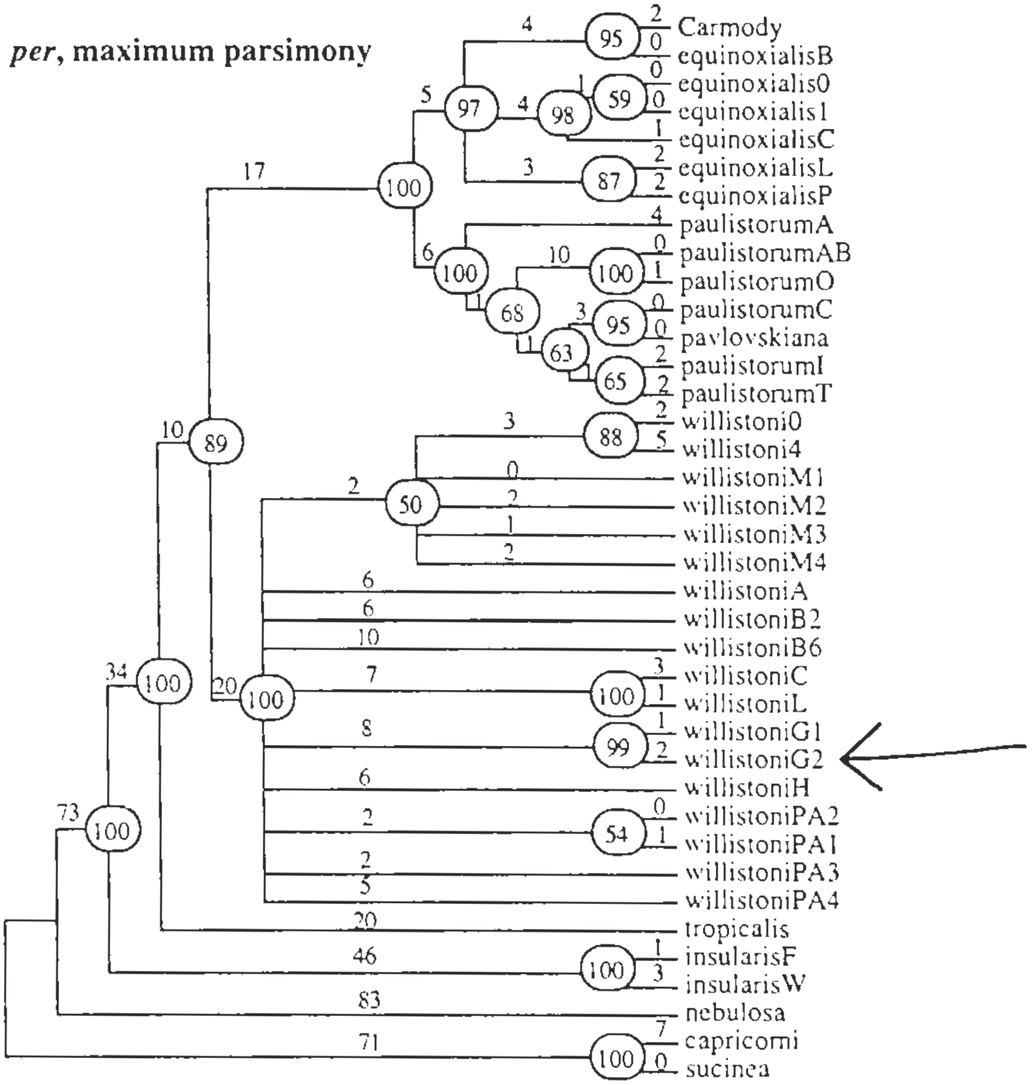


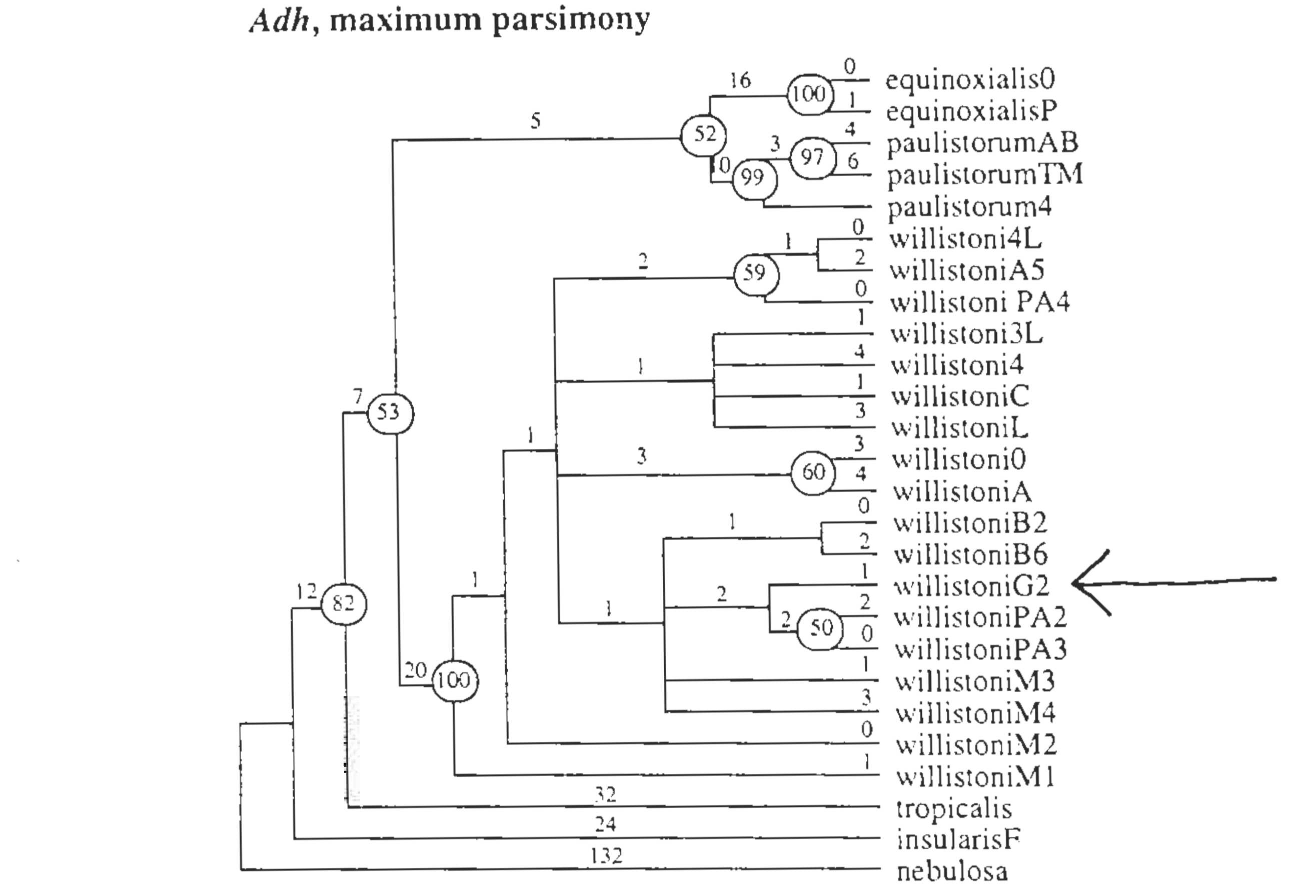
FIG. 2. Bootstrap 50%-majority-rule consensus tree (maximum parsimony) based on the entire *period* nucleotide dataset. Bootstrap values for each node are shown in ellipses. The number of nucleotide changes along each branch are shown above the branches.

Adh Dataset

Because over the entire *Adh* sequence transitions and transversion are approximately equal (Gleason 1996), they were not weighted differently in maximum-parsimony analysis. There were 1285 characters in this dataset, of which 85 were informative in a parsimony analysis. A heuristic maximum parsimony search produced 26 trees of length 322. The only differences among the trees lie in the arrangement of the *D. willistoni* strains. A 50%-majority-rule consensus tree shows the same topology for the species (Fig. 3), as the results of analysis of *per*. However, bootstrap values for this tree are mixed. Nodes joining all members of a single species are 99% or 100%. As with the *per* phylogenies, the node with the lowest support (53%) is the one joining the *D. paulistorum/D. equinoxialis* clade to *D. willistoni*. Similarly, the bootstrap value for the node joining *D. tropicalis* to the others is only 82%, as compared to 100% in the *per* tree. In addition, the node joining *D. equinoxialis* to *D. paulistorum* is only 52%, much lower than the 100% found for this node in the *per* maximum-parsimony tree. A different species topology was obtained using neighbor-joining (see below). In this case, *D. tropicalis* is the sister taxon to *D. equinoxialis*.

COI Dataset

An unweighted maximum parsimony search was initially done using the branch-and-bound option for the COI dataset, which includes a total of 495 bases. Six trees were found with length of 74. A 50%-majority-rule consensus tree (results not shown) indicates that there are several sources of ambiguity. In all trees, the *D. willistoni* strains are united, *D. tropicalis* and *D. insularis* are sister taxa, the Carmody strain is joined to the *D. equinoxialis* strains, and all of the *D. paulistorum* semispecies and *D. pavlovskiana* group together with the exception of the Amazonian semispecies (paulistorumA), which does not cluster with the other *D. paulistorum* semispecies. Branch-and-bound bootstrap analysis of this dataset indicates that the phylogeny is not well resolved (Fig. 4). The major contributing source of the low

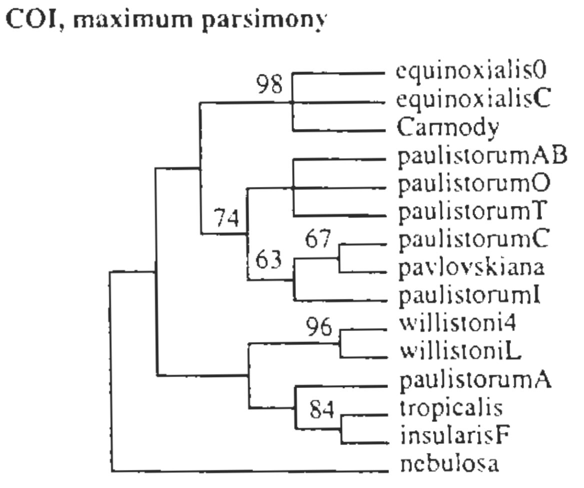


Adh, maximum parsimony

FIG. 3. 50%-majority-rule consensus tree of 26 minimal trees of length 322 using *Alcohol dehydrogenase* nucleotide sequences. Bootstrap values are shown for nodes represented in over 50% of bootstrap trees. Branch lengths (number of steps) are shown above the branches.

bootstrap values is probably the low number of informative sites ($n = 28$).

A similar topology was obtained by the neighbor-joining method, although some of the relationships among the strains were different (results not shown). Again, the *D. insularis/ D. tropicalis* clade is joined to *D. willistoni*, although the bootstrap value for this node (65%) is not very high. Carmody again clusters with *D. equinoxialis* and as before, the Amazonian semispecies does not cluster with the other *D. paulistorum* strains.



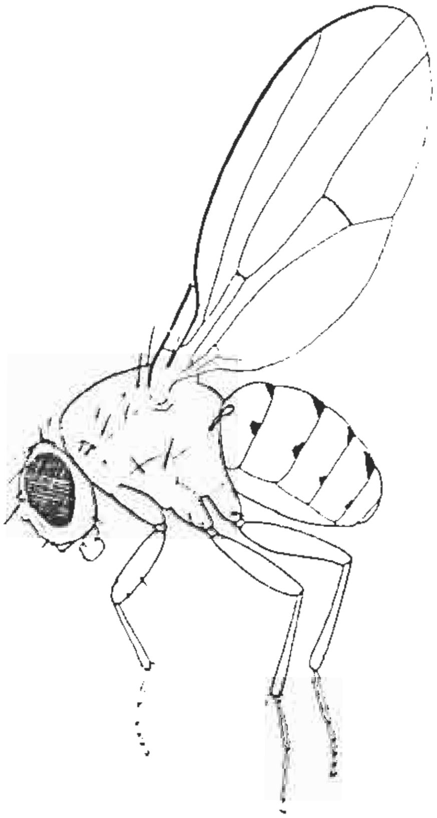
COI, maximum parsimony

FIG. 4. One of the six most-parsimonious trees derived from the branch-and-bound analysis with unweighted characters for the COI dataset. Bootstrap percentages greater than 50% of 100 replicates are shown at nodes.

Phylogenetic Analyses of Separate Datasets: Overlapping Strains

per Dataset

Six strains were sequenced for all three genes; these six were used in all subsequent analyses. A different *D. nebulosa* strain was used in the COI dataset as compared to the *per* and *Adh* datasets but this difference has been ignored. For *per*, the resulting dataset has 1216 characters, of which 79 are informative in a parsimony analysis. An exhaustive search produced one most-parsimonious tree of length 336; the next shortest tree is 339 steps. The topology of this tree was the same as that obtained for both the neighbor-joining and maximum-likelihood methods (Fig. 5a). For the maximum-likelihood tree, all branches are significant at the $P < 0.01$ level and the log-likelihood value is -3351.1. Bootstrap analysis using all three methods resulted in values equal to or greater than 79% for all nodes (Table 2).



A pomace fly, *Drosóphila* sp., 20 ×

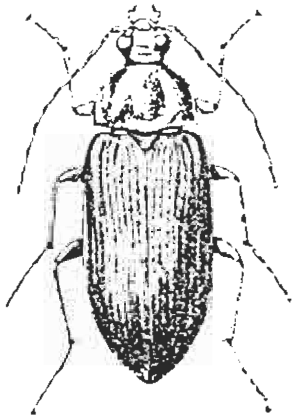
Family **Drosophilidae** – Pomace Flies or Small Fruit Flies: These flies are 3–4 mm in length and usually yellowish in color (Figure 513), and are generally found around decaying vegetation and fruit. This group is a large one (181 North American species), and many species are very common. The pomace flies are often pests in the household when fruit is present. The larvae of most species occur in decaying fruit and fungi. In the case of the larvae living in fruit, it has been shown that the larvae actually feed on the yeasts growing in the fruit. A few species are ectoparasitic (on caterpillars) or predaceous (on mealybugs and other small Homoptera) in the larval stage. Several species in this group, because of their short life span, giant salivary gland chromosomes, and ease of culturing, have been used extensively in studies of heredity.

Guana Island Coleoptera collected Oct. 1999
by Barry and Buena Valentine and Wenhua Lu

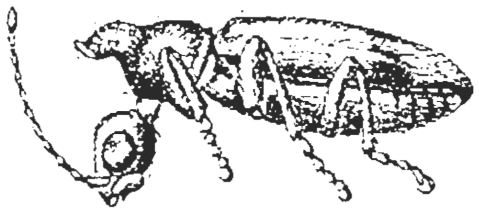
genera:species

- 3 : 3 Aderidae
  - Aderus?
  - Ganascus?
  - Gymnoganascus n. sp.
- 3 : 4 Alleculidae
  - Hymenorus wolcotti Campbell
  - Hymenorus n. sp.
  - Lobopoda (L.) thomasensis Campbell
  - Pachyhymenorus n. sp.
- 5 : 11 Anobiidae
  - Caenocara sp.
  - Cryptorama carinatum White
  - Cryptorama impunctatum White
  - Cryptorama megalops White
  - Cryptorama sp.
  - Petalium puertoricense Fisher
  - Petalium sp.
  - Protheca sp.
  - Protheca sp.
  - Tricorynus insulicola (Fisher)
  - Tricorynus pierrei (Lepesme) [probably]
- 1 : 1 Anthicidae
  - Anthicus sp.
- 4 : 4 Anthribidae
  - Acaromimus n. sp.
  - Ormiscus n. sp.
  - Toxonotus n. sp.
  - New genus, n. sp.
- 1 : 1 Apionidae
  - Apion metum Kissinger
- 3 : 3 Bostrichidae
  - Amphicerus cornutus (Pallas)
  - Melalgus femoralis (Fabricius)
  - Xylomeira tridens (Fabricius)
- 1 : 1 Brentidae
  - Exopleura monilis (Fabricius)
- 2 : 2 Bruchidae
  - ?
  - ?
- 1 : 1 Buprestidae
  - Micrasta ?ornata Fisher

See Next Page



Family **Allecúlidae**—Comb-Clawed Beetles: The members of this family are small beetles, 4–12 mm in length, elongate-oval, and usually brownish or black with a somewhat glossy or shiny appearance due to the pubescence on the body (Figure 306 B). They can be distinguished from related groups by the pectinate tarsal claws (Figure 247 B). The adults are found on flowers and foliage, fungi, and under dead bark; the larvae resemble wireworms and live in rotting wood, plant debris, or fungi.



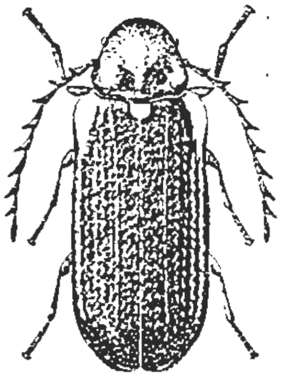
Family **Anthícidae**—Antlike Flower Beetles: These beetles are 2–6 mm in length and somewhat antlike in appearance, with the head deflexed and strongly constricted behind the eyes, and with the pronotum oval. The pronotum in many species (*Notóxus*, Figure 313 A, and *Mecinotársus*) has an anterior hornlike process extending forward over the head. Anthicids generally occur on flowers and foliage, some occur under stones and logs and in debris, and a few occur on sand dunes.

See Next Page

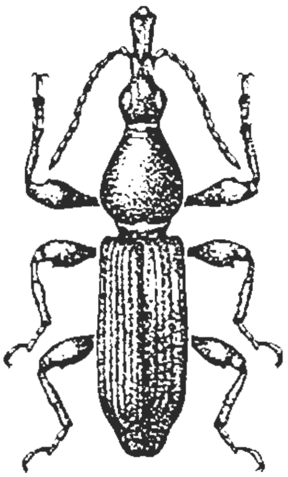
Family **Anobiidae:** The anobiids are cylindrical to oval, pubescent beetles, 1.0–9.0 mm in length; the head is deflexed and is usually concealed from above by the hoodlike pronotum. Most of them have the last three antennal segments enlarged and lengthened (Figures 249 C, and 294 B, D–F); a few have these segments lengthened but not enlarged, and a few have the antennae serrate or pectinate. About 260 species occur in North America.

Most anobiids live in dry vegetable materials such as logs and twigs or under the bark of dead trees; others pass the larval stage in fungi or in the seeds and stems of various plants. Some species, such as *Xestòbium rufovillòsum* (De Geer) (Figure 294 F), are called death-watch beetles because they make a ticking sound as they bore through wood.

Some of the anobiids are common and destructive pests. The drugstore beetle, *Stegòbium paniceum* (L.) (Figure 294 E), infests various drugs and cereals; the cigarette beetle, *Lasiodérma serricórne* (Fabricius) (Figure 294 C), is common in dried tobacco, museum specimens, and insect collections. Some wood-boring species, such as the furniture beetle, *Anòbium punctàtum* (De Geer) (Figure 294 B), bore in timbers, woodwork, and furniture.

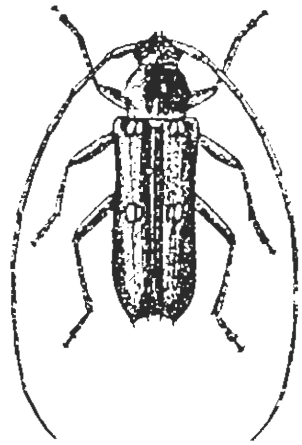


Family **Bréntidae** – Straight-Snouted Weevils: The brentids are narrow, elongate, cylindrical beetles, 10–30 mm in length, usually reddish or brownish and shining, with the snout projecting straight forward (Figure 328 A). The snout is generally longer and more slender in the female than in the male (Figure 329 G, H). This group is principally tropical, and only six species occur in North America. The only common eastern species is *Arrhenòdes minùtus* (Drury), which usually occurs under the loose bark of dead oak, poplar, and beech trees; the larvae are wood-boring, and sometimes attack living trees.



2 : 3 Cantharidae
Caccodes sp.
Caccodes sp.
Tytthonyx discolor Leng & Mutchler
1 : 1 Carabidae
?
14 : 16
Cerambycidae
Anelaphus nanus (Fabricius)
Ataxia alboscutellata Fisher
Curtomerus flavus (Fabricius)
Eburia quadrimaculata (Linnaeus)
Ecyrus hirtipes Gahan
Elaphidion irroratum (Linnaeus)
Elaphidion pseudonomon Ivie
Lagocheirus araneiformis (Linnaeus)
Leptostyloides similis (Gahan)
Merostenus attenuatus Chevrolat
Methia necydalia (Fabricius)
Neocompsa cylindricollis (Fabricius)
Neostizocera vanzwalenburgi Fisher
Styloleptus sp.
Urgleptes sp.
Urgleptes sp.
1 : 1 Ceratocanthidae
Ceratocanthus sp.
1 : 1 Chelonariidae
Chelonarium sp.
6 : 8 Chrysomelidae
Chalcosicya crotonis (Fabricius)
Cryptocephalus krugi Weise
Cryptocephalus solidus Weise
Homoschema nigriventre Blake
Homoschema obesum Blake
Longitarsis clanidotus Blake
Pachybrachys n. sp.
Syphrea sanctaecrucis (Fabricius)
1 : 2 Cicindellidae
Cicindella suturalis Fabricius
Cicindella trifasciata Fabricius
1 : 1 Ciidae
?
1 : 1 Cleridae
Neorthopleura murina (Klug)

Family **Cerambycidae** – Long-Horned Beetles: This family is a large one, with over 1200 species occurring in this country, and its members are all phytophagous. Most of the long-horns are elongate and cylindrical with long antennae, and many are brightly colored.



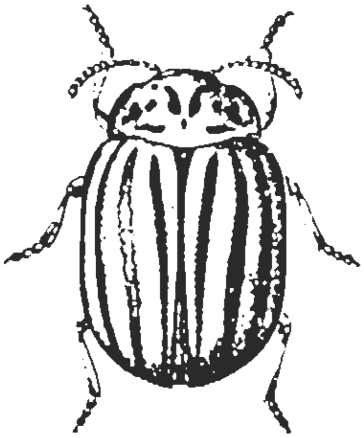
Most adult cerambycids, particularly the brightly colored ones, feed on flowers. Many, usually not brightly colored, are nocturnal in habit and during the day may be found under bark or resting on trees or logs; some of these make a squeaking sound when picked up.

Most of the Cerambycidae are wood-boring in the larval stage, and many species are very destructive to shade, forest, and fruit trees, and to freshly cut logs. The adults lay their eggs in crevices in the bark, and the larvae bore into the wood. The larval tunnels in the wood (Figure 314) are circular in cross section (thereby differing from most buprestid tunnels, which are oval in cross section) and usually go straight in a short distance before turning. Different species attack different types of trees and shrubs. A few will attack living trees, but most species appear to prefer freshly cut logs, or weakened and dying trees or branches. A few girdle twigs and lay their eggs just above the girdled band. Some bore into the stems of herbaceous plants.

See Next Page

Family **Chrysomélidae**—Leaf Beetles: The leaf beetles are closely related to the Cerambýcidae; both groups have a similar tarsal structure (Figure 251 A), and both are phytophagous. The leaf beetles usually have much shorter antennae and are smaller and more oval in shape than the cerambycids. The chrysomelids in the United States are all less than 13 mm in length; most of the cerambycids are larger. Many are brightly colored.

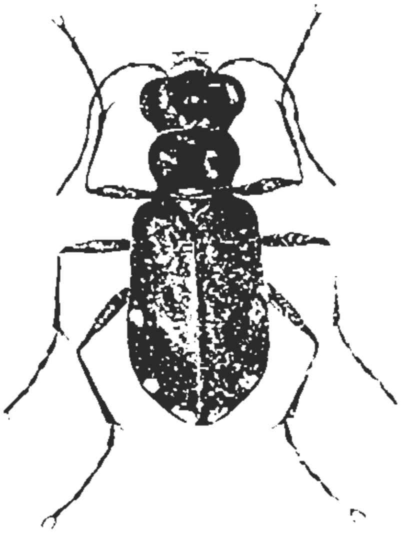
Adult leaf beetles feed principally on flowers and foliage. The larvae are phytophagous, but vary quite a bit in appearance and habits; some larvae are free feeders on foliage, some are leaf miners, some feed on roots, and some bore in stems. Many members of this family are serious pests of cultivated plants. Most species overwinter as adults.



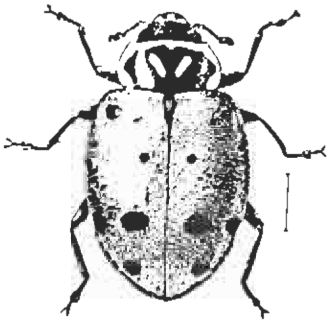
Family **Cicindèlidae**—Tiger Beetles: The tiger beetles are active, usually brightly colored insects found in open sunny situations; they are often common on sandy beaches. They can run or fly rapidly and are very wary and difficult to approach. When approached, they take flight quickly, sometimes after running a few feet, and usually alight some distance away facing the pursuer. They are predaceous and feed on a variety of small insects, which they capture with their long sicklelike mandibles; when handled, they can sometimes administer a painful bite.

The larvae are predaceous and live in vertical burrows in the soil in dry paths or fields or in sandy beaches. They prop themselves at the entrance of their burrow, with the traplike jaws wide apart, waiting to capture some passing insect. The larva has a hooklike spine on the fifth abdominal tergum with which it can anchor itself in its burrow and thus avoid being pulled out when it captures a large prey. After the prey is subdued, it is dragged to the bottom of the burrow, often a foot (0.3 m) underground, and eaten.

Adult tiger beetles are usually metallic or iridescent in color and often have a definite color pattern. They can usually be recognized by their characteristic shape (Figure 257), and most of them are 10–20 mm in length. Most of our tiger beetles belong to the genus *Cicindèla*.



4 : 7 Coccinellidae
- Cycloneda sp.
- Scymnus sp.
- Scymnus sp.
- Scymnus sp.
- Scymnus sp.
- ?
- ?



1 : 1 Corylophidae
- ?

±16:22 Curculionidae

See Next Page

- ?Acalles sp.
- ?Acalles sp.
- ?Acalles sp.
- Anthonomus sp.
- Anthonomus sp.
- Anthonomus sp.
- Anthonomus sp.
- Anthonomus sp.
- Decuanellus sp.
- Diaprepes abbreviatus (Linneaus)
- ?Euscepes sp.
- ?Euscepes sp.
- Huaca ayacho Clark
- Lembodes sp.
- Menoetius curvipes (Fabricius)
- Menoetius sp.
- Pseudomopsis cucubano Wolcott
- Sitophilus linearis (Herbst)
- Sternechus sp.
- Tyloderma sp.
- unknown tychiine
- ?

1 : 1 Dermestidae
- ?

3 : 8 Elateridae
- Ischiodontus sp.
- Conoderus rufidens (Fabricius)
- Conoderus bifoveatus (Palisot)
- Conoderus sp.
- Conoderus sp.
- Conoderus sp.
- ?Conoderus sp.
- ?

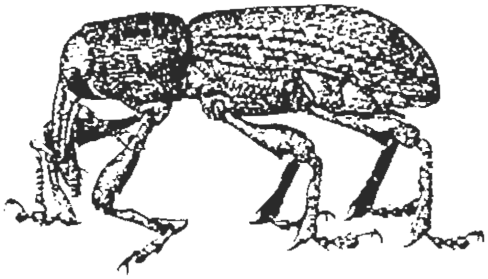
1 : 1 Endomychidae
- Eidoreus sp.

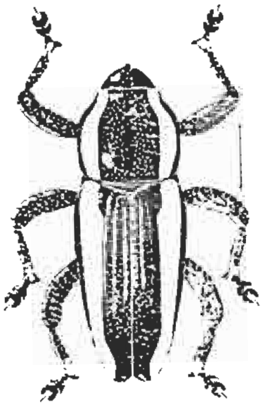
Family **Coccinéllidae**—Ladybird Beetles: The ladybird beetles are a well-known group of small, oval, convex, and often brightly colored insects. They may be distinguished from the chrysomelids, many of which have a similar shape, by the three distinct tarsal segments (chrysomelids appear to have four tarsal segments). Most of the ladybird beetles are predaceous, both as larvae and adults, and feed chiefly on aphids; they are frequently quite common, particularly on vegetation where aphids are numerous. Ladybirds hibernate as adults, frequently in large aggregations, under leaves or in debris.

The larvae of ladybird beetles (Figure 304 C) are elongate, somewhat flattened, and covered with minute tubercles or spines. They are usually spotted or banded with bright colors. These larvae are usually found in aphid colonies.

Two fairly common phytophagous species in this group are serious garden pests, the Mexican bean beetle, *Epilàchna varivéstis* Mulsant, and the squash beetle *E. boreàlis* (Fabricius). The Mexican bean beetle is yellowish, with eight spots on each elytron; the squash beetle is pale orange-yellow, with three spots on the pronotum and a dozen or so large spots arranged in two rows on the elytra, plus a large black dot near the tip of the elytra. These two species are the only large ladybird beetles in this country that are pubescent. The larvae of these species are yellow, oval in shape, with forked spines on the body. Both larvae and adults are phytophagous, and they are often very destructive.

Except for the two species of *Epilàchna*, the ladybird beetles are a very beneficial group of insects. They feed on aphids, scale insects, and other injurious insects. During serious outbreaks of aphids or scale insects, large numbers of ladybird beetles are sometimes imported into the infested areas to serve as a means of control: the cottony cushion scale, *Icérya púrchasi* Maskell, a pest of citrus in California, has been kept under control for a number of years by means of a ladybird beetle, *Rodòlia cardinàlis* (Mulsant), imported from Australia.

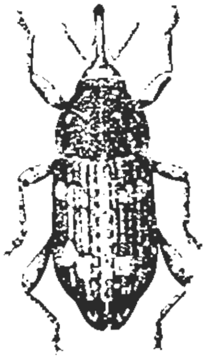




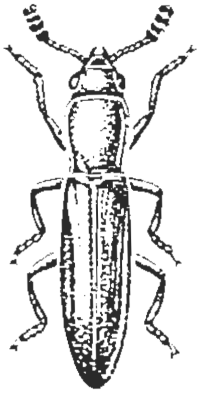
Family **Curculiònidae**—Snout Beetles: The members of this family are by far the most commonly encountered Curculionoidea, and are to be found almost everywhere; nearly 2500 species occur in North America. They show considerable variation in size, shape, and the form of the snout. The snout is fairly well developed in most species, with the antennae arising about the midlength of the snout (Figure 244 B); in some of the nut weevils (Figure 331 C) the snout is long and slender, as long as the body or longer.

All snout beetles (except a few occurring in ant nests) are plant feeders, and many are serious pests. Almost every part of a plant may be attacked, from the roots upward; the larvae usually feed inside the tissues of the plant, and the adults drill holes in fruits, nuts, and other plant parts.

Most snout beetles, when disturbed, will draw in their legs and antennae, fall to the ground, and remain motionless. Many are colored like bits of bark or dirt, and when they remain motionless they are very difficult to see. Some snout beetles (for example, *Conotrachèlus*, subfamily Cryptorhynchinae) are able to stridulate by rubbing hardened tubercles on the dorsum of the abdomen against filelike ridges on the underside of the elytra; these sounds in *Conotrachèlus* are extremely weak, and usually can be heard only by holding the insect to one's ear.

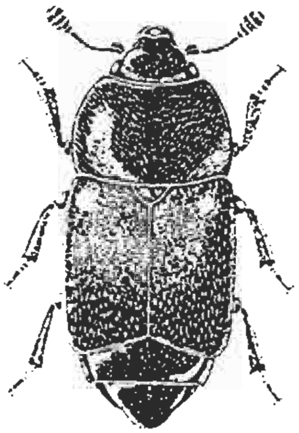


Family **Languriidae**—Lizard Beetles: The lizard beetles are narrow and elongate, 5–10 mm in length, and usually have the pronotum reddish and the elytra black (Figure 302 D). The adults feed on the leaves and pollen of many common plants, including goldenrod, ragweed, fleabane, and clover. The larvae are stem borers; the larvae of the clover stem borer (*Languria mozárdi* Latreille) attack clover and sometimes cause considerable damage.



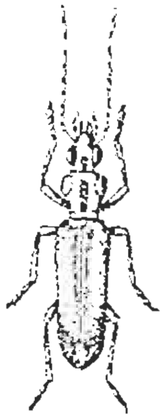
- 1 : 1 Histeridae
  - sp.
- 1 : 1 Hydrophilidae
  - Hydrophilus sp.
- 2 : 2 Languriidae → See Preceeding Page
  - Loberus testaceus Reitter
  - ?
- 1 : 1 Lathridiidae
  - Metophthalmus n. sp.
- 2 : 2 Monommidae
  - Aspathines aenea (Thomson)
  - Hyporrhagus marginatus (Fabricius)
- 5 : 7 Mordellidae → See Major Paper by Wenhua
  - Falsomordellistena danforthi (Ray)
  - Glipostenoda guana Lu & Ivie
  - Mordella atrata Melsheimer
  - Mordella summermanae Ray
  - Mordillistena lineata Ray
  - Tolidomordella basifulva (Quedenfeldt)
  - Tolidomordella leucocephala (Quedenfeldt)
- 1 : 1 Mycteridae
  - Physcius fasciatus Pic
- 1 : 1 Nitidulidae →
  - Stelidota sp.
- 4 : 5 Oedemeridae
  - Hyposclera sp.
  - Oxycopis desecheonis (Wolcott)
  - ?
  - – ?
  - ?
- 2 : 2 Phalacridae
  - Acylomus sp.
  - sp.
- 1 : 1 Ptinidae
  - Lachnoniptus lindae Philips
- 3 : 3 Scarabaeidae
  - Ligyrus cuniculus (Fabricius)
  - Phyllophaga sp.
  - Strategus talpa (Fabricius)
- 3 : 5 Scolytidae
  - ?
  - ?
  - ?
  - ?
  - ?
- 1 : 1 Silvanidae
  - Cathartus quadricollis (Guérin-Méneville)

→ See Next Page

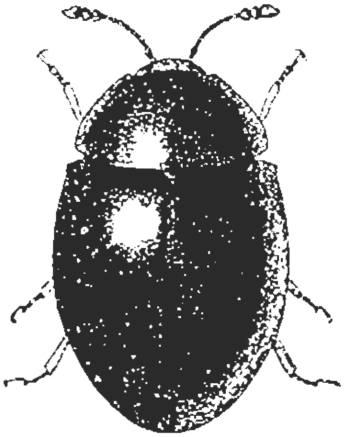


Family Nitidúlidae – Sap Beetles: The members of this family vary considerably in size, shape, and habits. Most of them are small, 12 mm in length or less, elongate or oval, and in a few the elytra are short and expose the terminal abdominal segments (Figure 301). Most nitidulids are found where plant fluids are fermenting or souring; for example, around decaying fruits or melons, flowing sap, and some types of fungi. A few occur on or near the dried carcasses of dead animals, and several occur in flowers. Others are very common beneath the loose bark of dead stumps and logs, especially if these are damp enough to be moldy.

Family **Oedemèridae** – False Blister Beetles: The oedemerids are slender, soft-bodied beetles, 5–20 mm in length (Figure 309 A). Many are black with an orange pronotum, while others are pale with blue, yellow, red, or orange markings; a common eastern oedemerid is yellowish brown with the tips of the elytra black. These beetles have a 5-5-4 tarsal formula, and the penultimate tarsal segment is dilated and densely hairy beneath (Figure 251 C). The pronotum is somewhat narrowed posteriorly and narrower than the base of the elytra, and the eyes are often emarginate. The adults are usually found on flowers or foliage, and are attracted to lights at night; the larvae live in moist decaying wood, especially driftwood.

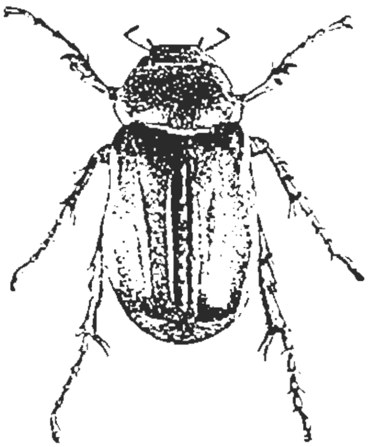


Family **Phalácridae** – Shining Flower Beetles: The phalacrids are oval, shining, cónvex beetles, 1–3 mm in length (Figure 303 A), and are usually brownish in color. They are sometimes quite common on the flowers of goldenrod and other composites; the larvae develop in the heads of these flowers.



Family **Scarabaèidae** – Scarab Beetles. This group contains about 1300 North American species, and its members vary greatly in size, color, and habits. The scarabs are heavy-bodied, oval or elongate, usually convex beetles, with the tarsi 5-segmented (rarely, the front tarsi are absent), and the antennae 8- to 11-segmented and lamellate.

The scarabs vary considerably in habits. Many are dung feeders, or feed on decomposing plant materials, carrion, and the like; some live in the nests or burrows of vertebrates, or in the nests of ants or termites; a few feed on fungi; many feed on plant materials such as grasses, foliage, fruits, and flowers, and some of these are serious pests of lawns, golf greens, or various agricultural crops.



4 : 4 Staphylinidae
?
?
?
?

4 : 4 Tenebrionidae
Diastolinus hummelincki Marcussi
Strongylium paddai Ivie & Triplehorn
Platydema micans Zimmerman
Nautes sp.

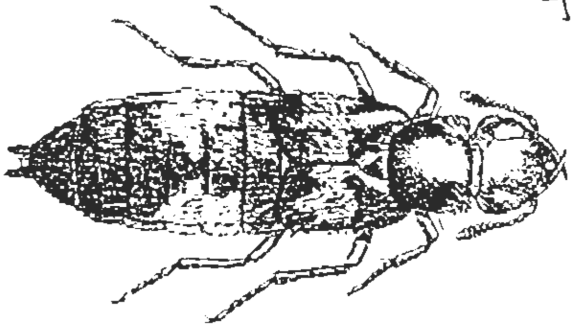
1 : 1 Throscidae
Aulonothroscus sp.

1 : 1 Trogidae
Omorgus suberosus (Fabricius)

1 : 1 Trogossitidae
Tenebroides sp.

1 : 1 Family unknown
?

45 familes
±120 genera
±148 species

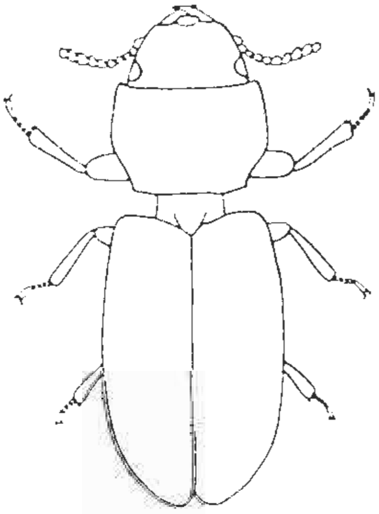


Family **Staphylinidae** – Rove Beetles: The rove beetles are slender and elongate, and can usually be recognized by the very short elytra; the elytra are usually not much longer than their combined width, and a considerable portion of the abdomen is exposed beyond their apices (Figure 266). The hind wings are well developed, and when at rest are folded under the short elytra. Rove beetles are active insects, and run or fly rapidly. When running, they frequently raise the tip of the abdomen, much as do scorpions. The mandibles are very long, slender, and sharp, and usually cross in front of the head; some of the larger rove beetles can inflict a painful bite when handled. Most of these beetles are black or brown in color; they vary considerably in size, but the largest are about 25 mm in length.

This is our largest family of beetles, with nearly 2900 North American species. These beetles occur in a variety of habitats, but are probably most often seen about decaying materials, particularly dung or carrion; they also occur under stones and other objects on the ground, along the shores of streams and the seashore, in fungi and leaf litter, and in the nests of birds, mammals, ants, and termites. Most species appear to be predaceous. The larvae usually occur in the same places and feed on the same things as the adults; a few are parasites of other insects.

Family **Trogositidae** – Bark-Gnawing Beetles: This group contains two subfamilies that differ rather markedly in shape: the Tenebroidinae are elongate, with the head about as wide as the pronotum, and with the pronotum rather widely separated from the base of the elytra (Figure 298); the Ostominae are oval or elliptical, with the head only about half as wide as the pronotum, and the pronotum is rather closely joined to the base of the elytra. The Ostominae are very similar to some nitidulids (for example, Figure 301 C), but may be separated by the characters given in the key (couplet 144); most Ostominae have long erect hairs on the elytra, while the similarly shaped nitidulids have the elytra bare or short-pubescent.

Trogositids are 2.6–22.0 mm in length, and most are blackish, bluish, or greenish; the majority are predaceous. The cadelle, *Tenebróides mauritánicus* (L.) (Figure 298), occurs commonly in granaries; it is believed to feed on both other insects in the grain and on the grain itself. *Temnochila viréscens* (Fabricius), a rather common and widely distributed species, is a bright blue-green beetle about 20 mm in length; it can administer a vicious bite with its powerful mandibles. Adults and larvae of trogositids are generally found under bark, in woody fungi, and in dry vegetable matter.



Barry D. Valentine
Columbus, Ohio
April, 2000

SYSTEMATICS

Tumbling Flower Beetles (Coleoptera: Mordellidae) of the Virgin Islands with Descriptions of New Species

WENHUA LU[1] AND MICHAEL A. IVIE[2]

Ann Entomol Soc Am 92(5): 656-701 (1999)

ABSTRACT Eight species of tumbling flower beetles in 4 genera (Coleoptera: Mordellidae) occur in the Virgin Islands: *Mordella atrata* Melsheimer, *M. summermanae* Ray, *Tolidomordella leucocephala* (Quedenfeldt) comb. nov., *T. basifulva* (Quedenfeldt) comb. nov., *Glipostenoda guana* sp. nov. (18° 29′ N, 64° 34′ W, Guana Island, British Virgin Islands), *Falsomordellistena danforthi* (Ray) comb. nov., *Mordellistena irfianorum* sp. nov. (18° 19′ N, 64° 43′ W, St. John, U.S. Virgin Islands), and *M. lineata* Ray. Males of *T. leucocephala* and females of *T. basifulva* are described for the first time, as are the male genitalia of *M. summermanae*, *T. leucocephala*, *T. basifulva*, *F. danforthi*, and *M. lineata*. Species of *Mordella*, *Tolidomordella*, and *Falsomordellistena* are new records from the Virgin Islands. Range extension of *M. summermanae* to Jamaica is reported. A key to the species is provided.

KEY WORDS Mordellidae, tumbling flower beetles, Virgin Islands, West Indies, genitalia

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MOST OF THE Virgin Islands, about a hundred isles, cays, and vegetated rocks, both British and American, lie on the Puerto Rico Bank and were united with Puerto Rico at glacial maxima (Lazell 1995). An American outlyer, St. Croix, with several small coastal cays, is on a separate bank and is often thought to be more closely allied biologically to the Lesser Antilles (Lazell 1972). We report known mordellid beetle faunas from the islands on both banks (Fig. 1).

In the West Indies (*sensu* Bond 1985, excluding continental shelf islands), *Glipa* and *Conalia* each had a species and *Mordella* had 7 in Blackwelder (1945). In his work on Puerto Rico, Ray (1937) listed 14 species of *Mordellistena*. Ray (1939) added another West Indian species to that genus. With an original description by Champion (1896), there was a total of 16 species of *Mordellistena* in Blackwelder (1945) from the West Indies. Maklin (1875, original description not read by authors) described *Mordellistena marginicollis* from Brazil, and Ray (1937) implied its presence in Puerto Rico by including it in his key (Wolcott 1950). Blackwelder (1945) did not list *M. marginicollis* from the West Indies and we have no evidence that it exists on the Puerto Rico Bank.

There has been no previous systematic work on tumbling flower beetles of the Virgin Islands. *Mordellistena ferruginea* (non-*Mordella ferruginea* F. 1775 or 1801) and *M. lineata* Ray were the only mordellids recorded nominally and anecdotally from the Virgin Islands (Miskimen and Bond 1970, Lazell 1995). Among the 7 *Mordella* species, *M. leucocephala* and *M. basifulva* were described by Quedenfeldt (1886). Since then, no one has applied these names to known populations (Wolcott 1950), not even in Ray's extensive work of 1939. However, Wolcott (1936) listed host plants for adults of both species and implied that specimens other than the types from Puerto Rico had been determined by E. A. Schwarz. We believe Quedenfeldt's description of *M. leucocephala* was based only on females and *M. basifulva* only on males. Here we describe the male of *M. leucocephala*. It is possible that the female of *M. basifulva* is represented by specimens from Puerto Rico. These species are placed in *Tolidomordella* in today's nomenclature (Ermisch 1949-1950, Jackman 1991).

Fabricius named 2 species "*Mordella ferruginea*." The 1st, *Mordella ferruginea* F. (1775) was moved to *Rhipiphorus* by Fabricius (1801). The 2nd, *Mordella ferruginea* F. (1801) is based on a type in Copenhagen labeled Essequibo, which is in Guyana, South America. The type specimen differs from the Puerto Rico Bank specimens in being larger, in having metallic reflection on the head, in having the antenna serrate, and in having a longer and narrower tibia with 4 transverse lateral ridges (examined by the junior author). Therefore, we believe *Mordella ferruginea* F. (1801) is not conspecific with the form from the Puerto Rico Bank. However, beginning with Quedenfeldt (1886), the name "*Mordella ferruginea*," transferred to *Mordellistena*, was used consistently by most authors for the Puerto Rico Bank species described herein.

The South American form named *Mordella ferruginea* by Fabricius (1801) is a primary junior homonym of *Mordella ferruginea* F. (1775). The situation is further complicated by the description of a European species, *Glipostenoda ferruginea* Horak (1995), which may be a congener. A solution to this problem is beyond the scope of this work.

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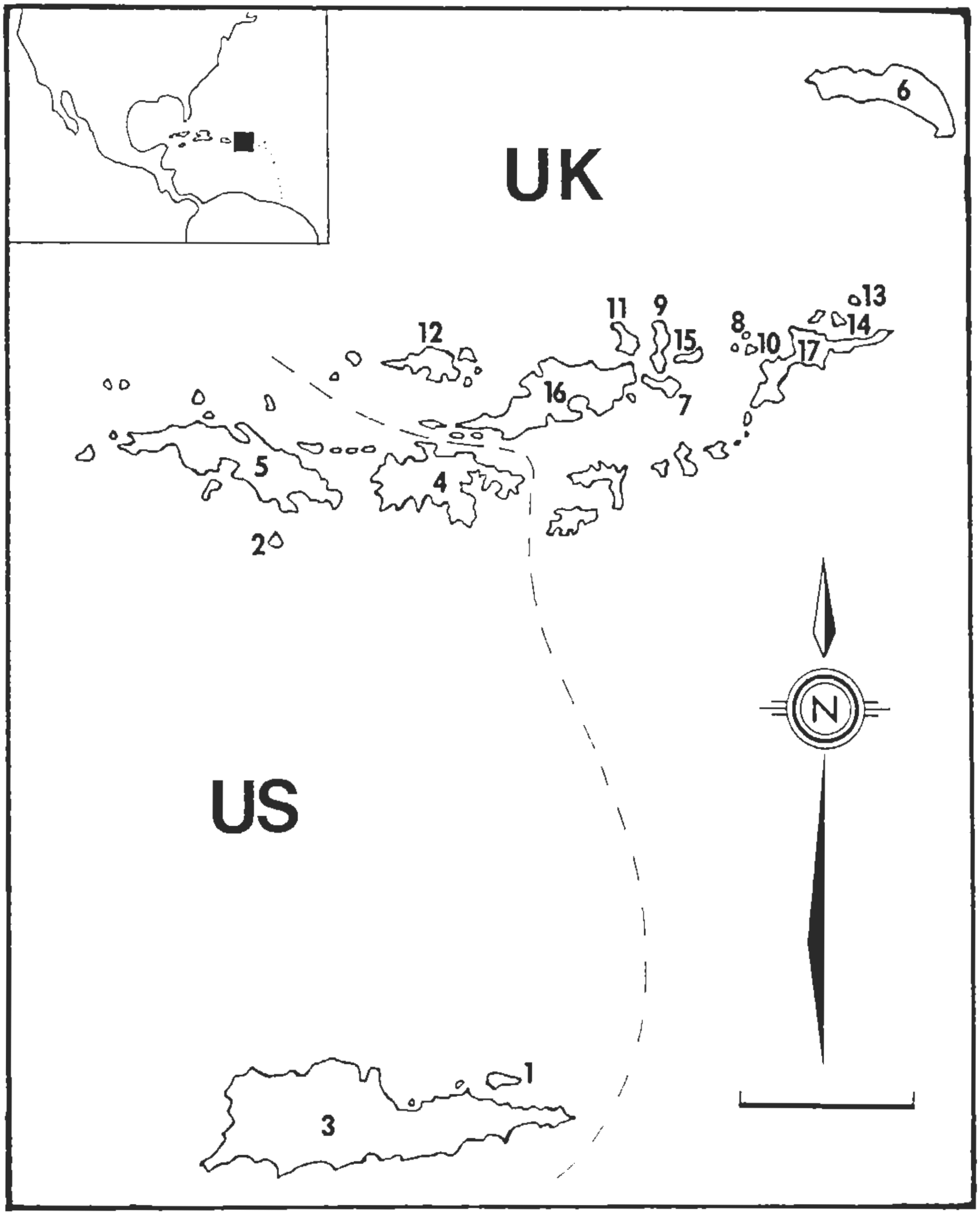

Fig. 1. The Virgin Islands. U.S. (American). 1. Buck. 2. Great St. James. 3. St. Croix. 4. St. John. 5. St. Thomas. UK (British). 6. Anegada. 7. Beef. 8. George Dog. 9. Great Camanoe. 10. Great Dog. 11. Guana. 12. Jost Van Dyke. 13. Necker. 14. Prickly Pear. 15. Scrub. 16. Tortola. 17. Virgin Gorda. Inset shows position, east of Puerto Rico and west of the Leeward Islands. Scale bar = 20 km.

There are some Fabrician names that might originate from the Virgin Islands but are not included above: *Mordella vittata* F. (1801) was not listed in Blackwelder (1945) under Mordellidae. *Mordella bifasciata* F. (1801), *M. hemorrhoidalis* F. (1801), *M. hamata* F. (1801), and *M. marmorata* F. (1801) were retained in this genus by Blackwelder (1945).

Because some descriptions are simplistic, contain errors, or provide no genitalic information, we redescribe most species or add to existing descriptions, following the guidelines of Franciscolo (1957), with emphasis on the genitalia. Length of a species is given as a range between the smallest and the largest (eye sighted) specimens measured in lateral view from the front edge of the pronotum to the tip of the elytron in an unaltered specimen. Elytral width is the maximum width across both elytra. Eye color varies among specimens because of different preserving materials and light angles; apical setae of the middle and posterior legs, as well as ridges and carinae on the posterior legs, are always black or much darker than the dermal color. Therefore, we do not mention these traits throughout this article. Tarsal ratios are the proportion of tarsomeres given from basal to apical segments and from anterior to posterior legs, respectively, but the legs are not scaled inter se, contra Franciscolo (1957). Observations using scanning electronic microscope (SEM) and genitalic terminology follow that of Lu et al. (1997). We deposited most specimens and the holotypes of *Glipostenoda guana* sp. nov. and *Mordellistena irfianorum* sp. nov. in the Department of Entomology, Montana State University (MTSU). Specimens that are in W.L.'s collection will eventually go to the U.S. National Museum of Natural History (USNM), or the Museum of Comparative Zoology, Harvard (MCZ).

Key to Species of Mordellid Beetles from the Virgin Islands

1. Posterior tibia with only a subapical ridge on outer face parallel to apical ridge; no other ridge on posterior tarsus 2
   Posterior tibia either with a fine carina along dorsal outer edge or some oblique lateral ridges on outer face other than the subapical ridge 3
2. Black, suboval, small, pygidium very short, flat at base . . . . *Mordella summermanae* Ray
   Black, cuneiform, large, pygidium twice as long as hypopygium . . *Mordella atrata* Melsheimer
3. Posterior tibia with a fine carina along dorsal outer edge in addition to subapical ridge; such carina also indicated on basitarsus 4
   Posterior tibia with some oblique ridges on outer face in addition to subapical ridge; such oblique ridges also indicated on tarsal segments 5
4. Female head and a semicircular spot on anterior pronotum yellow, elytron with 2 small anterior yellow spots and 1 large posterior yellow spot; male black with 1 large yellow spot on elytron before middle, another behind middle. . . . . . . *Tolidomordella leucocephala* (Quedenfeldt) comb. nov.
   Female head yellow, elytron with 2 small anterior yellow spots and 1 large posterior yellow spot; male black with a ferruginous humeral vitta covering the 2 small anterior yellow spots but not the large posterior yellow spot . . . . *Tolidomordella basifulva* (Quedenfeldt) comb. nov.
5. Head and pronotum black 6
   Derm generally ferruginous, at least pronotum so 7
6. Elytron black; 2 ridges on outer face of posterior tibia other than the subapical 1; 2 each on basal and 2nd segments of posterior tarsus. . . . . *Mordellistena irfianorum* sp. nov.
   Elytron with a flavous stripe running from base to apex, leaving suture and margin black; 2 ridges on outer face of posterior tibia other than the subapical 1; 2 on 1st segment, 1 on 2nd segment of posterior tarsus . . . . *Mordellistena lineata* Ray.
7. Head sometimes fuscous, otherwise totally ferruginous, including antenna . . . . *Glipostenoda guana* sp. nov.
   Head and thorax flavous; elytron fuscous with a flavous vitta at base, tapering caudad; at least 7 apical segments of antenna fuscous . . . . *Falsomordellistena danforthi* (Ray) comb. nov.

Mordella atrata Melsheimer (Fig. 2)

Mordella scutellaris F. Leng and Mutchler 1917, Ray 1939, Blackwelder 1945 (non-Fabricius 1801).

Mordella atrata Melsheimer, 1846; Liljeblad 1945.

Type Locality. Pennsylvania, USA.

Type. Not listed (Bright 1986). Ray (1939) used *M. scutellaris* F. (1801) for this species from Puerto Rico; Liljeblad (1945) pointed out that *M. scutellaris* was originally described as bicolored, and *atrata* was the oldest available name for the black mordellid otherwise resembling *scutellaris*. We compared our material with MCZ specimens determined by Liljeblad and follow Liljeblad (1945).

Length: 3.2–4 mm. Cuneiform, more robust in female than in male. Derm entirely black, often iridescent under light; pubescence on upper surface brownish, on scutellum cinereous; underside and basal pygidium with longer cinereous hairs.

Liljeblad (1945) has adequately redescribed the species except for the following characters: Middle tibia as long as its tarsus; penultimate segments of anterior and middle tarsi slightly enlarged and notched at apex. Posterior tibia with a short subapical ridge, parallel to apical margin, no continuous dorsal carina but with small granules scattered in an irregular line on dorsum; the same dorsal granules weakly indicated on basitarsus, much less so on 2nd segment of posterior tarsus. Outer spur of posterior tibia ⅓ (female) or ¼ (male) shorter than inner one. Tarsal ratios: 4-2-2-3–5, 3-2-2-4–8, 2-2-3-6. Pygidium long and stout, twice as long as hypopygium; hypopygium about twice as long as penultimate segments. Urosternites and genitalia as in Lu et al. (1997).

Previous Records. Cuba (Leng and Mutchler 1917), Puerto Rico, North, Central, and South Americas (Blackwelder 1945).

Material Examined. BRITISH VIRGIN ISLANDS: Guana, Quail Dove Ghut, 600 feet, 1, 20–25.IV.1993, flight intercept trap, W. P. Liao; Guana, 3, 10.X.1994, on sea grape blossoms, *Coccoloba uvifera*, W. Lu

# ERRATA
for

Lu, W., and M. Ivie. 1999. Tumbling flower beetles of the Virgin Islands with....Ann. Entomol. Soc. Am. 92(5): 686-701.

Fig. 2. *M. atrata.* A, antenna; L, posterior leg; P, maxillary palpus.

Fig. 3. *M. summermanae.* A, antenna; L, posterior leg; P, maxillary palpus; 8 and 9, male 8th and 9th sternites.

Fig. 4. *T. leucocephala* with sexual dimorphism in elytral patterns indicated. A, antenna; E, left elytron pattern; L, posterior leg; P, maxillary palpus; 8 and 9, male 8th and 9th sternites.

Fig. 5. *T. basifulva.* E, left elytron pattern; 8 and 9, male 8th and 9th sternites; LP, left parameron; RP, right parameron; D, dorsal branch; V, ventral branch; M, medial branch.

Fig. 6. *G. guana* with sexual dimorphism in antennae indicated. A, antenna; L, posterior leg; P, maxillary palpus; 8 and 9, male 8th and 9th sternites.

Fig. 7. *F. danforthi.* A, antenna; E, left elytron pattern; L, posterior leg; P, maxillary palpus; 8 and 9, male 8th and 9th sternites; LP, left parameron; RP, right parameron; D, dorsal branch; V, ventral branch.

Fig. 8. *M. lineata* with ridge variation of posterior leg indicated. A, antenna; E, left elytron pattern; L, posterior leg; P, maxillary palpus; 8 and 9, male 8th and 9th sternites; LP, left parameron; RP, right parameron; D, dorsal branch; V, ventral branch.

Fig. 9. *M. irfianorum.* A, antenna; L, posterior leg; P, maxillary palpus.

Ah, the failure of electronics! Wenhua attempted to correct "m" in the proofs to "mm" (meters to millimeters). The result transformed all the figure captions to nonsense, but the editor never noticed!

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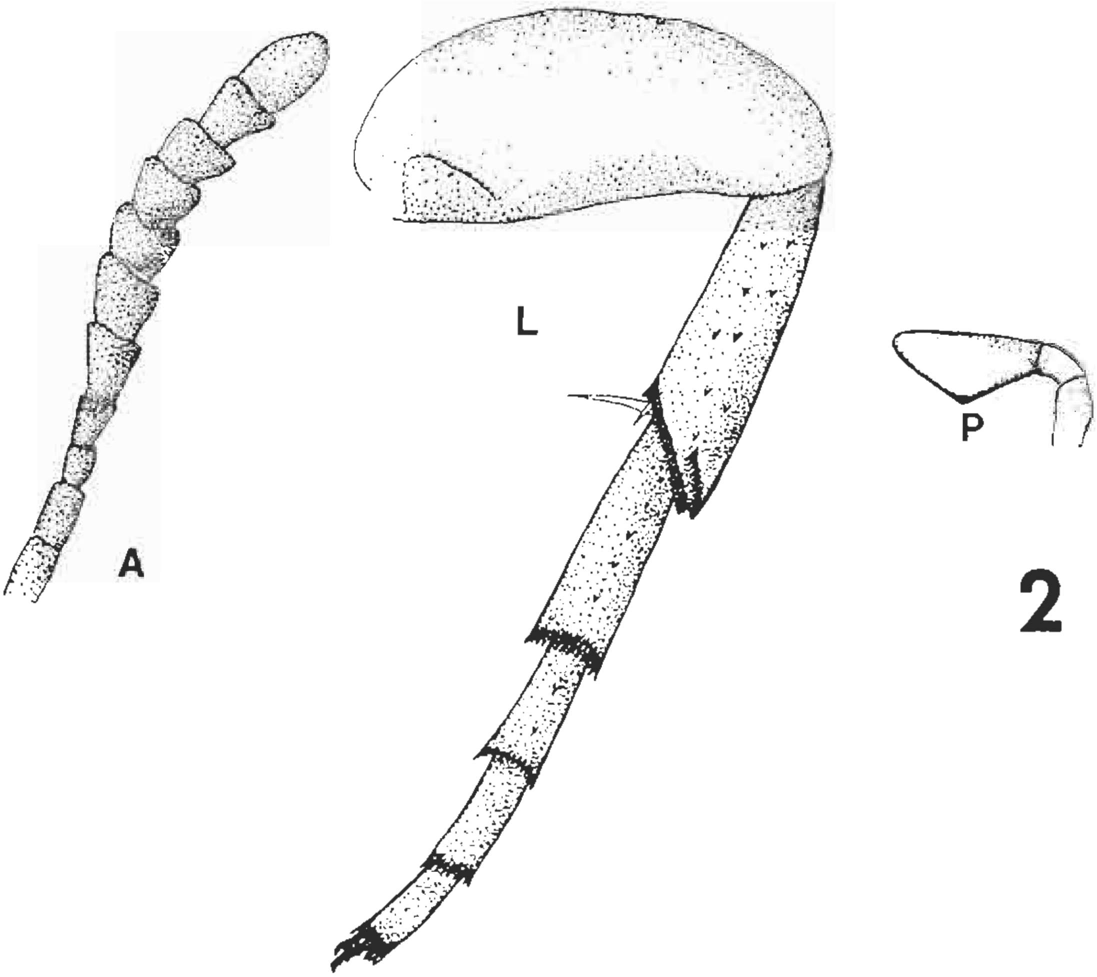

Fig. 2. A, antennae; L, posterior leg; P, maxillary palpus; 8 and 9m, male 8th and 9th sternites.

(MTSU); Guana, Muskmelon Bay, 1, 5.X.1995, sweeping on *Lantana involucrata*, W. Lu (W.L.).

Remarks. Champion (1889) and Liljeblad (1945) both mentioned that the 3rd segment of the antenna was a little longer than the 4th. We find that the 2 segments are of the same length. They did not mention the granules on the dorsum of the posterior tibia. All North American specimens in USNM and MCZ examined by W.L. have these granules.

Ray (1939) reported 5 *M. scutellaris* from Puerto Rico. W.L. was able to locate and examine these 5 specimens at USNM. Although Blackwelder (1945) made *atrata* a synonym of *scutellaris*, Ray's specimens are totally black instead of bicolored as in *scutellaris* sensu stricto. Despite the fact that many early workers called the all-black form *scutellaris*, most authors today accept Liljeblad's arrangement and so do we.

Mordella summermanae Ray (Figs. 3 and 10 A–C)

Mordella summermanae Ray, 1939.

Type Locality. Constanza, Dominican Republic.

Holotype. A unique female, 22.v.1927, A. Wetmore; USNM 52928. We could not locate this specimen, but we compared our material with specimens from the Dominican Republic that fundamentally fit Ray's (1939) description.

Length: 1.7–2.2 mm. Form short, suboval, elongate, broadest near base of pronotum. Derm fuscous to black, spurs of posterior tibia flavous; basal 4 segments of antenna less so; apical segments of antenna and legs (except for posterior tibia) fuscous. Upper surface covered with yellowish brown pubescence, hairs of underside cinereous.

Head big, as broad as pronotum; eye oval (pear-shaped, narrower anteriorly), reaching occiput, finely granulated with sparse short hairs; distance between eyes on vertex wider than 2 eyes combined. Antenna shorter than head and pronotum combined, scarcely reaching base of pronotum; segments 1 and 2 subequal, 3 and 4 subequal, shorter and narrower; 5 triangular, ⅓ longer than 4, and 3 times as broad at apex; 6–10 strongly serrate, twice as broad as long, each slightly shorter than 5; 11 rounded to apex, a little longer than

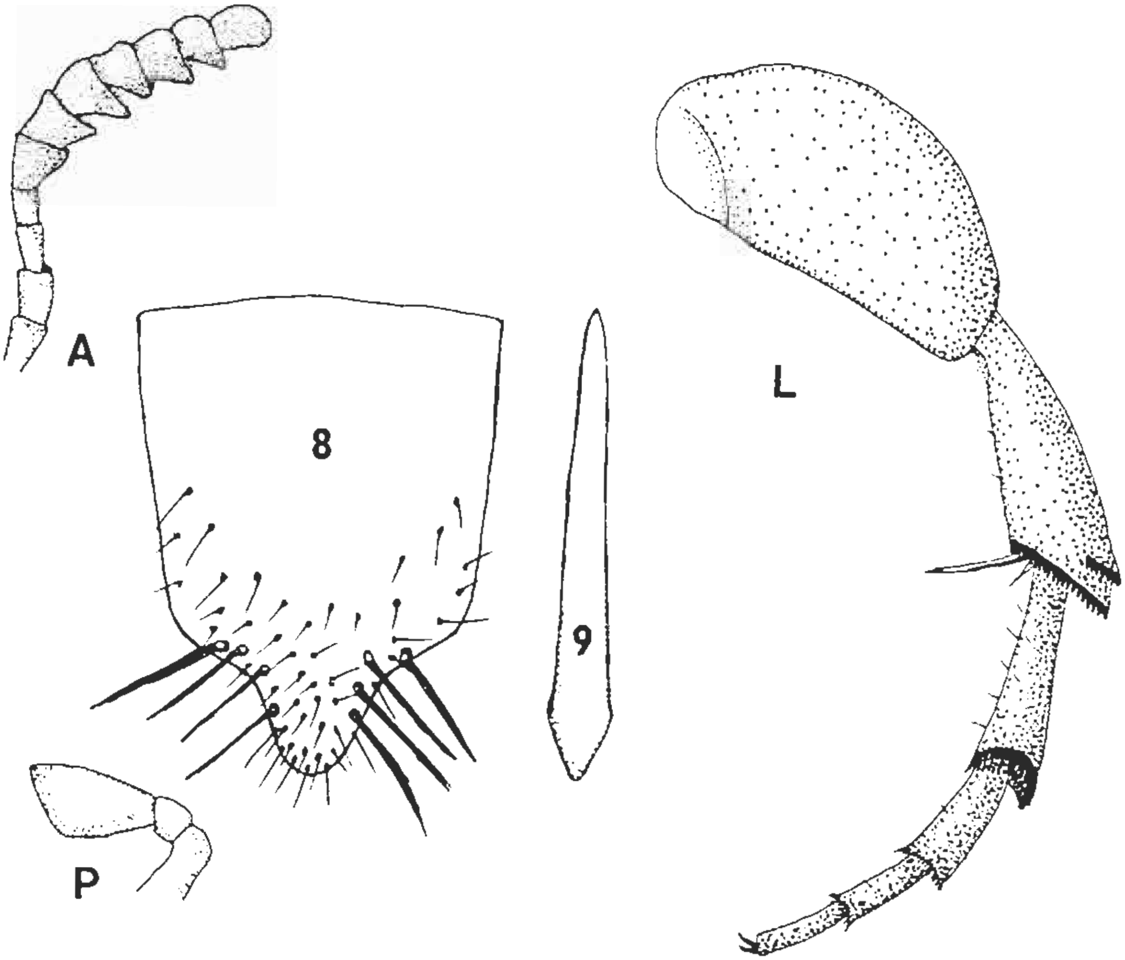

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Fig. 3. *M. summermanae.* (8) *M. lineata* with ridge variation. (9) *M. irfianorum.* A, antennae; L, posterior leg; P, maxillary palpus; 8 and 9m, male 8th and 9th sternites.

10. Distal segment of maxillary palpus isosceles triangular with outer side longer, almost equilateral in males.

Pronotum broader than long, widest subbasally, sides parallel; basal angles almost reticulate angles, base arcuate, basal lobe short, but broadly rounded. Scutellum very small, broadly triangular, apical angle rounded. Elytra about twice as long as broad, widest subbasally, attenuate apically; apices individually rounded with fine but distinct margin.

Middle tibia slightly longer than its tarsus or as long; penultimate segments of anterior and middle tarsi slightly enlarged and notched at apex. Posterior tibia with a short subapical ridge, parallel to apical margin. Outer spur of posterior tibia ⅓ as long as inner one. Tarsal ratios: 3-1-1-2-4, 3-1-2-3-8, 2-2-3-6.

Pygidium flat, short, but a quarter longer than hypopygium, very broad at base, but ⅓ longer than broad in dorsal view; sides straight, apex truncate; hypopygium 1.5–2 penultimate segments. Urosternites equal in length; furca twice as long as tube, tube as long as paramera, furca one and a half times as long as epimere; epimere wide and elliptical, twice as long as left parameron or one and a half times as long as right parameron; penis ~ 4.5 as long as epimere with a simple pointed tip.

Left parameron (Fig. 10B) short and flattened with a medial branch (Lu et al. 1997) apically; a dent at base of medial branch (Fig. 10A). Right parameron typical of type B (Fig. 10C) with an insignificant basal ridge (Lu et al. 1997); its ventral branch extremely long and thickened from base on, comparable to those of *Glipa* and *Hoshihananomia* (Lu et al. 1997), with a small prong (Fig. 10C, arrow).

Previous Records. Dominican Republic: Constanza (Ray 1939).

Material Examined. U. S. VIRGIN ISLANDS: St. Thomas, Est. Nazareth, 1, 27.VII.-19.X.1994, 40 feet flight intercept trap, M. A. and L. L. Ivie (MTSU). BRITISH VIRGIN ISLANDS: Guana, 8, 2–10.X.1994, sweeping on sea grape blossoms, *Coccoloba uvifera*, W. Lu (MTSU). JAMAICA: St. Catherine Parish, Little Goat Island, 5, 1.III.1995, W. Lu; Trelawny Parish, Good Hope, 1, 4.III.1995, sweeping on composite blossoms, W. Lu; Manchester Parish, 2.25 miles northwest Mandeville, Marshall's Pen, 2, 26.II.1995, W. Lu (W.L.). DOMINICAN REPUBLIC: Peravie, 17 km east San Jose de Ocoa, 1, 8.VIII.1979, G. B. Marshall; Peravie, 21 km northwest San Jose de Ocoa, 1, 9.VIII.1979, C. W. O'Brien (MTSU).

Remarks. In Ray's (1939) description the lighter color of the basal 4 segments of the antenna was not mentioned, and the width of segments 5–10 were said to be only "as broad as long." We have also observed that the frons, the mouthparts except the tip of the mandibles, and the anterior femur are often flavous. The right parameron embraces the left one, its small prong of the ventral branch articulates with the dent at the base of the medial branch of the left parameron.

The species is not often collected, but is occasionally numerous. This is the 1st record of it from the Virgin Islands and Jamaica.

Tolidomordella leucocephala (Quedenfeldt) comb. nov. (Figs. 4 and 10 D and F)

Mordella leucocephala Quedenfeldt, 1886.

Type Locality. 18° 29′ N, 64° 34′ W, Guana Island, British Virgin Islands.

Neotype. Quedenfeldt (1886) did not give any locality for his specimens and stated that the specimen given to him by C. Krug did not have locality data. His material was given to Obenthur who might have deposited it in France or Germany. Curators in the Humboldt Museum, Berlin, and the National Museum of Natural History, Paris, have not been able to locate his specimens. Because he described only the female, and the male characters are usually more important in identification for this group of beetles, we herein designate a male as the neotype, collected by W. Lu, 5.X.1996, on Guana Island, and deposited in MTSU.

Length: 1.9–2.7 mm. Form elongate, subparallel, broadest before base of pronotum. Male derm castaneous to black with frons, antenna, palpus, legs, and often apical pygidium fulvous; elytron with 2 large and transverse yellow spots: 1 occupying most of the basal 3rd of elytron, almost reaching base, the other behind middle; both spots not reaching sutural and side margins. Female head and a semicircle on anterior pronotum light yellow, leaving pronotum a large black basal margin; elytron with 2 small anterior yellow spots before middle: 1 round, near suture a little below base, the other transverse, lower down close to side margin; elytron with another large posterior yellow spot behind middle: transverse and oblong, not reaching suture but often touching side margin. Surface covered with pubescence partaking distinctly of ground colors.

Head small, slightly narrower than pronotum; eye oval, reaching occiput, moderately granulated with dense setae-like hairs. Antenna shorter than head and pronotum combined, not reaching base of pronotum; segment 3 distinctly small, triangular, not much longer than broad, 4 ≈⅓ wider at apex and slightly longer than 3; segments 5–7 subserrate, slightly increasing in width and length, 5 twice as long and broad as 3; 8–10 subequal, each as long as 7 and ⅓ longer than broad; 11 suboval, ⅓ longer and slightly broader in middle than 10. Distal segment of maxillary palpus boat-shaped or hammer-shaped in male, with apical side much less sclerotized; scalene triangular in female with outer side longer and rounded, apical side slightly shorter than inner side.

Pronotum ⅓ broader than long, widest in middle, evenly rounded to apex; basal angles obtuse, base arcuate, basal lobe broadly rounded. Scutellum small, triangular, rounded at apex. Elytra at least twice as long as broad, slightly narrower at base than pronotum, subparallel on basal two-thirds, then attenuate apically; apices individually rounded with fine but distinct margin.

Middle tibia as long as its basal 4 tarsal segments; penultimate segments of anterior and middle tarsi bilobed. In addition to a subapical ridge halfway across outer face and parallel to apical ridge, posterior tibia with a fine carina along dorsal outer edge, interrupted halfway to genu; another such carina, but more than halfway along dorsal outer edge on basitarsus. Outer spur of posterior tibia very short, ⅕ as long as inner one. Tarsal ratios: 2-1-1-1-4, 2-1-1-3-8, 3-4-5-10.

Pygidium conical, stout at basal two-thirds, then sharply attenuate to apex, curved down a little from side view, 2.5 times as long as hypopygium. Eighth sternite with a median protuberance long and rounded at apex, and a lateral lobe on each side; 9th sternite slender, with apical portion enlarged. Epimere 1.5 times as long as paramera, furca as long as tube, with furcal arms strongly thickened and hooked apically. Penis short, as long as pygidium, twice as long as epimere; its apical first third greatly flattened and enlarged, terminating in a round fleshy lobe.

Left parameron (Fig. 10D) bearing a highly developed and flap-like dorsal branch with setae all over inner surface, and a bare, blunt, and strongly sclerotized medial branch (Lu et al. 1997); inner surfaces of dorsal and medial branches normal to each other instead of in the same plane. Right parameron (Fig. 10E) bearing a dorsal branch highly developed, long, and flap-like with setae all over the inner surface, and a short, bare, truncate, strongly sclerotized ventral branch; basal angle of ventral branch with a sharp and long extension (Fig. 10 E and F, arrows); no setae on the outer surface (Fig. 10F).

Previous Records. Probably Puerto Rico (Quedenfeldt 1886) because the specimen's donor, C. Krug, was a resident there and Wolcott (1950) implied that the types were collected there by J. Gundlach. Puerto Rico (Leng and Mutchler 1914, Wolcott 1936).

Material Examined. Male: U.S. VIRGIN ISLANDS: St. John, Lameshur Bay, 1.III.1984, malaise trap, M. B.

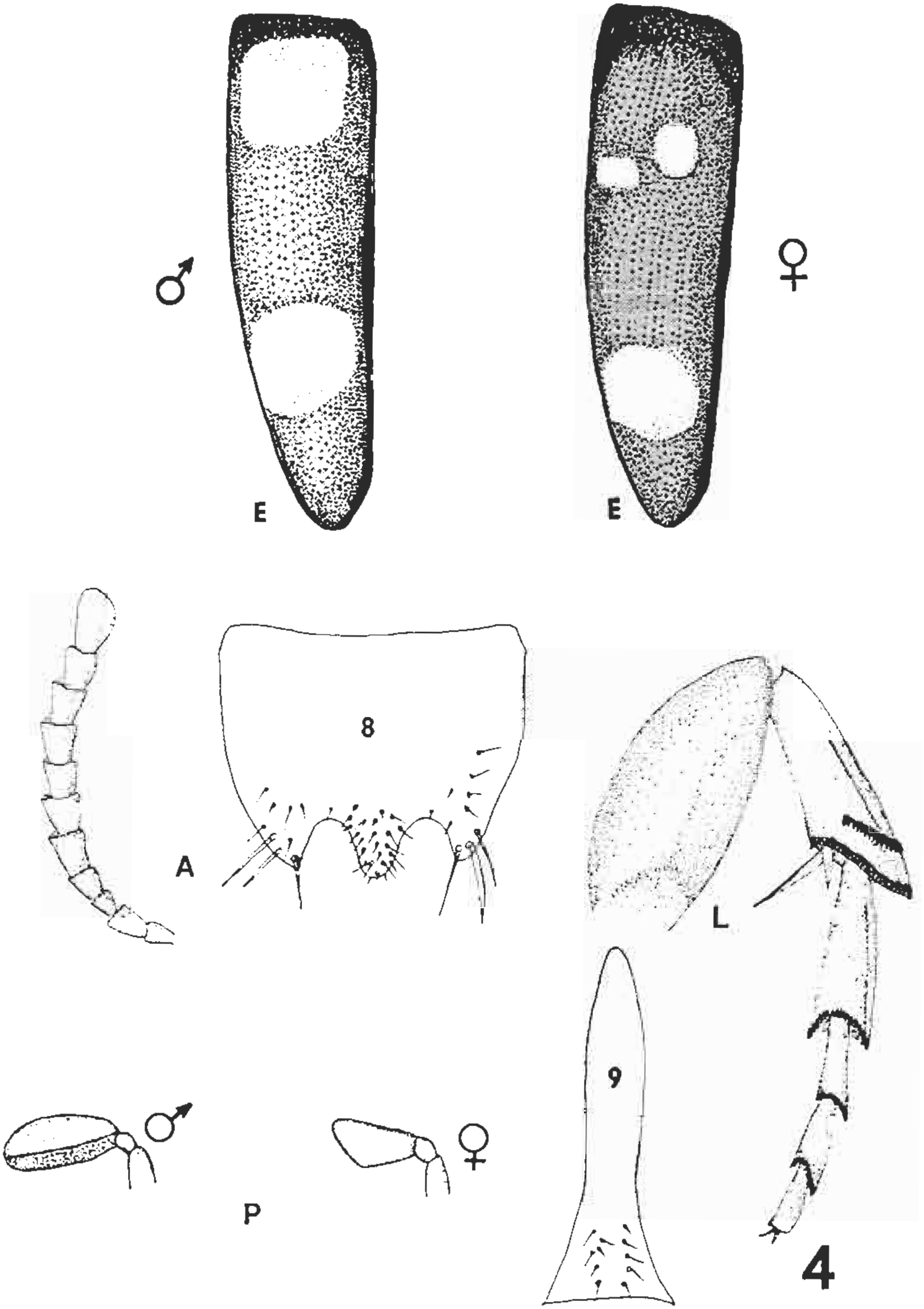

Fig. 4. *T. leucocephala* with sexual dimorphism in elytral patterns indicated. (8) *M. lineata* with ridge variation of posterior leg indicated. (9) *M. urfianorum*. A, antennae; E, left elytron pattern; L, posterior leg; P, maxillary palpus; 8 and 9m, male 8th and 9th sternites.

Muchmore; St. John, Lameshur Bay, 1, 21–28.VII.1994, UV light trap, M. S. Becker (MTSU). St. Thomas, East Botany Bay; 1, 29.VII–15.X.1994, M. A. and L. L. Ivie (MTSU). BRITISH VIRGIN ISLANDS: Necker, 1, 22–25.VII.1988, C. O'Connell (MTSU). Guana (in addition to neotype) – Sugarloaf Trail, 100–800 feet, 1, 9.X.1994, M. A. and L. L. Ivie; 0–80 m, 1, 10–25.VII.1988, S. E. Miller and C. O'Connell; 3, 1–14.VII.1984, S. E. Miller and P. M. Miller; 1, 16.X.1993, C. Bartlett and J. Cryan; 1, 19.X.1993, malaise trap, C. Bartlett and J. Cryan; 1, 18–19.X.1993, C. Bartlett and J. Cryan; 3, 10.X.1994, W. Lu; North Beach, 1, 11–16.X1992, malaise trap, R. R. Snelling; plantation area, malaise trap, 2, 16–20.X.1992, R. R. Snelling (MTSU); Iguana Trail, 2, 4.X.1996, W. Lu; Liao Weiping Trail, 7, 5.X.1996, W. Lu; Guail Dove Ghut, 2, 7.X.1996, W. Lu; Long Man's Point, 1 9.X.1996, W. Lu; Lower Iguana Trail, 2, 12.X.1996, W. Lu; Pyramid, 2, 13.X.1996, W. Lu (W.L.). PUERTO RICO: Ponce, Torres Finca, 1, 24.VIII.1933, *Ocotea* sp., R. G. Oakley (USNM).

Female. BRITISH VIRGIN ISLANDS: Guana – 1, 1–14.VII.1984, S. E. and P. M. Miller; Bigelow Road, 1, 17.VII.1994, at night, S. A. Bucklin (MTSU); Liao Weiping Trail, 2, 5.X.1996, W. Lu; Iguana Trail, 1, 6.X.1996, W. Lu; Quail Dove Ghut, 3, 7.X.1996, W. Lu; Long Man's Point, 1, 9.X.1996, W. Lu; Lower Iguana Trail, 1, 12.X.1996, W. Lu (W.L.). Great Camanoe, 2, 12.X.1996, W. Lu (W.L.).

Remarks. The colors of the head and thorax in the male can vary from fulvous to black, as can abdominal segments and legs in both sexes. W.L. examined and compared specimens totally fulvous, totally black, and intermediates. There are no differences in male genitalia and wing venation. We believe the difference in dermal color is because of age of the live animals. The elytral yellow spots of the male (Fig. 4) are about equal in size; the 1 posterior to the middle is as long as or slightly longer than the last apical portion of the elytron; the black band between the 2 yellow spots is at least as long as or longer than any other black band and a yellow spot combined. The head and a semicircle on the anterior pronotum are sometimes flavous in the male. This form is scarce but recorded from the islands of St. John, St. Thomas, Guana, and Great Camanoe.

Most specimens collected by W.L. during 1996 were on blossoms of pigeonberry, *Bourreria succulenta* (Boraginaceae), fiddlewood, *Citharexylum fruticosum* (Verbenaceae), and on leaves of dogwood, *Piscidia carthagenensis* (Leguminosae). A few were on blossoms of yellow cedar, *Tecoma stans* (Bignoniaceae) and tourist tree, *Bursera simaruba* (Burseraceae).

Tolidomordella leucocephala closely resembles *T. discoidea flaviventris* (Smith) from Florida and Texas in the male genitalia, wing venation, and male elytral pattern. However, *T. d. flaviventris* is not sexually dimorphic like *T. leucocephala*, and sometimes has a flavous humeral dash on the elytron, and the basal angle of the ventral branch of the right parameron does not have the sharp and pointed extension (Lu et al. 1997) of male *T. leucocephala*. Because of the basal angle extension, the base of the right parameron of *T. leucocephala* is very wide (Fig. 10 E and F).

Tolidomordella basifulva (Quedenfeldt) comb. nov. (Fig. 5)

Mordella basifulva Quedenfeldt, 1886.

Type Locality. 18° 00′ N, 66° 37′ W, Ponce, Puerto Rico.

Neotype. Quedenfeldt (1886) did not give any locality for his specimens. Wolcott (1950) implied that the types were collected by J. Gundlach in Puerto Rico. Because we could not locate Quedenfeldt's specimens, for reasons noted above, we herein designate a male as the neotype, collected by R. G. Oakley, 11.IX.1933, Ponce, Torres Finca, on *Ficus*, and deposited in USNM.

Length as in *T. leucocephala* but slightly narrower. Male similar to female *T. leucocephala* except for the following: Head fulvous with a dark cloud on vertex; pronotum with a large black spot on disc leaving marginal edges fulvous; elytral color various from fulvous to black, a wide humeral vitta fulvous all the way toward elytral suture, at least half way down the elytron, overwhelming the 2 small anterior yellow spots in the same location as in female *T. leucocephala*; basal 4 segments of antenna, underside of thorax, and legs lighter than elytra, from flavous to fulvous. Distal segment of maxillary palpus boat-shaped.

Median protuberance of 8th sternite long and pointed; 9th sternite elongate, with apical portion enlarged and strongly asymmetrical. Epimere twice as long as paramera, furca twice as long as tube, with furcal arms hooked but not thickened. Penis long, 3 times as long as epimere; its basal 2nd quarter slightly enlarged, but apical 1st quarter greatly enlarged, apical termination as in *T. leucocephala*.

Paramera similar to those of *T. discoidea flaviventris* (Lu et al. 1997); for right parameron, its ventral branch shorter than that of *T. leucocephala*, with a basal angle sharp but no extended root as in *T. leucocephala*; middle of dorsal branch of right parameron with some very short setae.

Previous Records. Puerto Rico (Quedenfeldt 1886, Leng and Mutchler 1914, Wolcott 1936).

Material Examined. U.S. VIRGIN ISLANDS: St. John, Estate Caneel Bay, Lind Point, 1, 2.I.1993, leaf litter (MTSU). BRITISH VIRGIN ISLANDS: Guana, Quail Dove Ghut, 1 male, 7.X.1996, *Acacia*, W. Lu (W.L.). Tortola, Sage Mountain, 450 m, 2 males, 4.X.1996, W. Lu (W.L.). PUERTO RICO (in addition to neotype): Mayaguez, 1 male, 21.VII.1933, coffee leaf, no collector, but the handwriting is R. G. Oakley's (USNM).

Remarks. All specimens of this type are males. Quedenfeldt (1886) did not mention the sex of his specimens but apparently named *T. basifulva* based on male specimens only. The fulvous humeral vitta on the elytron is so strong that the 2 anterior small yellow spots are sometimes merely suggestive. Four specimens from Puerto Rico – Ponce, 1, 11.IX.1933, *Ficus*, R. G. Oakley; Ponce, R. B. Noise F., 1, 12.I.1933, coffee,

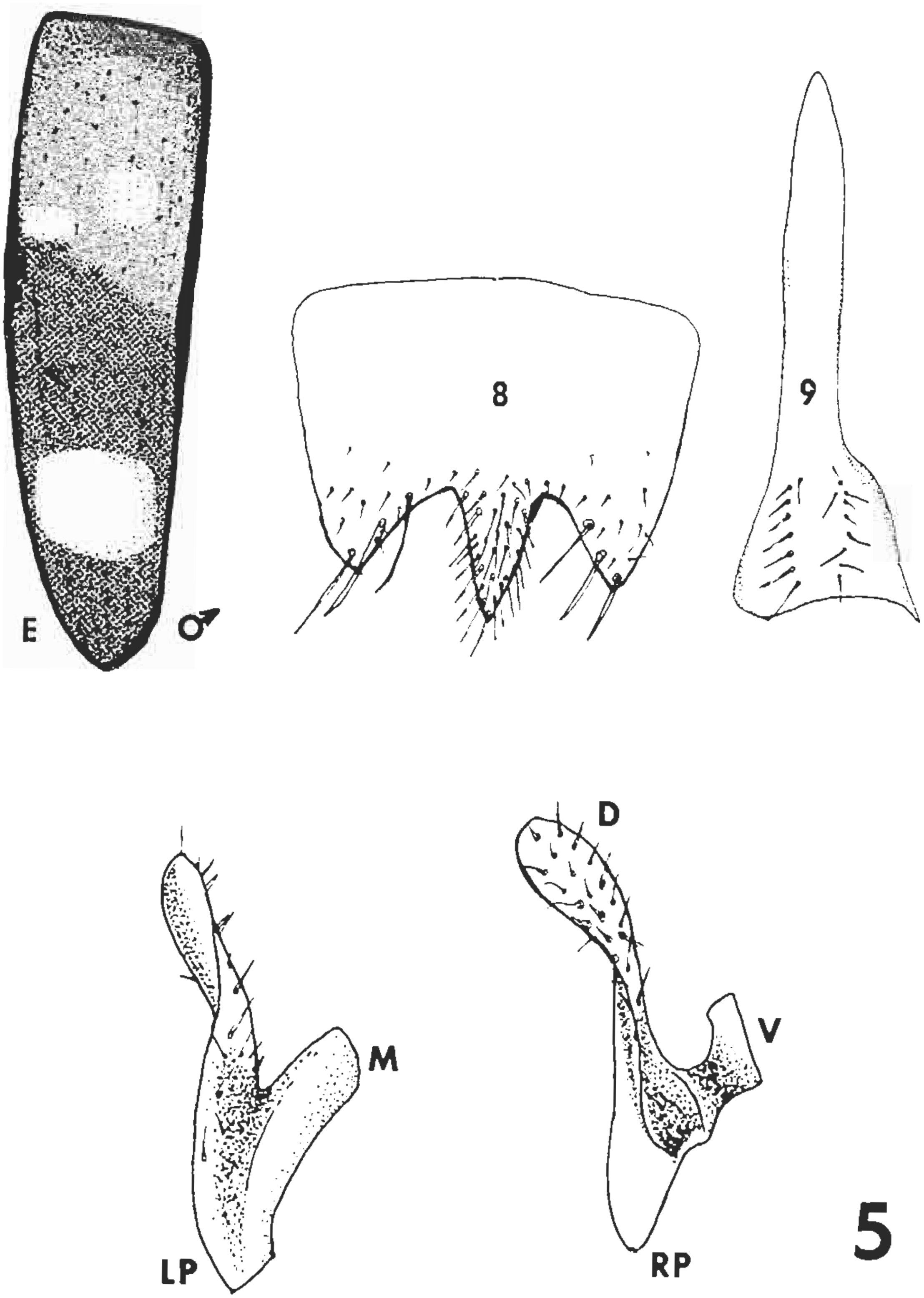

Fig. 5. *T basifulva* E. left elytron pattern; LP. left parameron; RP. right parameron; D. dorsal branch; V. ventral branch; (8) *M lineata* with ridge variation; (9) *M irfianorum*. A. antennae; M. medial branch.

R. C. Oakley (USNM); Naricao Forest Reserve, 1, 26.VII.1979, G. B. Marshall (MTSU); Maricao Forest, 2–3,000 feet, 1, 30.V–2.VI.1938, Darlington (MCZ) – have a yellow head as in female *T. leucocephala*, but the pronotum is entirely black, missing the anterior yellow semicircle characteristic of female *T. leucocephala*. The elytra are similar to those of female *T. leucocephala*. All specimens of this form are females; one of them was collected in the same locality, on the same date, on the same host plant, and by the same collector as the neotype. We thus believe that this form may be the female of *T. basifulva*. It appears that in the Virgin Islands *T. basifulva* is outnumbered by *T. leucocephala* and thus it is not surprising that we have not collected female specimens of *T. basifulva* there.

Glipostenoda guana sp. nov.

Mordellistena ferruginea F. Quedenfeldt 1886; Leng and Mutchler 1914, 1917; Wolcott 1936, 1950 (non-*Mordella ferruginea* Fabricius 1775 or 1801).

Mordellistena ferruginea (F.). Ray 1937, Miskimen and Bond 1970, Lazell 1995 (non *Mordella ferruginea* Fabricius 1775 or 1801).

Type Locality. 18° 29′ N, 64° 34′ W, Guana Island, British Virgin Islands.

Holotype. Male, collected by W. Lu, 10.X.1996, on Guana Island, and deposited in MTSU.

Length: 2.1–3.3 mm. Form elongate, narrow, sides subparallel, attenuate and rounded gradually caudad from apical quarter of elytra. Derm ferruginous; head and pronotum sometimes with fuscous clouds; basal segments of antenna, maxillary palpus, anterior and middle legs lighter (flavoferruginous), underside darker. Surface covered with fine pubescence partaking of ground color.

Head small and convex; eye large, hairy, and coarsely granulated, reaching occiput, emarginate behind antenna; eye width greater than its length, distance between eyes on vertex <2 eyes combined. Antenna filiform and long, antennal segments of males more slender than those of females, longer beyond base of pronotum, segment 5 shorter than 3 and 4 combined, segments 5–10 slightly decreasing in length and increasing in width, each segment ranging 2.5–2 times as long as broad in sequence. Antennal segments of females more stout, segment 5 as long as 3 and 4 combined, 5–10 obviously decreasing in length and increasing in width, each segment ranging 2–1 times as long as broad in sequence. Segment 11 slightly longer than 10, sides straight, apex rounded. Distal segment of maxillary palpus scalene triangular, inner side a little longer than apical side and shorter than outer side, apical side and angle rounded.

Pronotum a little broader than long, broadest at base; basal angles barely obtuse or nearly rectilinear, base arcuate, basal lobe short and broadly rounded. Scutellum triangular, sides straight, apical angle rounded. Elytra at least 2.5 times as long as broad, sides subparallel on basal 3 quarters, thence broadly rounded to apex; apices individually rounded. Metasternal plate with a transverse suture (TSM, Franciscolo 1962).

Middle tibia as long as its tarsus; penultimate segments of anterior and middle tarsi enlarged and emarginate at apex. In addition, to a short subapical ridge, posterior tibia with 2 long oblique ridges, extending halfway across outer surface; basitarsus with three 2nd tarsal segment with 2, short oblique ridges; basal ridge on basitarsus sometimes rudimentary. Outer spur of posterior tibia a quarter length of inner one. Tarsal ratios: 1-1-2-3-6, 1-1-2-3-6, 3-3-4-8.

Pygidium long, at least 2.5 as long as hypopygium in male, slightly shorter in female, conical, slender, and attenuate to apex. A small area in median protuberance of the 8th sternite without setae, and a large area in the basal two-thirds of 8th sternite less sclerotized; tube of phallobase short, as long as right parameron, furca longer than epimere; thus phallobase as long as paramera and epimere combined; epimere twice as long as right paramera. Penis slightly >3 times as long as epimere, and terminating in a simple lobe with a lateral flange (Fig. 10G, arrow) on each side.

Paramera typical of type D (Franciscolo 1957): mitten-like and more or less symmetric by branching dorso-ventrally. Dorsal branch of left parameron strongly sclerotized, thickened and triangular in apical cross section, longer by half than ventral branch, which is thin, sharp, bare, but sclerotized (Fig. 10H); basal prominence of dorsal branch blunt (Fig. 10H). Right parameron shorter and stouter than left, branching from basal ½ with a flap-like dorsal branch and a ventral branch shorter, bare, but strongly sclerotized (Fig. 10I).

Previous Records (as *Mordellistena ferruginea*). Puerto Rico (Quedenfeldt 1886, Leng and Mutchler 1914, Ray 1937). U. S. Virgin Islands: St. Thomas (Quedenfeldt 1886, Leng and Mutchler 1914, Wolcott 1950, Blackwelder 1945), St. Croix (Miskimen and Bond 1970). British Virgin Islands: Necker (Lazell 1995). A record for U. S. (Blackwelder 1945) has no known source. Quedenfeldt (1886) mentioned specimens from Columbia, South America.

Material Examined. We have collected and examined numerous specimens (now in MTSU – W.L.) from the Virgin Islands and only give island records (number of specimens) as follows. U. S. VIRGIN ISLANDS: St. Croix (8), St. John (37), St. Thomas (15). BRITISH VIRGIN ISLANDS: Guana (55−63), Jost Van Dyke (4), Necker (7−15), Virgin Gorda (4−2), Great Dog (−1), George Dog (−2), Great Camanoe (−19), Scrub Island (−1). PUERTO RICO: Ponce, 1 male, 1933-34, R. B. Oakley; Guanica, 1 female, 25.IX.1947, Caldwell; Rincon, 3, 1963, J. Maldonado; Rincon, 3, IV.1964, J. Maldonado (USNM); Mona Island, 7–13.XI.1992, 1, Snelling and Torres; Pico Atalaya, 1, 3.VII.1958, M. W. Sanderson; Guanica Forest Reserve, 1, 26.IX.1987, M. A. Ivie; Hwy. 371, 10 km, 25.VII.1979, G. B. Marshall; Maricao Forest Reserve, 1, 26.VII.1979, G. B. Marshall; Abajo Forest Reserve, 1, 27.VII.1979, G. B. Marshall; Guajataca Forest Reserve, 2, 27.VII.1979, G. B. Marshall; Toro Negro, 1, 22.VII.1979, C. W. O'Brien et al.; Maricao Forest Re-

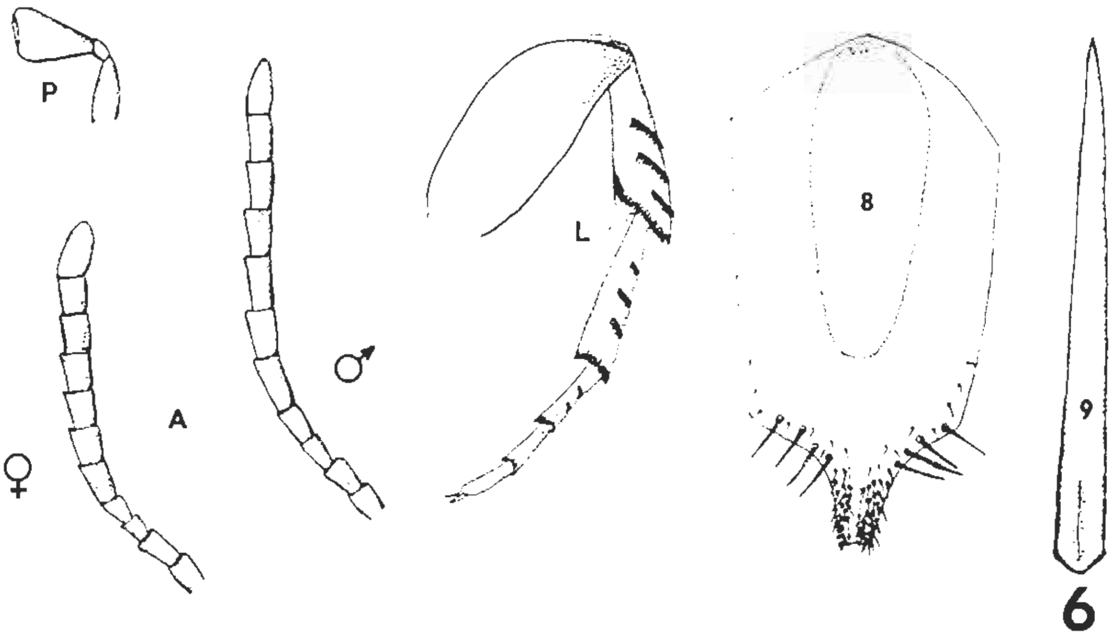

Fig. 6. *G. guana* with sexual dimorphism in antennae indicated. (8) *M. lineata* with ridge variation of posterior leg indicated. (9) *M. irfianorum*. A, antennae; L, posterior leg; P, maxillary palpus; 8 and 9m, male 8th and 9th sternites.

serve, 1, 25.VII.1979, B. O. O'Brien; Maricao Forest Reserve, 1, 26.VII.1979, B. O. O'Brien; Rio Abajo Forest Reserve, 24.VII.1979, B. O. O'Brien; Maricao Forest Reserve, 2, 25.VII.1979, C. W. O'Brien (MTSU).

Paratypes. The remaining 54 MTSU specimens listed above from Guana Island.

Etymology. Named for Guana Island as a noun in apposition.

Remarks. This is a very abundant species, can be found on blossoms of *Lantana, Acacia, Citharexylum fruticosum*, and various leguminous plants. The ridges on the posterior tibia and tarsus vary among individuals. An extremely small individual from St. John has only 1 long oblique ridge on the posterior tibia, in addition to the short subapical one; it has only 2 ridges on the basitarsus and 1 on the 2nd segment of the right tarsus, and a rudimentary 2nd on the 2nd segment of the left tarsus. The posterior tibia and basitarsus rarely show a rudimentary 4th ridge. The ferruginous color in this specimen and other small specimens collected on Guana and Virgin Gorda is so pale that it appears almost yellow. Newly emerged adults also are pale.

All 4 specimens from Jost Van Dyke are entirely black-headed. Their antennal segments 3 and 4 are short and narrow so that 5 is as long as 3 and 4 combined. Similar individuals were collected on St. John and Guana. There is a range of color variation on the head from flavoferruginous, fuscous, to entirely black, all with the same type of antennae, on the latter 2 islands. We observed no difference in the male genitalia and regard this color form on Jost Van Dyke as interisland variation.

Falsomordellistena danforthi (Ray) comb. nov.
(Fig. 7)

Mordellistena danforthi Ray, 1937; Wolcott 1950.

Type Locality. Villalba, Puerto Rico.

Holotype. Male, 21.VI.1934, C. M. Matos; USNM 51599. We examined both the holotype and allotype.

Length: 2.0–2.8 mm. Form elongate, sides subparallel. Derm flavous; elytron fuscous with a flavous, broad, humeral spot along base to suture, narrowing caudad to basal ⅓ of elytron; eye, apical 7 segments of antenna, posterior ventral abdominal segments, and pygidium fuscous. Surface densely covered with fine golden pubescence.

Ray (1937) has adequately described the species except for the following characters: Metasternal plate without TSM. Middle tibia as long as its basal 4 tarsal segments; penultimate segments of anterior and middle tarsi enlarged and slightly emarginate at apex. In addition to a short subapical ridge, posterior tibia with 2 long oblique ridges, extending halfway across outer surface; posterior basitarsus with three 2nd segment with 2, short oblique ridges; basal ridge on basitarsus sometimes rudimentary. Outer spur of posterior tibia ¼ as long as inner one. Tarsal ratios: 2-1-2-3–4, 3-2-3-4–9, 3-4-5-9.

Pygidium long, 2.5–3 times as long as hypopygium, shorter in females, conical, slender, and attenuate to apex. Median protuberance of 8th sternite appearing bifurcate due to setae and a less sclerotized area all the way to base, 9th sternite twice as long as 8th; furca twice as long as tube or paramera, and as long as epimere; epimere twice as long as right parameron;

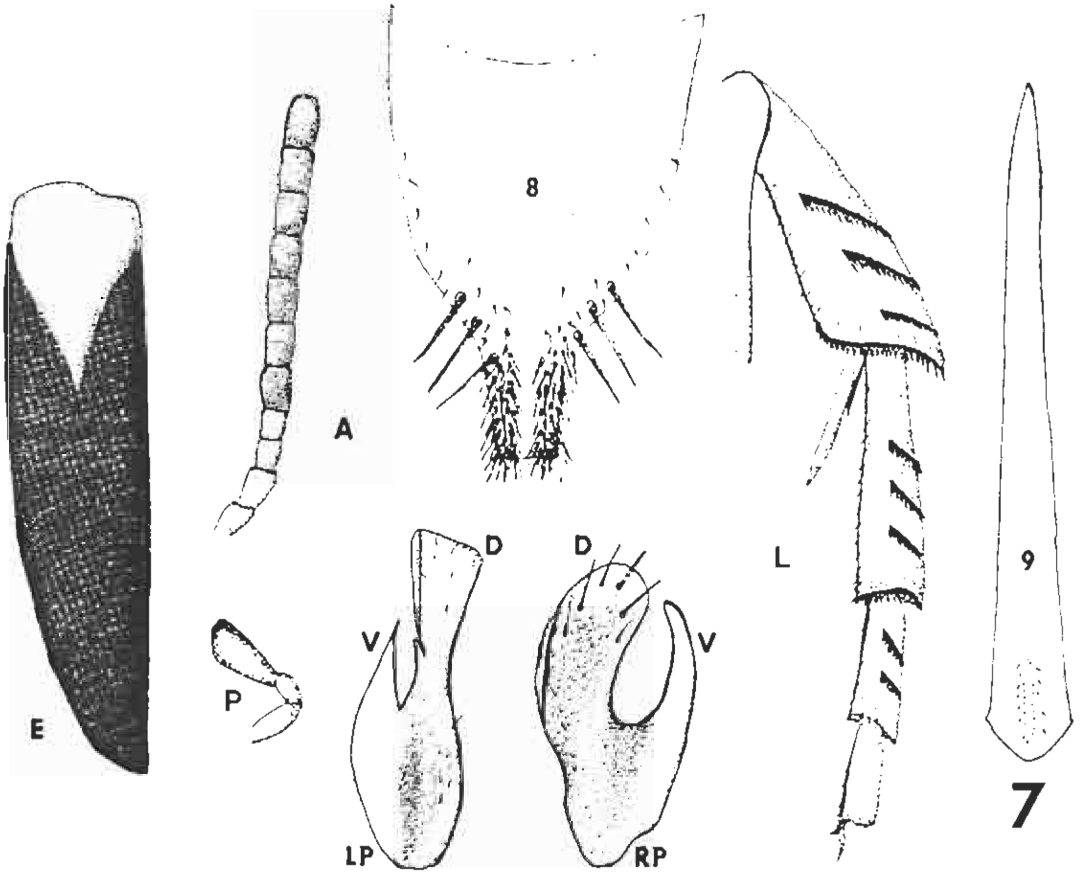

Fig. 7. *F. danforthi*. (8) *M. lineata* with ridge variation of posterior leg indicated. (9) *M. irfianorum* A, antennae; E, left elytron pattern; L, posterior leg; P, maxillary palpus; 8 and 9m, male 5th and 9th sternites; LP, left parameron; RP, right parameron; D, dorsal branch; V, ventral branch.

ventral branch of left parameron extremely narrow and pointed, basal prominence set off its dorsal branch by a split. Penis 4 times as long as epimere with a simple pointed tip, apical 1st and 3rd quarters enlarged with a constriction on apical 2nd quarter.

Previous Records. Puerto Rico (Ray 1937, Wolcott 1950).

Material Examined. U. S. VIRGIN ISLANDS: Great St. James, 1, 20.X.1994, M. A. Ivie (MTSU). St. John, 2, 15.VII.1994, beating at night, M. S. Becker; St. John, 1, 21–28.VII.1994, UV light, M. S. Becker (MTSU). BRITISH VIRGIN ISLANDS: Virgin Gorda, 1, 14.IV.1956, J. F. Clarke (USNM). Prickly Pear Island, 1, 6.IV.1958, J. F. Clarke (USNM). Guana, 1, 1–14.VII.1984, S. E. and P. M. Miller; 5, 4–10.X.1994, W. Lu (MTSU). Necker, 4, 30.IX.1996, *Citharexylum fruticosum*, W. Lu (W.L.). George Dog, 1 female, 30.IX.1996, *Lantana*, W. Lu (W.L.).

Remarks. One specimen from St. John (MTSU) has an additional rudimentary ridge on both the posterior tibia and the basitarsus. According to Ray (1937), the scutellum, apical two-thirds of the pygidium, and only 3 abdominal ventral segments were fuscous, but he also stated that "the abdominal segments of the female (except pygidium) lack the fuscous coloration of the male, and the general castaneous color is lighter." We have observed variation in the abdominal ventral segments from totally fuscous to totally flavocastaneous. The pygidium may be as he described or totally fuscous. We see no variation in the color of the scutellum, which is as flavous as the front part of the body or the humeral spots on the elytra. Ray (1937) described the eyes as "emarginate behind antennae." We find the eye is in fact almost rounded, but tapers acutely toward the antennal base; the width and length of the eye are about equal. In comparison, the width is longer than the length in *G. guana*. In other words, the distance between the eyes on vertex is about the width of the eyes combined in *F. danforthi*. We have also observed variation in elytral color in specimens from Guana. One has the humeral flavous spot on the elytron extending narrowly to the midpoint, then widening to the apex. Some have the flavous, broad, humeral spot covering the whole elytron; in this case, the appearance is very similar to *G. guana*, but the antennae remain diagnostically bicolored, the eyes are not broader than long, and *F. danforthi* lacks the TSM.

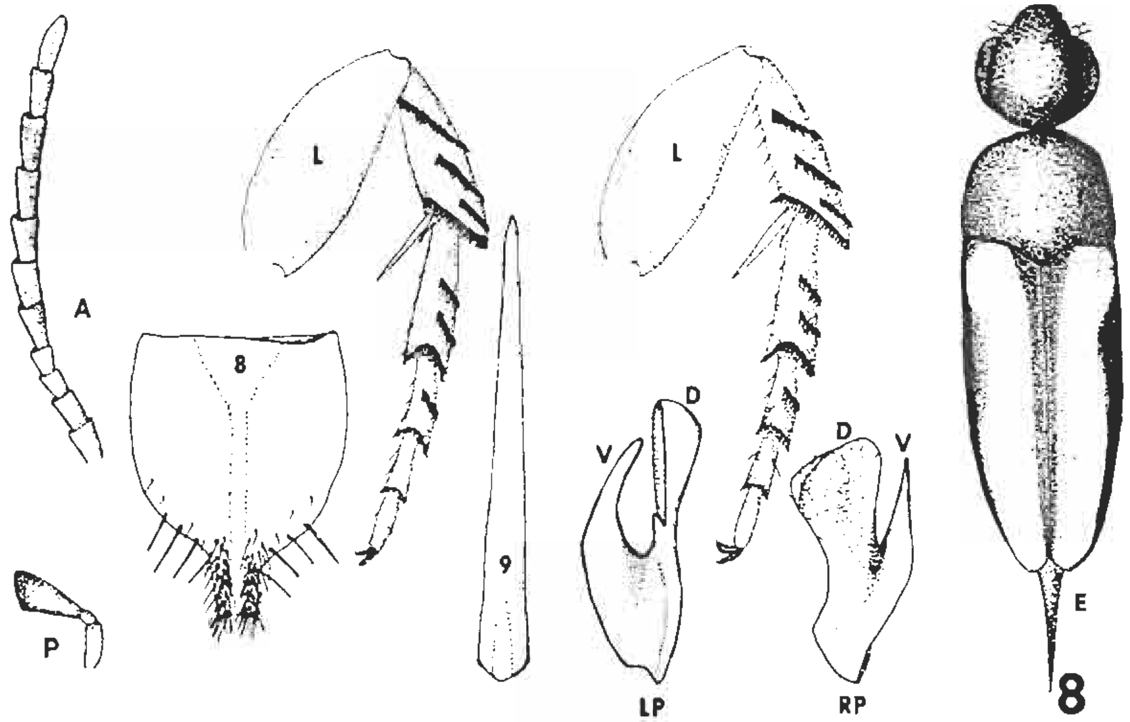

Fig. 8. *M. lineata* with ridge variation of posterior leg indicated. (8) *M. lineata* with ridge variation of posterior leg indicated; (9) *M. irfianorum*. A, antennae; E, left elytron pattern; L, posterior leg; P, maxillary palpus; 8 and 9m, male 8th and 9th sternites; LP, left parameron; RP, right parameron; D, dorsal branch; V, ventral branch.

Mordellistena lineata Ray (Fig. 8)

Mordellistena lineata Ray, 1937.

Type Locality. Guanica, Puerto Rico.

Holotype. Male, 26.VI.1934, C. M. Matos; USNM 51601. We examined both the holotype and allotype.

Length: 1.6–2.2 mm. Form elongate, narrow, sides subparallel, attenuate, and rounded gradually caudad from apical 3rd of elytra. Derm castaneous to black; frons of head, basal 4 segments of antenna, maxillary palpus, anterior and middle legs, and posterior leg other than femur flavocastaneous; a broad median stripe on each elytron flavocastaneous, reaching base of humerus, often narrowed in middle of elytral side margin, and extending to apex, leaving a narrow black line on each elytral side margin and a black sutural line. Surface covered with fine cinereous pubescence, except in the flavocastaneous area, where it partakes of the ground color.

Liljeblad (1945) has adequately redescribed the species except for the following characters: Metasternal plate with TSM. Middle tibia as long as its tarsus; penultimate segments of anterior and middle tarsi slightly enlarged and emarginate at apex. In addition to a short subapical ridge, posterior tibia with 2 long, oblique ridges, extending at least halfway across outer surface, basal ridge usually longer than the 2nd, sometimes extending entirely across outer surface to genu. Posterior basitarsus with two, 2nd with 1, short oblique ridges; basal ridge on basitarsus sometimes rudimentary. Outer spur of posterior tibia ⅓ as long as inner one. Tarsal ratios: 3-2-3-4–6, 2-1-2-3–6, 3-3-4-6.

Pygidium long, almost 3 times as long as hypopygium, shorter in female, conical, attenuate to apex. Median protuberance of 8th sternite appearing bifurcate due to setae and a less sclerotized area all the way to base, 9th sternite twice as long as 8th with a less sclerotized area at apex; furca twice as long as tube or paramera, and as long as epimere; epimere twice as long as right parameron; ventral branch of right parameron narrowly branched out, basal prominence of left parameron set off its dorsal branch by a split. Penis 3 times as long as epimere with apical 1st and 3rd quarters enlarged, its apex terminating in a finger-like lobe with a lateral flange on each side as *Glipostenoda ambusta* (LeConte) (Lu et al. 1997).

Previous Records. Puerto Rico. Guanica (Ray 1937), Mona Island (Wolcott 1950). British Virgin Islands: Necker Island (Lazell 1995).

Material Examined. U.S. VIRGIN ISLANDS: Buck Island (9), St. Croix (3), St. John (29), St. Thomas (3) (MTSU). BRITISH VIRGIN ISLANDS: Anegada (2), Beef Island (4–3), Guana (74–85), Necker (4–6), Tortola (1–1), Great Camanoe (–5), Great Dog (–1), George Dog, 2, 30.IX.1996, *Lantana*, W. Lu (W.L.). PUERTO RICO: Mona Island, Casuarina plantation, 1, 7–13.XI.1992, malaise trap, Snelling and Torres (MTSU).

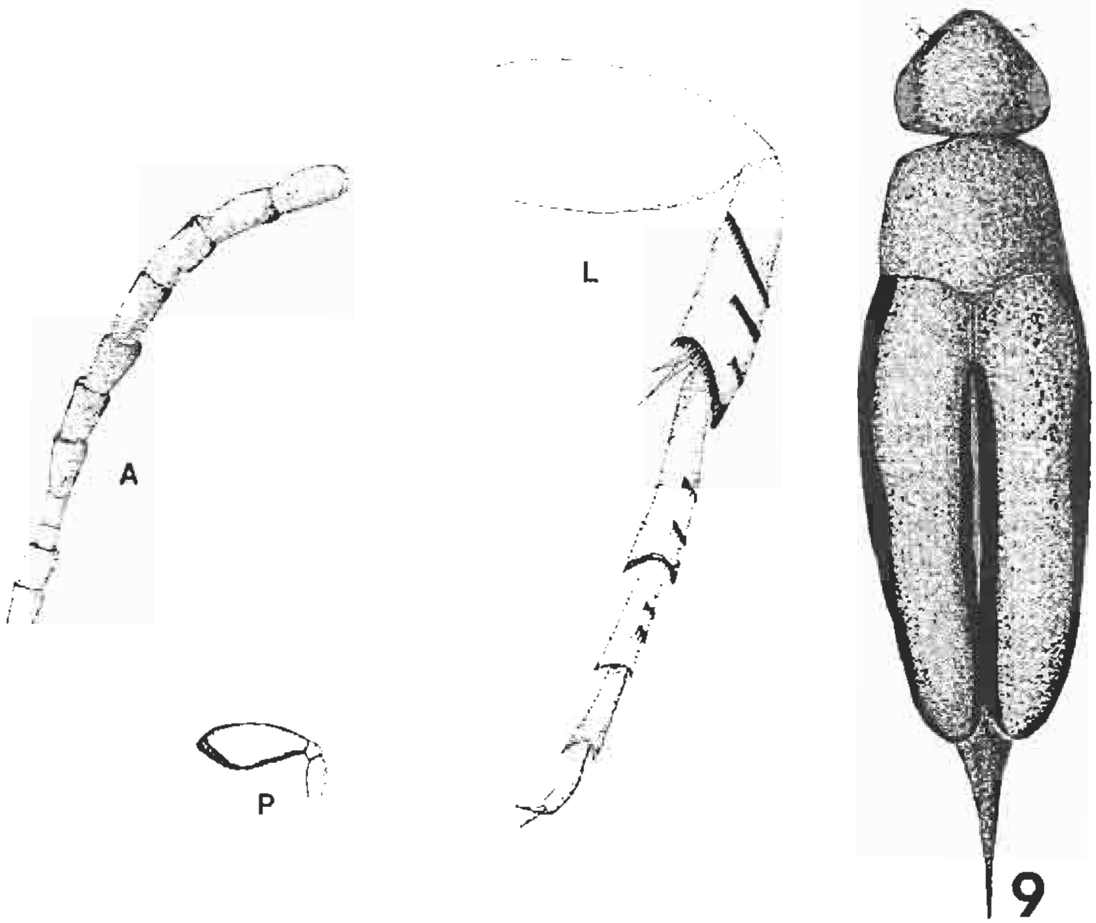

Fig. 9. *M. irfianorum.* A, antennae; L, posterior leg; P, maxillary palpus; 8 and 9m, male 8th and 9th sternites.

Remarks. The slightly enlarged and emarginate penultimate segments of anterior and middle tarsi are a giveaway character that this species does not belong to *Mordellistena*. The closest genus would be *Mordellina*, but the eyes are coarse and big in that genus, and the penultimate segments of anterior and middle tarsi should be the same as in *Mordellistena*. We retain this species in *Mordellistena* until we have a better understanding of the genera worldwide.

This species superficially resembles *Mordellistena angustiformis* Ray (1939), but the antenna is different from that species. In his original description, Ray stated, in an apparent lapse, that "7 apical segments of antennae" were flavocastaneous, lighter than basal segments. The reverse is true of all specimens we have examined, including the type. Ray also stated that the basal oblique ridge on the posterior tibia was "entirely across outer face." We find this character variable. Fewer than half the specimens examined are as described, all males. Most specimens have the basal ridge on the posterior tibia halfway across the outer surface or more, but not entirely, including both sexes. Occasionally the dermal color of some specimens is much lighter than black (probably newly emerged), but the even lighter stripes on elytra remain diagnostic. This is a very abundant species on flowers and dense vegetation, especially on leguminous *Acacia* species.

Mordellistena irfianorum sp. nov. (Fig. 9)

Type Locality. 18° 19′ N, 64° 43′ W, St. John, U.S. Virgin Islands.

Holotype. Female, collected by M. Becker and S. Bucklin, 6–27.VII.1994, flight intercept trap, East Hope, Bordeaux Mountain, 900 feet, St. John, and deposited in MTSU.

Length: 2.2 mm. Form elongate, sides subparallel. Derm castaneous to black; mouthparts, maxillary palpus, basal 4 segments of antenna, anterior leg, tibiae and tarsi of middle and posterior legs testaceous. Surface covered with long whitish pubescence, slightly golden on scutellum and on elytra, but pubescence on side and sutural margins partaking dermal color from basal ⅕ on, leaving most side and sutural margins black, widened slightly in middle of side margin; underside pubescence longer.

Head small; eye hairy, and moderately granulated, reaching occiput, suboval, not emarginate behind an-

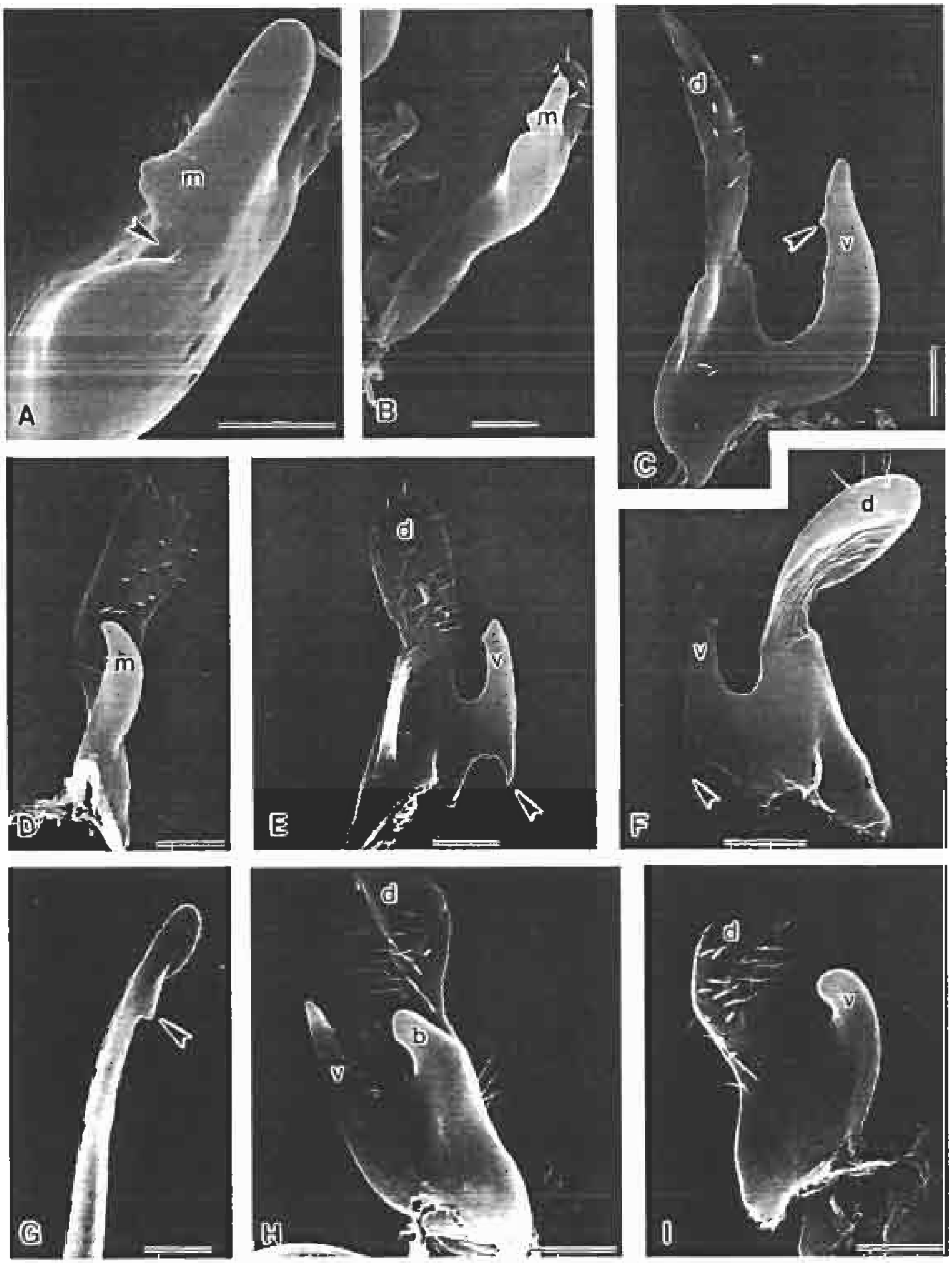

Fig. 10. SEM of genitalic. *M. summermanae* A and B, LP with arrow showing a dent on medial branch; C, RP with arrow showing a prong on ventral branch. *T. leucocephala*: D, LP; E and F, inner and outer surfaces of RP with arrows showing a sharp basal angle of ventral branch. *G. guana* G, lateral view of tip of penis with arrow showing a lateral flange; H, LP; I, RP. Scale bars A = 10 μm; B, C, and G = 30 μm; all others = 50 μm. b, basal prominence; d, dorsal branch; v, ventral branch; m, medial branch; otherwise as above.

tenna. Antenna filiform and long, reaching base of pronotum; segments 1 and 2 subequal, 3 and 4 shorter and narrower, four ≈ ⅓ longer than 3; 5–10 each as long as 3 and 4 combined, increasing in width, 11 apically rounded, slightly longer than 10. Distal segment of maxillary palpus elongate-triangular, apical side slightly shorter than inner side.

Pronotum ≈¼ broader than long, sides rounded; basal angles acute, base arcuate, basal lobe conspicuous, rounded. Scutellum small, triangular. Elytra at most 2.5 times as long as broad, sides narrower at base than in middle, broadly rounded to apex; apices individually rounded. Metasternal plate with TSM.

Middle tibia as long as its tarsus; penultimate segments of anterior and middle tarsi emarginate (but not bilobed) at apex. In addition, to a short subapical ridge, posterior tibia with 2 long oblique ridges, basal 1 extending entirely across outer surface; basal and 2nd tarsal segments each with 2 short oblique ridges. Inner spur of posterior tibia ⅔ length of basitarsus, outer spur short, ¼-⅕ length of inner one. Tarsal ratios: 1-1-1-2–3, 3-3-4-8–16, 3-4-5-9. Pygidium long, 3 times as long as hypopygium, conical, slender, and attenuate to apex.

Material Examined. U.S. VIRGIN ISLANDS: St. John, East Hope, Bordeaux Mountain., 900 feet, 1 female, 6–27.VII.1994, flight intercept trap, M. Becker and S. Bucklin (MTSU). PUERTO RICO: Cambalache, 1 female, 7.XI.1947, J. S. Caldwell (USNM).

Paratype. The remaining specimen from Puerto Rico.

Etymology. The Island Resources Foundation of St. Thomas, IRF, has provided support. We name this species for IRF in the genitive neuter pleural.

Remarks. This species looks very much like *M. lineata* at 1st glance and we have the same difficulty in placing it in any other known genus as we do for *M. lineata*. The 2 ridges on posterior 2nd tarsus and the entirely black elytra distinguish it from *M. lineata*. The specimen from Puerto Rico is mutilated, missing antennae as well as tibiae and tarsi of most legs.

Acknowledgments

This article is dedicated to the memory of M. S. Collins, whose advice and encouragement were invaluable to this project and the career of W.L. We are indebted to P. W. Johnson (University of Rhode Island) for SEM work. This project was funded in part by Island Resources Foundation, The Conservation Agency, Rhode Island Agricultural Experiment Station, contribution number 3724, and Montana State University. Without a Smithsonian Institution Short-Term Visitor Award to W.L. and the support of T. L. Erwin, this work wonld not have been completed.

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**CONTRIBUTIONS
OF THE
AMERICAN ENTOMOLOGICAL INSTITUTE**

Volume 30, Number 5

REVISION DEL GENERO *PACHODYNERUS* SAUSSURE (HYMENOPTERA: VESPIDAE, EUMENINAE)

by

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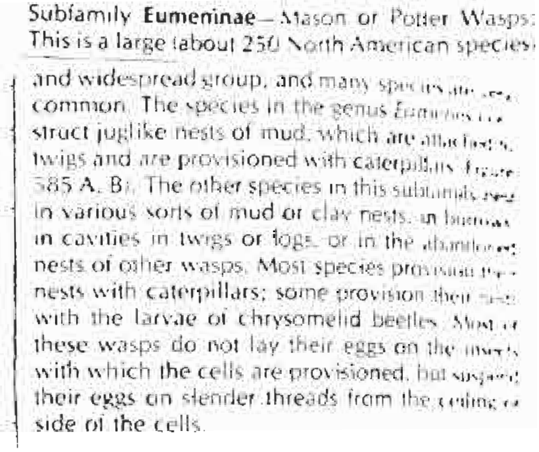
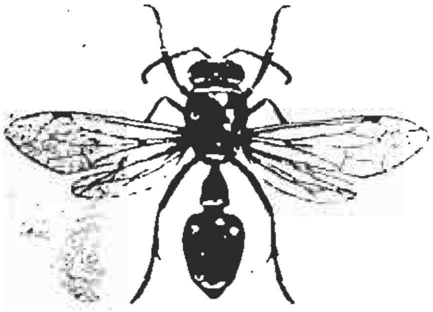


Subfamily **Eumeninae**—Mason or Potter Wasps: This is a large (about 250 North American species) and widespread group, and many species are very common. The species in the genus *Eumenes* construct juglike nests of mud, which are attached to twigs and are provisioned with caterpillars (Figure 585 A, B). The other species in this subfamily nest in various sorts of mud or clay nests, in burrows, in cavities in twigs or logs, or in the abandoned nests of other wasps. Most species provision their nests with caterpillars; some provision their nests with the larvae of chrysomelid beetles. Most of these wasps do not lay their eggs on the insects with which the cells are provisioned, but suspend their eggs on slender threads from the ceiling or side of the cells.



Pachodynerus atratus (Fabricius)
(Fig. 56)

Vespa atrata Fabricius, 1798: 262 macho y hembra "America meridionalis insulis" (Lectotipo de St.Thomas en Copenhagen). Fabricius, 1804: 260. Saussure, 1875: 379. Dalla Torre, 1894: 137 (cat.); 1904: 66 (cat.). Schulz, 1912: 82. Zimsen, 1964: 401. Menke 1986: 655. (designación de lectotipo, loc. tipo St. Thomas).

Rhynchium atratum; Dewitz,1881: 200.

Monobiella atrata; Ashmead, 1900: 312 (cat.); 1902: 209. Wolcott, 1924 (1923): 41; 1936: 568. Miskimen y Bond, 1970: 109 (de St.Croix, probablemente mal identificada).

Odynerus atratus; Zavattari, 1912: 192.

Pachodynerus atratus; Bequaert, 1929: 558. Wolcott, 1941: 156 (etología en Puerto Rico); 1951 (1948): 861 (etología). Simonthomas, 1984: 94. Menke, 1986: 653.

Odynerus aethiops Cresson MS; Wolcott, 1924 (1923): 41; 1936: 568; 1951 (1948): 861. (Nomen nudum).

Con *cinerascens* esta especie constituía el subgénero *Monobiella*, siendo sus características morfológicas principales el no tener una lamela sobre la cara posterior del propodeo, los ángulos póstero-laterales del propodeo proyectados y el T1 con una carena transversal más o menos definida. Esta especie es de color negro brillante, mientras que *cinerascens* es opaca.

Hembra. Largo del ala anterior 7,5 mm. *Coloración* negra azabache. Son de color parduzco: mandíbula, tégula, tibias y tarsos en parte. Alas subhialinas, anteriores ahumadas en la zona costal. *Morfología.* Sin rebordes internos junto a los ocelos posteriores. Clípeo, proporción entre largo y ancho 0,94; ápice subigual a la distancia interalveolar, proporción entre AAC y DIA 1,06; área central del clípeo con puntos finos alargados y estriolado longitudinal y puntos finos aislados; área lateral con micropunteado y puntos finos dispersos.
Carena occipital próxima al borde inferior del ojo por una distancia igual a 1,25 veces el diámetro del ocelo anterior. Gena ancha, proporción respecto del ancho del ojo 0,8. Reborde posterior de la depresión cefálica aquillado. Con 1 fovea cefálica. Escudo con puntos finos separados por 0,5 veces su diámetro, más espaciados medial y posteriormente; superficie entre puntos lisa y brillante. Pronoto con punteado irregular, con puntos poco profundos separados por menos de 0,5 veces su diámetro. Proporción entre el largo y el ancho del tórax 1,08. Cara superior del postescutelo ancha, sin cresta definida. Fémures anteriores sin carena longitudinal. Cara posterior del propodeo muy cóncava, brillante, con pocas estrías finas. Lamela propodeal ausente o reducida a una carena vestigial. Angulos póstero-laterales proyectados hacia atrás y hacia abajo en forma de diente aguzado. Caras anterior y dorsal de T1 separadas por una carena transversal. T2 con banda apical poco definidas con puntos finos más o menos densos, en el resto del tergo con puntos muy finos aislados.

Macho. Largo del ala anterior 6,2 mm. *Coloración* similar a la hembra. Clípeo negro con una banda amarilla mediana longitudinal que nace en la base y se ensancha hacia el ápice; cara inferior del escapo también amarilla. *Morfología.* Clípeo con micropunteado denso, regular, y algunos puntos finos aislados; sin protuberancias medianas presentes; ápice levemente cóncavo; proporción entre AAC y DIA 1,40. Carena occipital próxima al borde inferior del ojo por una distancia igual a 2,3 veces el diámetro del ocelo anterior. Antena con 9 flagelómeros. Mandíbula con diente basal oblicuo, bajo; protuberancia basal ausente. Proporción entre el largo del gonocoxito y la espina parameral 1,26.

Material revisado. PUERTO RICO. Adjuntas; Coamos Springs; Mayaguez; Ensenada Honda; Rincón; Rio Piedras; San Juan; Ponce; Bahía Las Cabezas; Morovis; Ensenada Honda. ISLAS VIRGENES. St. Thomas, Magens Bay; Brit. Virgin Isl.; Guana Isl. ISLAS SOTAVENTO. Montserrat, Belham River; St.Kitts, Muddy Ponds; St. Maarten, Cul du Sac Reward. BARBADOS. St. Eustacius. *Colecciones*: IFML; USNM, CAS, AMNH, UCZ, UCD, BMNH, NHML, MACN.

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In Press Ecological Entomology

Reduced flight capability in British Virgin Island populations of a wing-dimorphic insect: the role of habitat isolation, persistence, and structure

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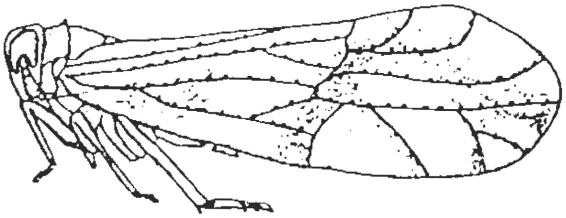

Family **Delphácidae:** This is the largest family of planthoppers, and its members can be recognized by the large flattened spur at the apex of the hind tibiae (Figure 202 C, *sp*); most species are small, and many have reduced wings. The sugarcane leafhopper, *Perkinsiélla sacchárida* Kirkaldy, which at one time was a very destructive pest in Hawaii, is a member of this family.

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Abstract. 1. The effects of habitat isolation, persistence, and host-plant structure on the incidence of dispersal capability (per cent macroptery) in populations of the delphacid planthopper *Toya venilia* were examined throughout the British Virgin Islands. The host plant of this delphacid is salt grass *Sporobolus virginicus*, which grows either in undisturbed habitats (large expanses on intertidal salt flats and around the margins of salt ponds, or small patches of sparse vegetation on sand dunes along the shore), or in less persistent, disturbed habitats (managed lawns).

2. Both sexes of *T. venilia* were significantly more macropterous in disturbed habitats (77.1% in males, 12.5% in females) than they were in more persistent, undisturbed habitats (19.2% in males, < 1% in females).

3. Males exhibited significantly higher levels of macroptery (26.9 ± 7.6%) than did females (2.0 ± 1.7%), and per cent macroptery was positively density dependent for both sexes in field populations.

4. There was no evidence that the low incidence of female macroptery in a subset of island populations inhabiting natural habitats (1.7 ± 1.2%) was attributable to the effects of isolation on oceanic islands. The incidence of macroptery in British Virgin Island populations of *T. venilia* was not different from that observed in mainland delphacid species existing in habitats of similar duration.

5. Rather, the persistence of most salt grass habitats throughout the British Virgin Islands best explains the evolution of flight reduction in females of this island-inhabiting delphacid.

6. Males were significantly more macropterous in populations occupying dune vegetation (37.6 ± 9.8) than they were in populations occupying salt flat-pond margin habitats (7.6 ± 5.6%). By contrast, females exhibited low levels of macroptery in both dune (0%) and salt flat-pond margin habitats (< 1%). Variation in salt-grass structure probably underlies this habitat-related difference in macroptery because flight-capable males of planthoppers are better able to locate females in the sparse-structured grass growing on dunes. This habitat-related difference in male macroptery accounted for the generally higher level of macroptery observed in males compared to females throughout the islands.

7. The importance of habitat persistence and structure in explaining the incidence of dispersal capability in *T. venilia* is probably indicative of the key role these two factors play in shaping the dispersal strategies of many insects.

Key words. Delphacid planthopper, dispersal, flightlessness, habitat isolation, habitat persistence, habitat structure, host plant architecture, life history evolution, *Sporobolus virginicus*, *Toya venilia*, wing polymorphism.

Introduction

With the evolution of flight in insects came an increased ability to track changing resources, negotiate structurally complex habitats, locate mates, and escape predators (Southwood, 1962; Roff & Fairbairn, 1991; Wagner & Liebherr, 1992; Denno, 1994a; Denno *et al.*, 1996, in press). Moreover, associated with the appearance of flight capability was the tremendous diversification of the class Insecta (Wagner & Liebherr, 1992). As a consequence of the association between flight capability and the increased radiation and success of the insects, reasons underlying the secondary loss of wings or flight capability, which has occurred repeatedly throughout the Insecta (Roff, 1990; Wagner & Liebherr, 1992), are not immediately apparent.

One of the keys to understanding the evolution of flight reduction in insects lies in elucidating the costs associated with building and maintaining wings and flight muscles, and in demonstrating how such costs are levelled against other life-history traits (Roff, 1986; Denno *et al.*, 1989; Zera & Denno, 1997). Most often, the diversity of costs associated with flight capability are imposed on reproduction (Roff, 1984; Srygley & Chai 1990; Marden & Chai 1991; Roff & Fairbairn, 1991; Zera & Denno, 1997). Such reproductive penalties are revealed most easily by comparing the reproductive success of the volant and flightless wing forms of wing-dimorphic insects (Roff, 1986; Denno *et al.*, 1989, in press; Roff & Fairbairn, 1991; Langellotto *et al.*, in press). In general, flightless females have higher fecundity, reproduce at an earlier age, and produce larger progeny than their flight-capable counterparts (Solbreck, 1986; Roff & Fairbairn, 1991; Denno, 1994b; Zera & Denno, 1997). Similarly, flightless males can acquire matings more successfully and sire more offspring than macropterous males (Novotný, 1995; Langellotto *et al.*, in press). Indeed, such wing-form comparisons provide widespread evidence for an antagonistic trade-off between flight capability and reproductive success across a wide variety of insect taxa including crickets, planthoppers, aphids, thrips, true bugs, and beetles (Utida, 1972; Roff, 1984; Zera, 1984; Solbreck, 1986; Crespi, 1988; Denno *et al.*, 1989; Dixon, 1998; Langellotto *et al.*, in press).

Although flightless forms clearly have an inherent reproductive advantage, they are extremely sedentary and are unable to effectively exploit ephemeral habitats, track spatial changes in food availability, manoeuvre efficiently in heterogeneous habitats, or locate widely scattered mates (Waloff, 1983; Roff 1990; Denno *et al.*, 1991, 1996, in press; Langellotto, 1997; Langellotto *et al.*, in press). Thus, the dispersal strategy that evolves in a particular species will reflect a balance between the advantage of increased reproductive success resulting from flight loss and the need for wings to track resources (Roff, 1990; Zera & Denno, 1997).

Among those selective forces considered central in shaping the evolution of insect dispersal strategies are habitat isolation, persistence, and structure (Southwood, 1962, 1977; Roff, 1990; Denno *et al.*, 1991, in press; Wagner & Liebherr, 1992; Travis & Dytham, 1999). In general, theory predicts reductions in flight capability for species exploiting habitats that are very isolated, persistent, or dense and low-profile in structure (Southwood, 1962; Roff, 1990; Langellotto, 1997; Denno *et al.*, in press). In particular, habitat isolation has been a longstanding but controversial explanation for the evolution of flightlessness in insect taxa inhabiting oceanic islands (Darwin, 1876; Roff, 1990). The argument asserts that the constant loss of emigrants from oceanic islands should select against flight capability (see Roff, 1990), however the spatial scale at which habitat isolation selects against dispersal has been a subject of considerable debate (Roff, 1990; Wagner & Liebherr, 1992; Denno *et al.*, in press). Notably, recent modeling efforts have shown that the propensity to disperse generally declines with increased habitat fragmentation, but that the predicted outcome depends on patterns of habitat availability and persistence (Travis & Dytham, 1999).

Isolation, and other habitat-related hypotheses for the evolution of flightlessness in insects, have proved difficult to test empirically, however, primarily because of the difficulty of assessing the dispersal ability of the inhabitants (Denno *et al.*, 1991, 1996, in press). Wing-dimorphic insects such as delphacid planthoppers (Hemiptera: Delphacidae) are ideal for investigating the effects of habitat factors on dispersal because migratory adults (macropters with fully-developed wings) and flightless adults (brachypters with reduced wings) are so easily recognised (Denno *et al.*, 1991). Moreover, the proportion of macropters in a population can be used as a reliable index of the incidence of potential dispersal (Denno *et al.*, 1991, in press). Testing the habitat isolation-flightlessness hypothesis has been challenging as well because comparisons of the incidence of dispersal between island and mainland populations are frequently confounded by other factors such as habitat persistence and structure (Roff, 1990; Denno *et al.*, in press).

Using British Virgin Island populations of the wing-dimorphic delphacid *Toya venilia* (Fennah), the objectives for this study were threefold. First, the incidence of dispersal (% macroptery) was compared between populations of *T. venilia* inhabiting undisturbed (relatively persistent) and disturbed habitats throughout the British Virgin Islands with the expectation of higher levels of macroptery in disturbed habitats. Second, to test the hypothesis that flight reduction is more prevalent on oceanic islands, the incidence of macroptery in island populations of *T. venilia* was compared with known levels of macroptery in mainland populations of other grass-inhabiting delphacid species. For this analysis, possible differences in habitat persistence were controlled by comparing the incidence of dispersal capability between taxa inhabiting habitats of similar age. Last, the incidence of macroptery was compared between populations of *T. venilia* inhabiting two structurally different and habitat-associated growth forms of its host grass *Sporobolus virginicus* (L.) (dense stands on salt flats and sparse stands on beach dunes). Because vegetation structure (dense versus sparse) is known to influence the ability of male planthoppers to locate mates (Denno, 1994b; Langellotto, 1997; Denno *et al.*, in press), its contribution to habitat-related variation in the incidence of dispersal capability in *T. venilia* populations was examined. Ultimately, this information was used to assess the relative contribution of habitat isolation, persistence, and vegetation structure to the dispersal strategy of this oceanic island-inhabiting planthopper.

Methods

Study organisms

Toya venilia is Caribbean in distribution, having been recorded from the British Virgin Islands, Puerto Rico, and Montserrat (Fennah, 1959). This delphacid is multivoltine and monophagous on the perennial salt grass *Sporobolus virginicus*. Like most delphacids, *T. venilia* is wing dimorphic with both macropters and brachypters occurring in most populations. Wing form in planthoppers is determined by a developmental switch that responds to environmental cues (Denno, 1994b). The sensitivity of the switch, however, is heritable and under polygenic control (Iwanaga & Tojo, 1986; Denno, 1994b; Zera and Denno, 1997). Of all the proximate cues known to affect wing form in planthoppers, population density is by far the most influential (Denno & Roderick, 1990). For most delphacids, the production of the macropterous wing form is density-dependent (Denno *et al.*, 1985; Denno, 1994b). The threshold density that triggers the production of macropterous forms, however, can differ among species, among populations of the same species, and even between the sexes of the same species (Kisimoto, 1965; Denno *et al.*, 1991). Thus, macroptery may or may not be correlated between the sexes of a species (Denno *et al.*, 1991; Denno, 1994a). Moreover, patterns of density-dependent macroptery in the sexes, be they the same or different, can be maintained under common environmental conditions suggesting an underlying genetic basis (Denno *et al.*, 1991).

Besides allowing for habitat escape and the colonisation of new habitats (Southwood, 1962, 1977), wings also function in mate location (Ichikawa, 1977; Hunt & Nault, 1991; Langellotto, 1997). In planthoppers, only males search actively for stationary females (Ichikawa, 1977; Claridge & de Vrijer, 1994; Langellotto *et al.*, in press) and acoustic communication is essential for locating mates (Claridge, 1985; Denno *et al.* 1991, Heady and Denno, 1991; Heady, 1993). Both males and females communicate through substrate-transmitted vibrations, whereby calls are produced by vibrating their abdomens (Claridge, 1985). Vibrations are transferred to the host plant through the legs or mouth parts (Claridge, 1985). Planthoppers sitting on the same host plant or on adjacent plants in physical contact can sense each other's calls from as far away as 1 m (Ichikawa & Ishii, 1974). However, planthoppers resting on neighboring but slightly separated plants do not detect each other's presence (Ichikawa & Ishii, 1974). Sexually mature males and virgin females call spontaneously on their food plants. After sensing each other, they begin to alternate calls in a duetting fashion (Claridge, 1985; Ichikawa & Ishii, 1974; Heady & Denno, 1991). During duetting, males move toward stationary females, and after locating a female, courtship ensues, followed by mating (Ichikawa & Ishii, 1974; Heady & Denno, 1991).

Given their substrate-borne system of mate location, it is not surprising that vegetation structure has a major impact on the ability of the male wing forms of planthoppers to locate mates. When host plants are isolated and do not come into contact, flight is essential for mate location because only macropterous males can fly among plants, locate females effectively, and acquire matings (Langellotto, 1997). Macropterous males also locate females much more effectively than brachypters under low female-density conditions (Langellotto, 1997). In contrast, in contiguous vegetation, brachypterous males obtain most matings apparently due in part to their inherent ability to displace rival macropters aggressively during courtship (Langellotto *et al.*, in press).

The host plant of *T. venilia* is salt grass *S. virginicus*, a perennial that grows in several different habitat types throughout the Caribbean including most of the vegetated British Virgin Islands (Chase, 1971; Acevedo-Rodriguez, 1996; Table 1). Salt grass grows on intertidal salt flats and around the margins of salt ponds, where it often occurs in dense, expansive, pure stands, frequently in association with mangroves. It also occurs as small patches on the dunes of sandy beaches and the bases of cliffs along the shore. In this beach-dune habitat, the structure of the grass stand is sparse, with culms growing further apart than those occurring on tidal flats. *Sporobolus virginicus* is also grown in managed, suburban habitats where it is encouraged by home owners as a lawn grass in low-lying areas. Although frequently disturbed by mowing, the dense structure of the grass in lawns is more like that of grass growing on salt flats than dunes. Such structural variation in grass form may influence the dispersal strategy of the resident *T. venilia*, particularly the males.

Study sites

The British Virgin Islands lie 100 km east of Puerto Rico and comprise more than 50 small islands and islets between 18°18' and 18°46' N, and 64°15' and 64°52' W (Fig. 1). Among the largest Islands are Tortola (64 km^2), Anegada (34 km^2), Virgin Gorda (21.5 km^2), and Jost van Dyke (9 km^2). Other islands (e.g. Guana, Beef, Great Camanoe) measure <5 km^2, and others yet (e.g. Necker, Great Dog, and Salt) are very small (<1 km^2).

All eleven islands visited supported at least one population of salt grass (Table 1). Although vast expanses of salt grass occurred on the intertidal flats of some islands (e.g. Anegada, Beef, and Virgin Gorda), and wide swaths (5 - 20 m) surrounded salt ponds on others (e.g. Guana, Great Camanoe, and Tortola), only single small patches occurred on the upper beach and dunes of other islands (e.g. Great Dog and Great Thatch). On some islands such as Guana, salt-pond and dune populations of salt grass co-occurred, but in this case they grew on either side of a central ridge (266 m) and were separated by 500 m. Moreover, these were the only two stands of salt grass on Guana. With the exception of the expansive salt flats on Beef Island (Airport and Trellis Bay area) and Anegada (Flamingo Pond area), salt grass populations were generally small and isolated.

Incidence of dispersal capability in planthopper populations inhabiting undisturbed and disturbed habitats throughout the British Virgin Islands

The incidence of dispersal capability in populations of *T. venilia* (per cent macroptery in both sexes) was compared between undisturbed (relatively persistent) and disturbed habitats (relatively temporary) throughout the British Virgin Islands over the course of a 3-year period (1996-1998). For this comparison, stands of salt grass growing on salt flats, along the margins of salt ponds, and on the upper reaches of beaches and dunes showed no signs of disturbance and were considered relatively persistent habitats for *T. venilia* (Table 1). By contrast, managed lawns and cattle-trampled and browsed stands of salt grass surrounding some salt ponds were regarded as disturbed habitats (Table 1). Using a combination of D-vac and sweep-net sampling, 18 populations (16 undisturbed and 2 disturbed) were assessed in disjunct stands of salt grass on 11 islands: Anegada (The Settlement and Flamingo Pond), Beef (Bridge, Airport, West Trellis Bay, and East Trellis Bay), Great Camanoe (Lee Bay), Great Dog (South Side), Great Thatch (North Side), Guana (Salt Pond and North Beach), Jost van Dyke (Great Harbor), Necker (North Side), Salt (North Side), Tortola (Belmont Pond and Josiah Bay), and Virgin Gorda (Biras Creek and Pond Bay).

For this assessment, planthoppers were sampled in 1996 using a sweep-net (38 cm diameter) and in 1997 and 1998 using a portable D-vac (1 HP Echo, model PB210E, Gempler's, Mount Horeb, Wisconsin). Extraction of most planthoppers from the dense stands of salt grass required a prolonged period of vacuuming with this portable D-vac in 1997. To achieve more time-efficient extraction of planthoppers in 1998, the conventional sampling head of this D-vac (0.093 m^2) was constricted to 0.031 m^2 by fitting the sampler with a smaller cylindrical plastic head (40 cm long, 20 cm diameter). One sample with this modified D-vac consisted of either 20 or 40 placements of the D-vac head on the vegetation, depending on the size of the grass stand. Each sample with the sweep net consisted of 20 or 50 sweeps to and fro while walking through the stand. The number and size of samples at each site and the date on which they were taken are shown in Table 1. Given the slow extraction of planthoppers in 1997, a consistent number of samples was not taken. Rather, the vegetation was vacuumed at each location for approximately 30 min. Planthopper samples were bottled in 95% ethanol and returned to the laboratory where the incidence of macroptery (%) in both sexes of *T. venilia* was determined for each population.

The incidence of macroptery (%) in males and females of *T. venilia* was compared between persistent and disturbed habitats using t-tests on angular-transformed data (SAS, 1990). For these analyses, only one value of macroptery (%) was used for each population, and if a population was sampled several times, macroptery was averaged across dates to generate this value. Populations from which fewer than five individuals of either sex were sampled were not included in the analysis.

Incidence of dispersal capability in island and mainland taxa: habitat isolation vs persistence

To test whether flightlessness was more prevalent on oceanic islands, the incidence of macroptery in British Virgin Island populations of *T. venilia* was compared with published levels of macroptery for mainland-inhabiting delphacids (extracted from Denno *et al.*, 1991). Because habitat persistence has a strong influence on the dispersal strategies of planthoppers (Denno, 1994a; Denno *et al.*, 1991, 1996, in press), it was essential to make the island and mainland comparison between taxa occupying similarly persistent habitats. Thus, it was necessary to quantify habitat persistence roughly for several *T. venilia* populations.

Habitat persistence for a particular species depends on the relationship between the generation time of the organism (τ) and the length of time the habitat remains favourable for development (H) (Southwood, 1962; Southwood *et al.*, 1974). Persistent habitats are characterised by $H/\tau >> 1$ and temporary habitats by $H/\tau \approx 1$ (Southwood, 1962). Habitat persistence was quantified for three populations of *T. venilia* (Guana, Salt Pond; Beef, East Trellis Bay; Great Camanoe, Lee Bay) by multiplying habitat age (years) by the maximum number of generations/habitat/year; thus, habitat persistence was expressed as the maximum number of generations attainable during the existence of the habitat (see Denno *et al.*, 1991).

Minimum estimates of habitat age were obtained by questioning senior residents of the islands, in particular Oscar Chalwell from Guana/Tortola, who placed minimum estimates of the salt grass habitats sampled on Guana, Beef, and Great Camanoe at 64, 60, and 60 years respectively. Estimates of the annual number of generations for these populations of *T. venilia* were predicted from an existing model established explicitly for planthoppers: *number of annual generations* = 10.12 - 0.157(*°N*) (from Denno, 1994b). By substituting the latitudes of Guana (18°29'N), Beef (18°26'N), and Great Camanoe (18°28'N) into this equation, the number of annual generations for the three populations of *T. venilia* was estimated at 7.2. Thus, habitat persistence (maximum number of generations attainable) was estimated at 460, 432, and 432 generations respectively for the Guana, Beef, and Great Camanoe populations.

The mean incidence of macroptery (per cent) in these three populations of *T. venilia* was then compared with the mean level of macroptery in mainland taxa of delphacids in three ways. First, the observed incidence of macroptery in these three British Virgin Island populations was compared with expected levels of macroptery predicted by a model describing the relationship between habitat persistence and macroptery for mainland delphacid species: *macroptery* (%) = -5.450 + 1/(*habitat persistence*$^{0.045}$ - 0.095) (from Denno *et al.*, 1991). Expected macroptery for the British Virgin Island populations was obtained by substituting habitat persistence values for the three British Virgin Island populations into the mainland-derived model. Observed and expected levels of macroptery were compared using a paired t-test on angular-transformed data (SAS, 1990). Due to small sample size (n = 3), a power analysis was performed where power = $1 - \beta$, the probability of committing a Type II error (Zar, 1996).

Second, the observed level of macroptery in the three British Virgin Island populations of *T. venilia* was compared with that for six species of mainland delphacids [*Laodelphax elegantulus* (Boheman), *Muirodelphax exiguus* (Boheman), *Paraliburniella dalei* (Scott), *Pissonotus piceus* (Van Duzee), *Prokelisia dolus* Wilson, and *Ribautodelphax angulosis* (Ribaut)] existing in similarly persistent grassland habitats (150-350 generations) (extracted from Denno *et al.*, 1991). For this and the following analysis, the incidence of macroptery (%) in British Virgin Island and mainland taxa was compared using a t-test on angular-transformed data.

Third, macroptery in British Virgin Island populations of *T. venilia* was compared with that observed in populations of seven mainland species [*Delphacodes detecta* (Van Duzee), *D. penedetecta* Beamer, *Neomegamelanus dorsalis* (Metcalf), *N. penelautus* (McDermott), *Prokelisia dolus* Wilson, *P. marginata* Van Duzee, and *Toya propinqua* (Fieber)] occupying the same low-profile habitat type (grasses growing on marshes and dunes) along the Gulf of Mexico shore (extracted from Denno, 1978; Denno *et al.*, 1991). For this analysis, no estimates of habitat persistence were required, although the habitats of all the delphacids were generally very persistent (>500 years; see Denno *et al.*, 1991).

For these three analyses, the incidence of macroptery in British Virgin Island populations should be less than that for mainland taxa if oceanic isolation were an important contributor to the evolution of flightlessness in delphacids. Thus, one-tailed tests were used to assess significance (SAS, 1990). Moreover, for all three analyses, the assessment of macroptery was limited to the female sex because the dispersal strategies of female planthoppers are not compromised by possible flight constraints associated with mate location, as is the case for males (Denno, 1994a; Denno *et al.*, 1991, in press).

Habitat structure and the incidence of macroptery in planthopper populations

The stand area (m^2) of salt grass growing on salt flats, around pond margins, and on beach dunes was estimated visually or by pacing at each of the 18 locations visited (Table 1). Stand area was compared between the salt flat-pond edge habitat and the beach-dune habitat using a t-test. Also, the structure of salt grass (culm density, culm length, and above-ground biomass) was determined by clip-quadrat sampling for stands growing in the two major habitat types (salt flats-pond edges vs dunes) on three islands (Beef, Guana, and Necker) (Denno and Roderick, 1992). Five samples were taken in each habitat type on the three islands during 19-23 October, 1998. Each sample consisted of the removal of all above-ground grass within a 0.047 m^2 wire frame. Subsequently, culm density (number per m^2), culm length (cm) and wet weight biomass (g per m^2) were determined. Because island effects were minimal (ANOVA), t-tests were used to compare culm density, culm length, and grass biomass between the two habitat types. For these analyses, the five habitat samples were averaged within each island resulting in a sample size of three for each habitat type.

The influence of habitat structure on the dispersal capability of both sexes of *T. venilia* was examined by comparing the incidence of macroptery between populations occurring in the two habitat types (sparse stands of salt grass occurring on dunes and dense stands growing on salt flats or around salt pond margins). For each sex, the incidence of macroptery (%) in the two habitat types was compared using a t-test on angular-transformed data. Similarly, a t-test on angular-transformed data was used to compare macroptery (%) between the sexes within each habitat. Sites at which < 10 individuals were collected were excluded from the analysis. The expectation was to find higher levels of macroptery in males inhabiting the dunes than in males inhabiting the salt flats because flight is likely to be essential for mate location in the sparsely structured habitat. Habitat-related variation in salt grass structure was not envisioned to influence macroptery in females because they do not search actively for mates. Because macroptery is density dependent in most planthoppers (Denno *et al.*, 1994), the slopes of the relationship between macroptery in both sexes (angular-transformed) and population density in the two habitats (dune and salt flat) were tested to see whether they differed from zero (t-test on the regression coefficients). To test further for habitat effects on the incidence of macroptery, the slopes of the relationship between macroptery (%) and population density (number per m^2) were compared between the two habitat types using ANCOVA with density as the covariate (SAS, 1990). This analysis was run separately for each sex.

Estimates of population density were necessary for the above approaches. D-vac sampling during 1998 allowed for the association of variation in the incidence of macroptery (%) in *T. venilia* with absolute population size (number per m^2). Sweep-net sampling, however, provided only a relative density estimate. To convert sweep-net counts to absolute density data, side-by-side, replicated D-vac (3, 40 placement) and sweep-net (5, 20 sweep) samples were taken on 23 October 1998 in an expansive stand of salt grass located at the margin of Salt Pond on Guana Island. The resulting planthopper counts from D-vac (17.5 ± 7.6 m^{-2}, mean ± SEM) and sweep-netting (18.8 ± 7.8 per 20 sweeps) provided a conversion factor (number of planthoppers per m^2 = number of planthoppers per 20 sweeps/1.07), which then allowed for the transformation of sweep-net data taken from other sampling locations to absolute densities. All absolute densities (number per m^2) for sweep-sampled populations were estimated using this conversion factor (see Table 1). It was not possible to establish a separate conversion factor in dune vegetation because all dune habitat patches were very small (< 80 m^2) and not easily swept. Regardless, absolute estimates of planthopper density were obtained by D-vac sampling in most dune-grass populations (Table 1).

Results

Incidence of dispersal capability in planthopper populations inhabiting undisturbed and disturbed habitats throughout the British Virgin Islands

Males of *T. venilia* were significantly more macropterous in disturbed stands of salt grass growing in lawns or cattle-trampled habitats (77.0 ± 1.0%, mean ± SEM) than they were in undisturbed stands of salt grass growing on salt flats or dunes (19.2 ± 6.4; t = 2.88, $P < 0.05$; Fig. 1). Female planthoppers were also more macropterous in disturbed habitats (12.5 ± 12.5%) than those inhabiting undisturbed stands of salt grass (0.4 ± 0.3%; t = 2.66, $P < 0.05$; Fig. 2). The pattern of elevated macroptery in disturbed habitats prevailed in both sexes even though males were significantly more macropterous (26.9 ± 7.6%) than females (2.0 ± 1.7%) in all habitats sampled (t = 3.60, $P < 0.01$) (compare Figs. 1 and 2).

Incidence of dispersal capability in island and mainland taxa: habitat isolation vs persistence

Together, three lines of evidence suggest that the incidence of macroptery in British Virgin Island populations of *T. venilia* is not significantly lower that exhibited by mainland delphacids. First, the observed levels of macroptery in British Virgin Island populations of *T. venilia* (1.7 ± 1.2%, mean ± SEM) were not significantly lower than predicted values (5.5 ± 0.03%) obtained by substituting habitat persistence values for the British Virgin Island populations into a model based entirely on mainland delphacid species (paired t = -2.35, NS; Fig. 3). Had the error associated with the full regression model been taken into account in the analysis (Fig. 3) however, the one-tailed P value (0.072) would most certainly be larger. Moreover, given an average difference of 3.85% macroptery between expected (mainland) and observed (island) data, a power analysis on arcsin-transformed data revealed that the likelihood of detecting a difference between the two samples, if indeed it existed, was 43%. Thus, the hint of a difference in macroptery between British Virgin Island and mainland populations does not even verge on significance.

Second, the average incidence of macroptery in British Virgin Island populations of *T. venilia* (1.7 ± 1.2%) did not differ from that for six species of mainland delphacids (1.4 ± 1.1%) existing in similarly persistent grassland habitats ($t = 0.16$, NS). Third, macroptery in British Virgin Island populations of *T. venilia* (1.7 ± 1.2%) did not differ from that observed in populations of seven mainland species of delphacids occupying the same type of low-profile grassland habitats (marshes and dunes) along the shore of the Gulf of Mexico (3.4 ± 1.8%) ($t = -0.59$, NS).

Together, these data suggest that with habitat persistence controlled, habitat isolation at the scale of oceanic islands contributes little to explaining the dispersal strategy of *T. venilia* in the British Virgin Islands. Be it an island or mainland population, habitat persistence appears to be the most crucial factor shaping the dispersal strategy of female delphacid planthoppers (Fig. 3).

Habitat structure and the incidence of macroptery in planthopper populations

On average, stands of salt grass were significantly smaller on dunes (48 ± 9 m^2, mean ± SEM, $n = 5$) than on salt flats and around the margin of salt ponds (1595 ± 471 m^2, $n = 11$) ($t = 2.52$, $P < 0.05$). Moreover, culms of salt grass grew significantly denser

(3753 ± 352 culms m^{-2} vs 2232 ± 364) and longer (49 ± 2 cm vs 33 ± 3) on salt flats than on dunes ($t_{culm\ density} = 3.0$, $P < 0.01$; $t_{culm\ length} = 4.77$, $P < 0.001$). Also, the above-ground biomass (wet-weight) of salt grass was significantly greater for salt flat (2755 ± 221 g m^{-2}) than for dune vegetation (761 ± 228 g m^{-2}; $t = 6.28$, $P < 0.001$).

Males of *T. venilia* were significantly more macropterous in populations occupying dune vegetation (37.6 ± 9.8%) than they were in populations occurring in stands of salt grass growing on intertidal flats and around salt ponds (7.6 ± 5.6%) ($t = 3.28$, $P < 0.01$). This habitat-related difference in male macroptery accounted for most of the disparity in macroptery between the sexes of *T. venilia* throughout the British Virgin Islands (compare Figs. 1 and 2). Moreover, there was a significant positive relationship between macroptery in males (%) and population density in both dune [macroptery = - 24.12 + 2.64(density), $R^2 = 0.93$, $P < 0.01$] and salt-flat [macroptery = - 0.94 + 0.14(density), $R^2 = 0.54$, $P < 0.01$] habitats (Fig. 4). However, the slope of the relationship between macroptery and density was significantly steeper for males in dune-inhabiting populations than for males occupying salt flats (ANCOVA, $F = 96.5$, $P < 0.001$), further indicating a habitat effect on dispersal capability.

In contrast, there was no difference between the incidence of macroptery in female planthoppers in dune (0%) and salt-flat (0.6 ± 0.5%) ($t = 1.11$, NS) populations (Fig. 2). Also, the incidence of macroptery in female (0.6 ± 0.5%) and male (7.6 ± 5.6%) planthoppers did not differ in the salt flat habitat ($t = 1.45$, NS). In the dune habitat, however, males were significantly more macropterous (37.6 ± 9.8%) than females (0% ± 0) ($t = 5.95$, $P < 0.01$). Thus, habitat structure appears to have a selective influence on the dispersal strategy only of male planthoppers. Macroptery was significantly density dependent for females inhabiting the salt flat-pond edge habitat (macroptery = - 0.85 + 0.57(density), $R^2 = 0.39$, $P < 0.05$; Fig. 4), a slope that did not differ from that for males in this habitat (ANCOVA, $F = 3.24$, NS). Density-dependent macroptery was not detected for females occurring in the dune habitat (0% macroptery at all densities), probably because the high densities that occurred occasionally in salt flat habitats (>35 planthoppers per m^2) were never observed in dune vegetation (Fig. 4).

Discussion

Both sexes of *T. venilia* exhibit elevated macroptery in disturbed habitats (managed lawns) and reduced flight capability in natural, more persistent habitats (salt flats, salt ponds, and dunes) throughout the British Virgin Islands, a pattern that has been reported for many insects including other delphacid species (Roff 1990; Denno *et al.*, 1991; Novotný, 1994). Dispersal capability is apparently retained to track the frequent changes in resource quality and abundance that occur in disturbed and temporary habitats (Southwood, 1977; Denno *et al.*, 1991, 1996). Although the incidence of macroptery in populations of *T. venilia* is generally low in undisturbed habitats (<30% on average), the dispersal strategies of males and females are clearly different (Figs. 1 and 2). Males exhibit higher levels of macroptery (26.9 ± 7.6%) than do females (2.0 ± 1.7%), but this difference in dispersal ability is habitat dependent, with males significantly more macropterous than females in dune habitats (37.6 vs 0%) but not in salt flat-pond edge habitats (7.6 vs 0.6%). For both sexes, the occurrence of the macropterous form in field populations is positively density dependent

(Fig. 4). Thus, fluctuations in population density in the field, coupled with density-dependent macroptery, probably explain much of the within-habitat variation in the incidence of dispersal (Figs. 1 and 2). The mechanism underlying the disparity in macroptery between the sexes of *T. venilia* is probably a genetically-based difference in the induction of macropters under crowded conditions, a well documented occurrence for other species of delphacids (Kisimoto, 1965; Denno *et al.*, 1991, 1994).

The selective forces underlying the discrepant dispersal strategies of the sexes of this planthopper probably involve several habitat-related factors. Of the major habitat-associated factors thought to influence the dispersal strategies of insects, namely persistence, structure, and isolation (Roff, 1990; Denno *et al.*, 1991, 1996, in press), only habitat persistence and structure showed an effect on island populations of *T. venilia*. There was little evidence that the low incidence of dispersal in several island populations (1.7 ± 1.2% in females) was attributable to the effects of isolation on oceanic islands (Fig. 2). Three analyses revealed that the low level of macroptery in several British Virgin Island populations of *T. venilia* was no different than that observed in mainland delphacid species existing in habitats of similar duration. Rather, the persistence of the natural salt grass habitats throughout the British Virgin Islands probably best explains the evolution of flight reduction in this island-inhabiting delphacid (Fig. 3). That flight capability is retained under certain conditions on oceanic islands is evidenced by the high incidence of macroptery (25%) in females of *T. venilia* exploiting the disturbed lawn habitats on Anegada (Fig. 2).

It might be argued that the assessments of habitat age, and thus persistence for salt grass habitats in the British Virgin Islands (~ 450 possible planthopper generations) are underestimates. This is probably the case. Nonetheless, two lines of evidence suggest that brachyptery increases very rapidly in populations of wing-dimorphic planthoppers given the appropriate circumstances. First, with an increase in habitat persistence, dispersal capability (% macroptery) in field populations declines sharply, suggesting that when the demand for flight is relaxed, flight capability diminishes rapidly (Denno *et al.*, 1991; Fig. 3). Planthoppers existing in habitats lasting only 30 generations are nearly as brachypterous (> 90%) as species occupying habitats a thousand times more persistent. Second, macropterous and brachypterous lines of the planthopper *Nilaparvata lugens* Stål can be established after only 30 generations of selection in the laboratory on an initial population consisting of an equal mix of both wing forms (Marooka & Tojo, 1992). Thus, both field data on habitat persistence (Denno *et al.*, 1991, 1996) and selection experiments in the laboratory (Marooka *et al.*, 1988; Marooka & Tojo, 1992) suggest that dispersal characters respond very rapidly to selection over the course of ecological time. Therefore, the habitats of *T. venilia*, even though possibly underestimated in age, have probably persisted long enough for the dispersal strategy of this planthopper to stabilise. The reduction in dispersal capability of planthoppers in persistent habitats is probably attributable to the reproductive advantage of brachypterous adults (Denno *et al.*, 1989; Zera and Denno. 1997; Langellotto *et al.*, in press).

Other studies have also shown that habitat persistence rather than oceanic isolation underlies the dispersal strategy of other planthopper species and insects. For example, the incidence of macroptery in Hawaiian island delphacids is low (1.26 ± 0.25%), not different from the mainland average (1.50 ± 1.15%) (Denno *et al.*, in press), and very similar to the level observed in British Virgin Island populations of *T. venilia* (1.7 ± 1.2%). Notably, habitat persistence and dimensionality were controlled in the Hawaiian island-mainland comparison, whereby the incidence of macroptery was compared only between taxa inhabiting persistent, low-profile vegetation. Similarly, in an extensive analysis of the effects of habitat isolation on the dispersal strategies of a wide diversity of insect taxa (Orthoptera, Hemiptera, Thysanoptera, Psocoptera, Neuroptera, Coleoptera, and Diptera), Roff (1990) showed that oceanic islands do not have higher-than-expected incidences of flightlessness than mainland faunas.

Habitat isolation may contribute to reduced dispersal capability via migrant loss only in the very smallest of habitat patches (Roff, 1990). The highly fragmented yet persistent salt marshes in southern California may provide an example where isolation contributes to the evolution of flightlessness in delphacids. In these habitats, dispersal is virtually absent in populations of *Prokelisia dolus* (0.16 ± 0.36% macroptery; Denno *et al.*, 1996), a level below that (5-8%) predicted by habitat persistence alone (see Denno *et al.*, 1991). By contrast, males of *T. venilia* were much more macropterous (32.2 ± 11.4%) in the small, isolated patches of salt grass on dunes than they were in the large expanses of salt grass associated with salt flats (5.7 ± 3.3%). Although this pattern is attributed here to the constraints associated with mate finding, it illustrates that flight capability can be retained when necessary even in the smallest and most isolated habitats. Therefore, it is argued that at the scale of oceanic islands, and perhaps also at much smaller spatial scales, isolation *per se* plays little role in the dispersal strategies of planthoppers.

Habitat type (dune vs salt flat-pond edge vegetation) influenced the incidence of macroptery in *T. venilia*, but only in the male sex (Fig. 4). Macroptery in males was almost five times higher in dune habitats (38%) than in salt flat and salt pond vegetation (8%). Higher levels of macroptery in male planthoppers than in females are symptomatic of the difficulties associated with mate location, because only the male sex searches actively for mates (Denno *et al.*, 1991, in press; Claridge and de Vrijer, 1994; Denno, 1994a; Langellotto, 1997). Variation in salt-grass structure, coupled with a generally low population density (25 ± 5 adults per m^2; Table 1), probably underlies this habitat-related difference in macroptery in males of *T. venilia*. The sparse structure of dune vegetation apparently favours the retention of wings because macropters are better able to negotiate such habitats and locate calling females, an effect that has been shown for other delphacid species (Langellotto, 1997). Brachypterous males neither sense nor locate calling females efficiently in heterogeneous vegetation. The situation is reversed in contiguous vegetation, such as the dense stands of salt grass on intertidal flats, a situation where brachypterous males of other planthopper species have been shown to be more successful in locating males and outcompeting macropters for access to them (Langellotto, 1997).

Macroptery was density dependent in the males of *T. venilia*, but the slope of the relationship was significantly steeper in populations occupying dune vegetation than in salt-flat/pond-margin vegetation, further corroborating the effect of habitat type on the incidence of dispersal capability (Fig. 4). A difference in the slope of this relationship is consistent with the view that there is a genetic difference between dune and salt flat-inhabiting populations of *T. venilia*, whereby the density that triggers the production of macropters in males differs between the two populations (Denno *et al.*, 1991, 1996). An independent assessment using Amplified Fragment-Length Polymorphism markers also found a significant genetic difference between the dune and salt-pond populations of *T. venilia* on Guana Island (D.J. Hawthorne, unpublished). This is a remarkable finding considering that these two disjunct populations are separated by only 500 m, albeit by an upland ridge. Other marsh-inhabiting planthopper species with similarly low incidences of macroptery (< 20%) show no evidence for the genetic subdivision of populations at such a small spatial scale, although their habitats are relatively contiguous (Peterson & Denno, 1997, 1998). Apparently, the homogenising effects of gene flow between these two populations on Guana Island are offset by the strength of habitat-related differences in selection for the enhancement of flight capability in one habitat and its reduction in the other. The strength of the opposing forces, however, may be less than it appears because gene flow between populations of *T. venilia* depends not only on the fraction of macropters in the population but also on the flight capability of the individuals. One study with gerrids suggests that the flight capability of the macropterous morph decreases as the proportion of macropters declines in the population (Fairbairn & Desranleau, 1987). Thus, for a planthopper species that averages < 30% macroptery, males may be relatively weak fliers, simply flitting around within the habitat in search of females, a behaviour that may diminish frequent gene flow between disjunct populations.

It has been argued that isolation may promote macroptery because only winged adults can colonize small, isolated, and extinction-prone patches (see Travis & Dytham, 1999). If this were the case for the dune-inhabiting populations of *T. venilia*, one should expect to see elevated levels of macroptery in both sexes in such habitats because planthoppers mate only after they have dispersed to new habitats (reviewed in Denno & Roderick, 1990). In the three years of sampling dune vegetation, not one macropterous female was found, even though macropterous males were relatively abundant (Table 1). Moreover, on Guana Island, the extensive Salt Pond population would be the closest source of colonists for the dune-inhabiting population on North Beach. Yet, it is these two populations that show evidence for genetic divergence. Macropterous males in the dune population are more genetically related to their brachypterous counterparts in the dune population than they are to brachypters in the salt-pond population (D.J. Hawthorne, unpublished). Together, these data do not suggest that macroptery in dune populations results from selective colonization by macropters. Rather, within-habitat selective pressures associated with mate finding appear to be a more parsimonious explanation for elevated macroptery in males.

The lability of dispersal characters in delphacid planthoppers, coupled with their wing-dimorphism, allows one to tease apart the selective effects of habitat persistence and structure that interact to shape the dispersal strategies of insects. For planthoppers exploiting low-profile host plants, there is an inverse relationship between habitat persistence and dispersal capability (% macroptery), with volant species predominating in temporary habitats and flightless taxa occurring primarily in long-lived habitats (Denno *et al.*, 1991). Habitat dimensionality and macroptery are related positively, with flight reduction evident in species exploiting low-profile vegetation, and wing retention characteristic of arboreal species (Denno, 1994b). Habitat persistence and dimensionality interact such that flight is retained in species exploiting arboreal habitats, even though habitats are persistent (Denno *et al.*, in press). Thus, the effect of habitat persistence on the incidence of flight capability is realised only for species occupying low-profile habitats such as *T. venilia*.

In addition to the three-dimensional nature of the habitat, finer-scale differences in habitat structure also affect the dispersal strategies of planthoppers, particularly for males. It is argued here that the difference in the structure of salt grass between dune and salt-flat habitats influences the searching efficiency of the male wing forms of *T. venilia*, and hence their mating success. Macropterous males of other delphacids are far more effective at locating females in sparse vegetation and under low-density conditions than are brachypters (Langellotto, 1997). The enhanced incidence of macroptery in males of *T. venilia* occupying sparsely vegetated dune habitats probably also reflects the advantage of flight in mate location.

Historically, coastal strand, marsh, and dune communities have been targeted as habitats where isolation may promote the evolution of flightlessness in insects (see Roff, 1990; Wagner & Liebherr, 1992). Recent studies in these same habitats have played a pivotal role in both challenging the significance of isolation and in demonstrating the importance of habitat persistence and structure in the evolution of insect dispersal strategies (Denno *et al.*, 1991, 1996, in press).

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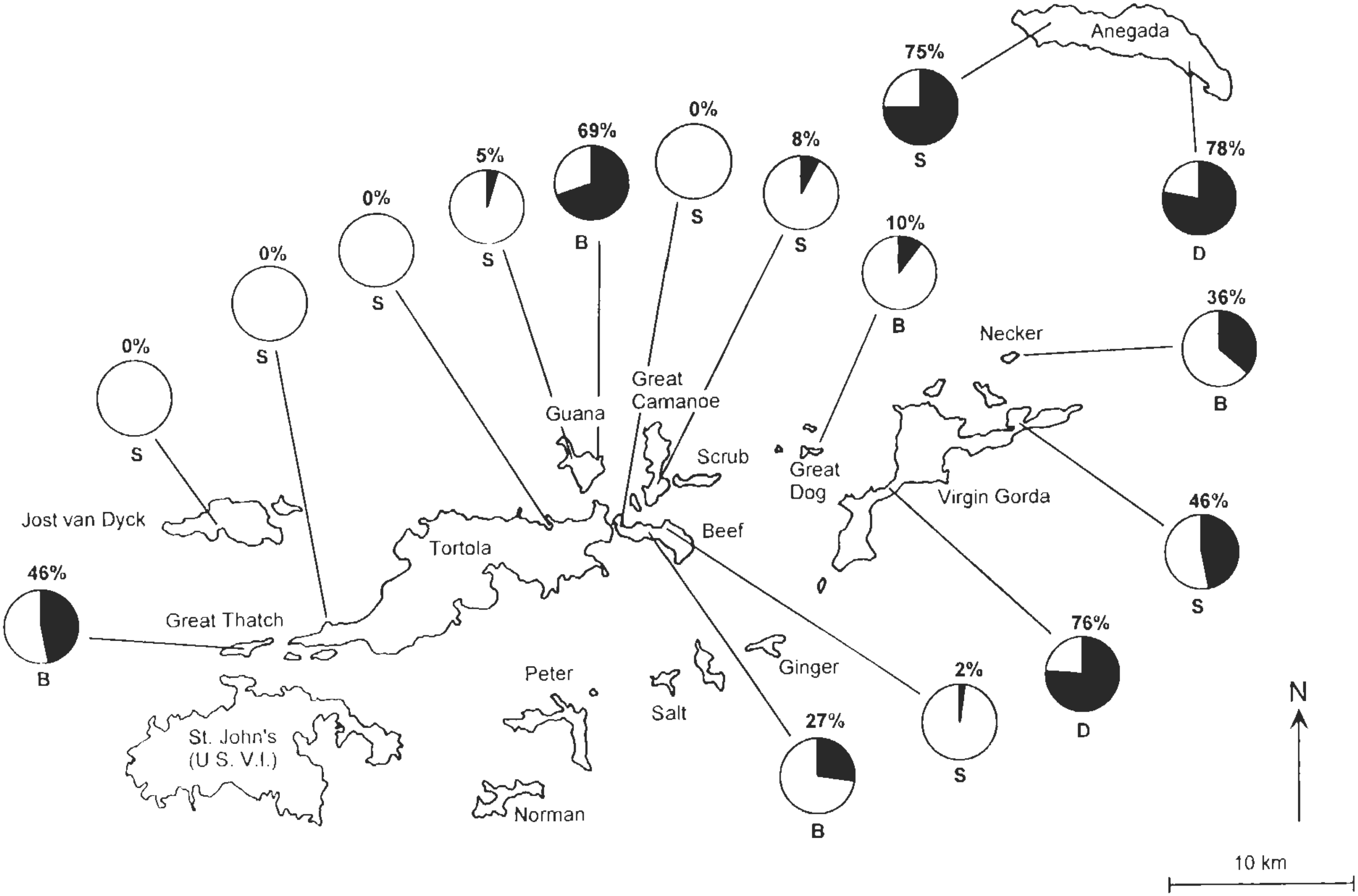
Figure Descriptions

Fig. 1. Incidence of dispersal (% macroptery in males) in populations of the planthopper *Toya venilia* inhabiting salt flat-pond edge habitats (S), beach-dune habitats (B), and disturbed habitats (D) throughout the British Virgin Islands. The black portion of each pie diagram reflects the percentage of macropters in each population.

Fig. 2. Incidence of dispersal (% macroptery in females) in populations of the planthopper *Toya venilia* inhabiting salt flat-pond edge habitats (S), beach-dune habitats (B), and disturbed habitats (D) throughout the British Virgin Islands. The black portion of each pie diagram reflects the percentage of macropters in each population.

Fig. 3. Relationship between macroptery (%) and habitat persistence (the maximum number of generations attainable) for the females of 41 field populations (35 species) of mainland-inhabiting species of delphacid planthoppers (○) (data from Denno *et al.* 1991) and 3 British Virgin Islands populations (Beef, Guana, and Great Camanoe) of the delphacid *Toya venilia* (•). The observed levels of macroptery in island populations of *T. venilia* were not significantly different from those expected using the mainland model (*macroptery* (%) = -5.450 + 1/(*habitat persistence*$^{0.045}$ - 0.095; paired t-test, NS) (model adapted from Denno *et al.*, 1991). Thus, with habitat persistence controlled, the incidence of dispersal in field populations was the same for British Virgin Island and mainland taxa of planthoppers.

Fig. 4. Relationship between the incidence of macroptery (%) in males and females of the planthopper *Toya venilia* and population density (number per m^2) in two salt-grass habitats (dense stands of *Sporobolus virginicus* growing on salt flats or along edges of salt ponds and sparse stands inhabiting beach dunes) in the British Virgin Islands. For males, macroptery was significantly density dependent in both habitats, but the slopes of the relationship differed (ANCOVA, $F = 96.5$, $P < 0.001$). Macroptery was significantly density dependent for females inhabiting the salt flat-pond edge habitat (macroptery = - 0.85 + 0.57(density), $R^2 = 0.39$, $P < 0.05$), but density-dependent macroptery was not detected for females occurring in the dune habitat.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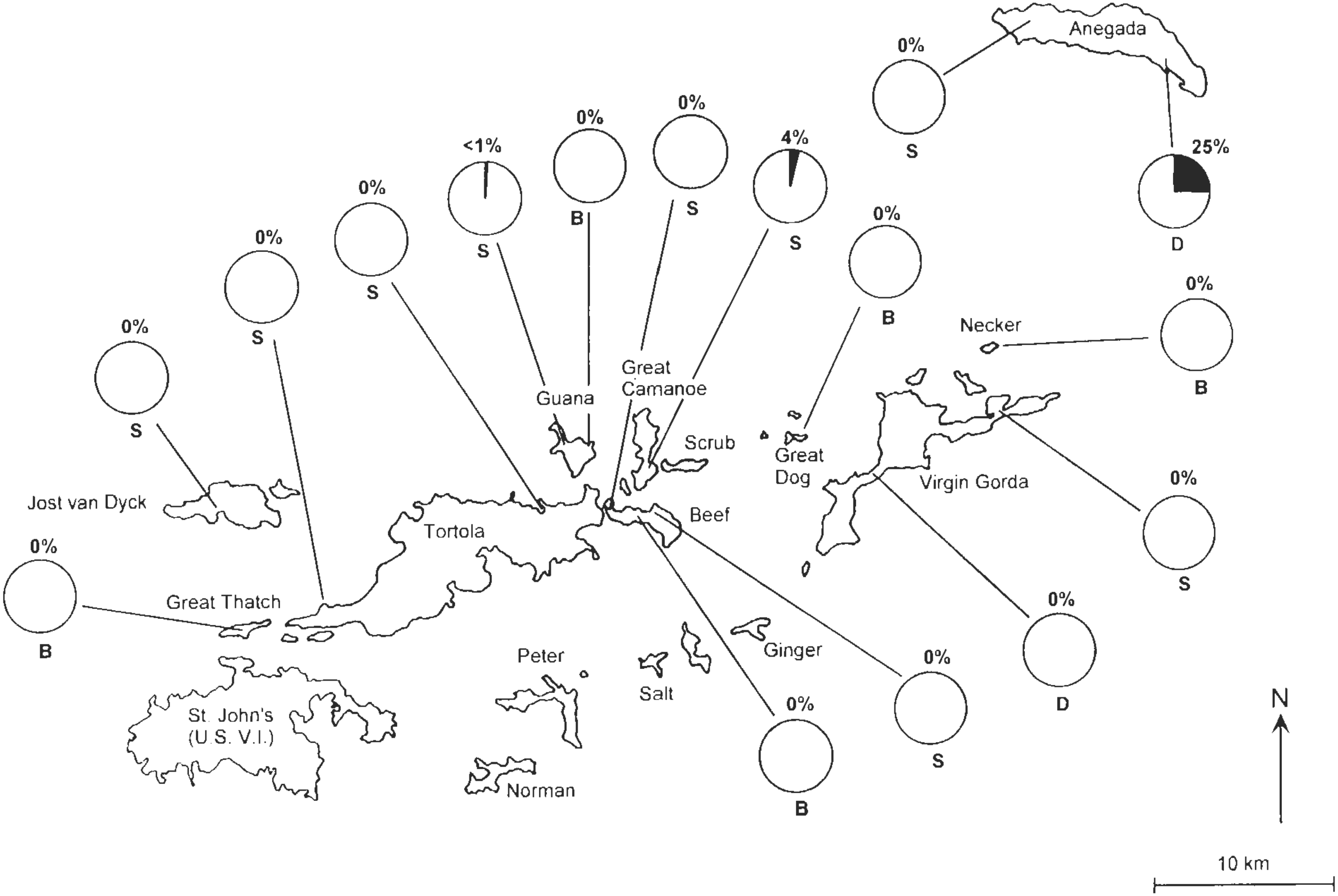
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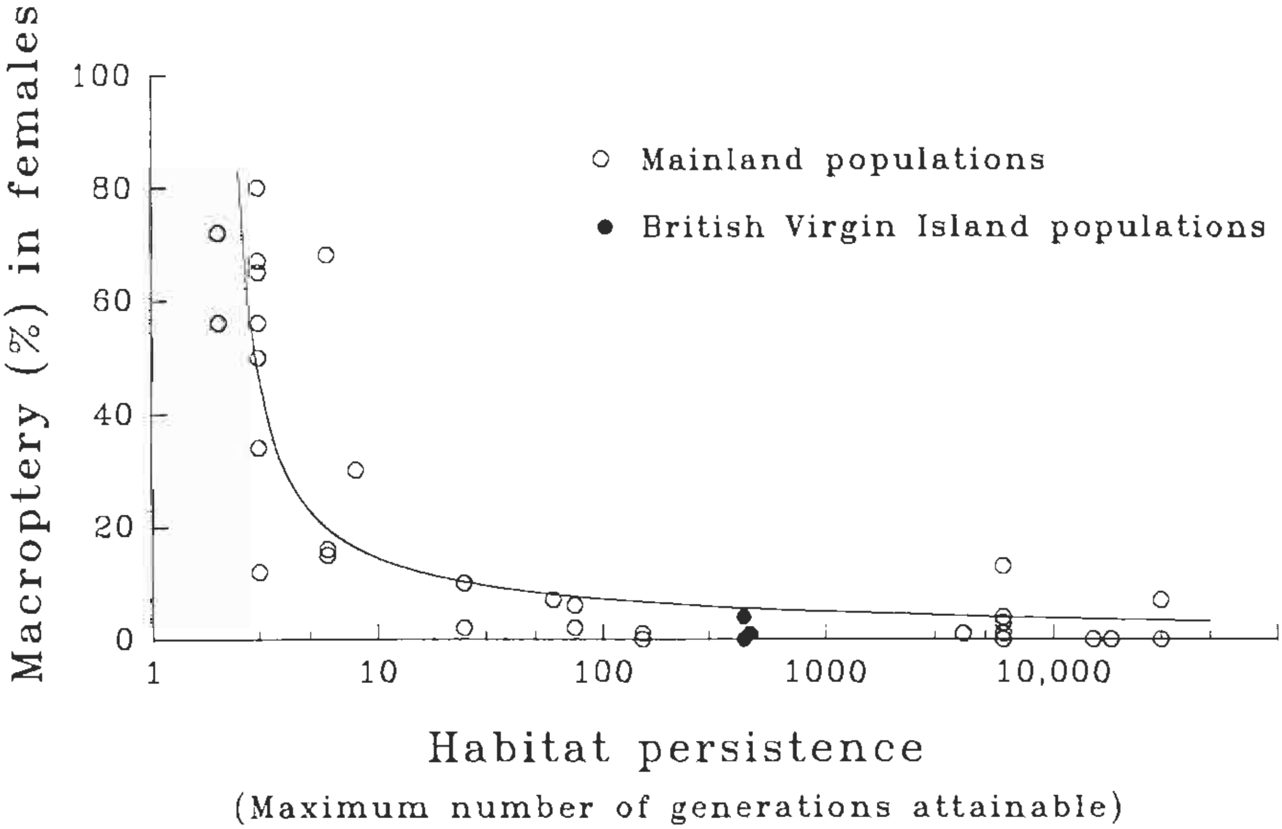
Macroptery (%) in females
100
80
60
40
20
0
1
10
100
1000
10,000
○ Mainland populations
● British Virgin Island populations
Habitat persistence
(Maximum number of generations attainable)

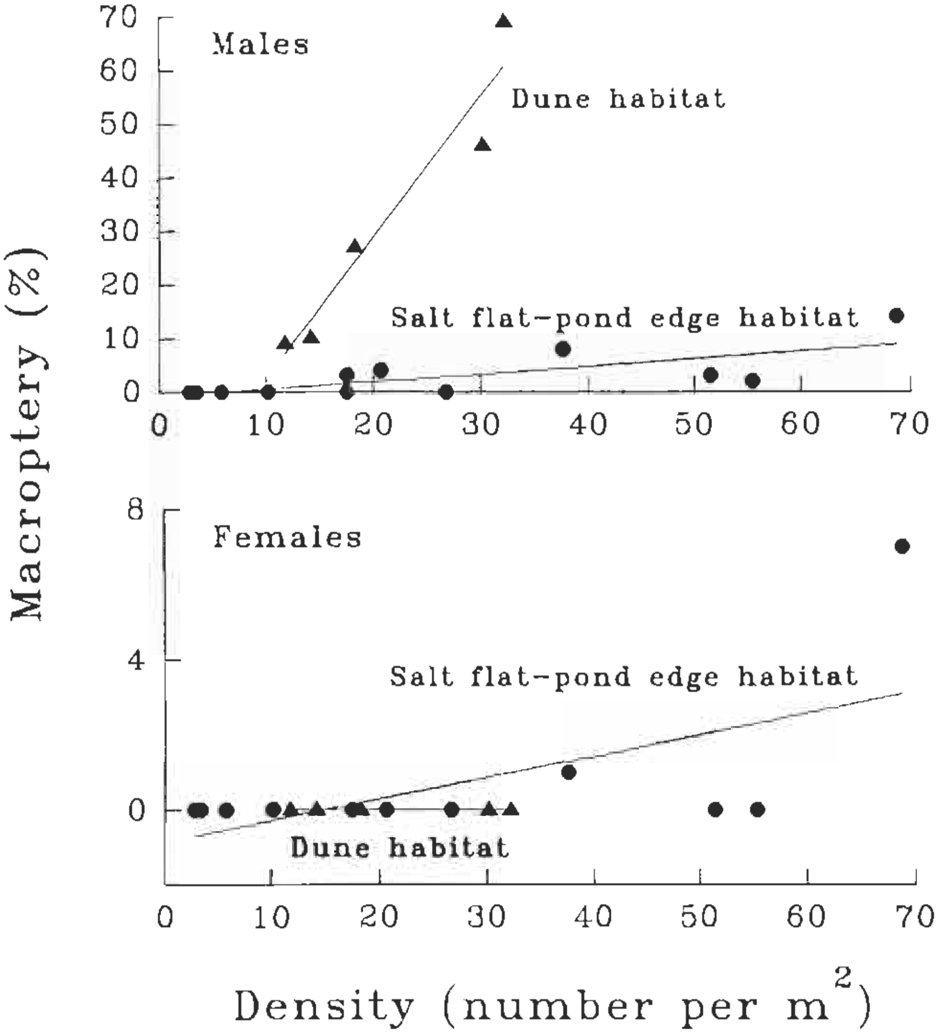
Macroptery (%)
Males
Dune habitat
Salt flat-pond edge habitat
70
60
50
40
30
20
10
0
0
10
20
30
40
50
60
70
Females
Salt flat-pond edge habitat
Dune habitat
8
4
0
0
10
20
30
40
50
60
70
Density (number per m^2)

Table 1. Habitats, density, and macroptery of populations of the planthopper *Toya venilia* on salt grass *Sporobolis virginicus* throughout the British Virgin Islands. The location (island and sample site) and date of samples are shown as is the sample size (total number of planthoppers taken at each site) and number of samples (sweeps or D-vac placements) per site. Populations are sorted by habitat, either salt flat/salt pond, beach/dune, or disturbed.

Island, sample site, date	**Habitat**	**Density (number per)**		**Macroptery (%)**			**Sample size**	**Sample no.**
	(area, m^2)	**20 sweeps**	**m^2**	**Males**	**Females**	**Overall**	**total (male, female)**	**and type**
Salt-flat and salt-pond populations								
Anegada, Flamingo Pond, 19/10/97	Salt flat (5000+)			75	0	50	6 (4, 2)	D-vac
Beef, Bridge, 16/10/96	Salt flat (500)	3.0	2.8	0	0	0	15 (3, 12)	2, 50 sweep
Beef, Airport, 16/10/96	Salt flat (3000)	3.6	3.4	0	0	0	27 (6, 21)	3, 50 sweep
Beef, Airport, 22/10/98	Salt flat (3000)	28.7	26.7	0	0	0	86 (42, 44)	3, 20 sweep
Beef, E Trellis Bay, 17/10/98	Salt flat (3000)	59.7	55.5	2	0	1	179 (93, 86)	3, 20 sweep
Great Camanoe, Lee Bay, 17/10/96	Pond edge (800)	74.0	68.8	14	7	7	185 (35, 150)	1, 50 sweep
Great Camanoe, Lee Bay, 14/10/98	Pond edge (800)	55.3	51.5	3	0	1	166 (38, 128)	3, 20 sweep
Guana, Salt Pond, 15/10/96	Pond edge (2000)	40.4	37.6	8	1	2	202 (38, 164)	5, 20 sweep
Guana, Salt Pond, 14/10/98	Pond edge (2000)	22.2	20.7	4	0	1	111 (24, 87)	5, 20 sweep
Guana, Salt Pond, 23/10/98	Pond edge (2000)	-	17.5	0	0	0	66 (32, 34)	3, 40 D-vac
Guana, Salt Pond, 23/10/98	Pond edge (2000)	18.8	17.5	3	0	1	94 (26, 68)	5, 20 sweep
Jost Van Dyke, S side 18/10/98	Pond edge (600)	11.0	10.2	0	0	0	22 (9, 13)	2, 20 sweep
Salt, N Side, 15/10/98	Pond edge (200)	-	-	-	-	-	2 (nymphs)	D-vac
Tortola, Belmont Pond, 23/10/98	Pond edge (150)	-	5.8	0	0	0	22 (9, 13)	3, 40 D-vac
Tortola, Josiah Bay, 16/10/98	Salt flat (300)	-	-	0	0	0	40 (9, 31)	D-vac
Virgin Gorda, Biras, 23/10/97	Salt flat (2000)	-	-	46	0	40	15 (13, 8)	D-vac

Beach and dune populations								
Beef, W Trellis Bay, 17/10/98	Beach/dune (60)	19.7	18.3	27	0	8	59 (18, 41)	3, 20 sweep
Great Dog, S Side, 15/10/98	Beach/dune (50)	-	14.2	10	0	7	15 (10, 5)	1, 40 D-vac
Great Thatch, N Side, 18/10/98	Beach/dune (30)	-	30.2	46	0	32	19 (13, 6)	1, 20 D-vac
Guana, North Beach, 21/10/98	Beach/bank (25)	-	32.5	69	0	44	57 (36, 21)	2, 40 D-vac
Necker, N Side, 24/10/97	Beach/dune (75)	-	-	48	0	30	43 (25, 18)	D-vac
Necker, N Side, 19/10/98	Beach/dune (75)	12.6	11.8	9	0	3	38 (11, 27)	3, 20 sweep
Disturbed habitat populations								
Anegada, Settlement, 20/10/97	Lawn (300)	-	-	78	25	62	13 (9, 4)	D-vac
Virgin Gorda, Pond Bay, 22/10/97	Cattle pond (300)	-	-	76	0	49	39 (25, 14)	D-vac

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Nest Growth and Survivorship in Three Species of Neotropical *Nasutitermes* (Isoptera: Termitidae)

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Thorne and Haverty: Growth and survival of *Nasutitermes* nests

ABSTRACT Long-term growth and survivorship of individual arboreal nests were studied in three species of Neotropical termites in the genus *Nasutitermes*. Of the 29 *N. corniger* and seven *N. ephratae* nests monitored in an area of young second-growth in Panama, 12 (41%) *N. corniger* and four (57%) *N. ephratae* nests remained active throughout the 9 to 11 month study. There was no significant difference in survivorship between small and large nests of either species. In surviving *N. corniger* nests with a single queen, the net increase in volume was highly correlated ($r = 0.87$, $n = 9$) with queen wet weight. There was a marked seasonality to nest expansion in both *N. corniger* and *N. ephratae*, with growth occurring almost exclusively during the wet season. Seventeen *N. acajutlae* nests were monitored for 4 to 9 years on Guana Island, British Virgin Islands. Four of the 17 (23.5%) *N. acajutlae* nests survived the study period, and two more abandoned their original nest and relocated. Within this limited sample of colonies, *N. acajutlae* nests that were large (> 150,000 cm^3) at the beginning of the study had a higher probability of survival than did small (< 100,000 cm^3) nests. Nest budding, relocation, and resprouting are mechanisms that *Nasutitermes* may use to create a new nest for all or a portion of an established colony. The ontogeny of incipient *Nasutitermes* colonies is discussed as a sequence in which a young colony remains cryptic within wood, building its population size to a point where the colony can maintain and defend a nest. Early in a wet season, termites then venture from within wood to build and occupy a small arboreal nest.

KEY WORDS *Nasutitermes acajutlae, Nasutitermes corniger, Nasutitermes ephratae*, termite colony survivorship, termite colony longevity, arboreal nests

THE TROPICOPOLITAN TERMITE genus *Nasutitermes* (Termitidae: Nasutitermitinae) is the most speciose of all isopteran genera, containing 74 described species from the Neotropics alone (Constantino 1998). Unlike most termites, many species of *Nasutitermes* build arboreal carton nests composed of masticated wood and occasionally other materials such as sand cemented together with salivary and fecal fluids (Light 1933; Emerson 1938; Thorne et al. 1996a). The majority of nest-building termites construct mounds on the ground, but nesting in trees has enabled species of *Nasutitermes* and several other genera to colonize and exploit a new habitat (Emerson 1938; Noirot 1970).

Nasutitermes nests are built on the trunk or on or around a branch of a host tree. Typically, the termites build a network of trails or "galleries" from the nest to other regions of the tree, down the trunk (sometimes within the trunk), and/or along the underside of branches to connect the nest with other food sources in the area. *Nasutitermes* nests reach enormous sizes in some species, occasionally exceeding 2 m in height (e.g., *N. acajutlae* Collins et al. 1997; Haverty et al. 1997; *N. rippertii* (Rambur) Scheffrahn, personal communication). In all species of arboreal *Nasutitermes*, nests are built with reinforced, dense zones of carton that act to protect at least the queen cell from vertebrate predators, damage from a falling branch, or toppling of the nest due to a storm or decay of its host tree (e.g., Hubbard 1877; Andrews 1911; Emerson 1938; Thorne 1980; Lubin and Montgomery 1981). These termite nests thus represent the focal reproductive location for the colony, the hub of its foraging network, and a substantial investment of time and energy in construction and maintenance.

In this paper we report on long-term studies of arboreal nest growth and survivorship in three species of Neotropical *Nasutitermes*. "Nest growth" refers to the expansion of their carton nest by the termites housed within; "nest survivorship" means survivorship of the termite colony, or portion of the colony, active within the nest. Twenty nine nests of *N. corniger* (Motschulsky) and seven nests of *N. ephratae* (Holmgren) were followed for 9 to 11 months in Panama, and 17 nests of *N. acajutlae* (Holmgren) were monitored for 4 to 9 years on Guana Island, British Virgin Islands. We tested the null hypothesis that colonies in large and small nests have an equal probability of survival, even though larger nests have a greater volume and physical structure to protect them from injury or disturbance, and they have already survived through the early age classes. The processes of incipient nest formation and relocation of established nests are also discussed.

Materials and Methods

Study Area. All of the individual *N. corniger* (N = 29) and *N. ephratae* (n = 7) nests monitored in Panama were located in an area of young second-growth that had been burned 3 to 6 years previously, with only small trees left standing, near Frijoles, a settlement on the south shore of the Panama Canal, Panama (9°09' N, 79°51'W) (Thorne 1983). Every arboreal nest within that region of second-growth was included in the study. All nests were located within a radius of 0.5 km. The *N. acajutlae* nests (N = 17) were on or near the flats of White Bay Beach of Guana Island, a small (340 ha; highest peak 246 m), but biologically diverse, reserve in the British Virgin Islands (Lazell 1996). The majority of *N. acajutlae* nests on the White Bay Beach flats were part of the study, however not every nest in the area was included because some were too high in the canopy to measure accurately. In the Panama site by agreement with the landowner, and on Guana Island because it is managed as a conservation area, all nests were left undisturbed by humans during the course of the study.

Nest Measurements. Individual nests included in this study were all accessible by standing or climbing. Measurements of the hemiaxes (height, width, and depth) were taken with a measuring tape and recorded on each monitoring date. The position of these measurements was generally at the maximum dimension of height, width, or depth, although if the nest had an exaggerated protrusion that compromised the typically ellipsoidal shape (irregularities most likely to occur in *N. corniger*), account was taken and the recorded measurement was the "best fit" to a more regular ellipsoid. Nest volumes (cm^3) were estimated as the volume of an ellipsoid ($4/3\ \pi\ a\ b\ c$, where a, b, and c are lengths of the hemiaxes) (Thorne 1980, 1983, 1984, 1985; Levings and Adams 1984; Leponce et al. 1995). [Note that Weigert (1970) and Weigert and Coleman (1970) used nest length x width x height as an index of arboreal *Nasutitermes* nest volume, and Clarke (1993) used the maximum perimeter of arboreal *Nasutitermes* as a volumetric correlate]. In Panama, portions of all host tree trunks or branches encased by the nest were measured. Their volumes were calculated as cylinders, and subtracted from the total nest volume measurement to yield the volume of the nest carton. On Guana Island the *N. acajutlae* nests were built on substantially larger trees (often on mature sea grape, *Coccoloba uvifera*; Polygonaceae), and were typically perched on the trunk, on a branch, or at the junction of the trunk and a branch. Wood from the host tree did penetrate nests, but for practical reasons the volume of enclosed wood could not be measured precisely. Because these *N. acajutlae* nests were much larger than the Panama series in total and in proportion to wood encased by the nest, host tree wood was not measured or subtracted from the calculation of nest volume.

In Panama, nest measurements were taken during the months of May to July, 1979, with additional nests added to the study group throughout that time as different areas of the site were explored (two additional nests were added to the study in October 1979). A total of 29 *N. corniger* nests were included in the study, along with seven *N. ephratae* nests within the same site. Further measurements on the Panama nests were taken October 1979 to January 1980, with the final measurement of surviving nests made on 1 April 1980.

A total of 17 nests of *N. acajutlae* were measured on Guana Island. One was first measured in July 1989, and 11 additional nests were first measured in October 1992. Subsequent measurements were made in October of 1993, 1994, and 1998. An additional nest added to the study in 1993 and four more nests were added in 1994.

At the same time that individual nests were measured, photographs of each nest were taken from a specific position and orientation and repeated at each monitoring interval to record the nest profile(s). Scale rulers included in the photos could be used subsequently to check measurements, and photos could be compared to document nest growth.

Nest Dissections. Weights of queens in *N. corniger* colonies were determined following complete dissection of the nest and removal of the queen from the royal cell. Entire carton nests were excised from the host trees (wood encompassed by the nest included in the sample), placed in thick plastic bags, and transported to the Smithsonian Tropical Research Institute's laboratory on Barro Colorado Island, Republic of Panama. Colonies were refrigerated for 24 – 48 h to inactivate the termites. Nests were then sequentially shaved and shaken over a collection tray, allowing termites to fall from the exposed galleries. Upon location of the royal cell, the sides were scraped carefully to open the royal chamber and collect the queen(s).

Data Analysis. Nest volumes were calculated for each observation and plotted over the entire length of each study to visualize the variation in growth rate for the nests of all three species of *Nasutitermes*. Initial size of nests of *N corniger* and *N. acajutlae* were stratified into small (< 3,000 cm^3 and < 100,000 cm^3, respectively) and large (>6,000 cm^3 and > 150,000 cm^3, respectively) size categories. Survivorship of small and large nests was compared with logistical regression (SAS 1998) and contingency table analysis (Steele and Torre 1980). Chi-square values were tested at the $\alpha = 0.05$ level.

Newly Constructed Nests. Observations on incipient nest formation and on nest relocation were made during the course of the study in both sites. Recognition of these events was possible because of long-term familiarity with established nests, making new nests that appeared during the course of the research available for investigation.

Voucher Specimens. Voucher specimens are deposited in the USNM collection of the Smithsonian Institution.

Results

Nest growth and survivorship. Of the 29 *N. corniger* nests, 12 (41%) survived the 9 to 11-month study period. Of those, only two (17% of the survivors) did not grow at all in external dimensions, but one increased in volume from 296 cm^3 on 22 June 1979 to 14,781 cm^3 on 5 January 1980, a 4,893% increase in volume in just 6.5 months (Fig. 1, 2). Thirteen of the 17 *N. corniger* nests that ultimately died during the study (76%) showed no signs of growth even during the period that they remained active (Fig. 3). There was no relationship between nest volume for *N corniger* at the beginning of monitoring and at the end of the monitoring period ($r = 0.32$, $n = 12$) (Fig. 4). Thus nest size at the beginning of the study was not a good predictor of nest size at the end of the study.

The volume of *N. corniger* nests at the beginning of monitoring (May, June, or July 1979) associated with survivorship to April 1980 is shown in Fig. 5. The two nests for which measurements did not begin until October 1979 (both of which died before April 1980) were not included in this analysis because of a different total monitoring interval. We tried a simple fit using logistical regression and found no significant relationship between initial nest size and survival ($\chi^2 = 0.74$). To test the original hypothesis (Ho: $P_S = P_L$, where P_S = probability of survival of small nests, and P_L = probability of survival of large nests), we compared the probability of survival of nests with volumes less than 3,000 cm³ at the beginning of monitoring (P_S = 0.375) versus survivorship of nests with a first recorded volume exceeding 6,000 cm³ (P_L = 0.60). There was no significant difference in survivorship over the 9 to11-month period between small and large nests of *N. corniger* (χ^2 = 0.86), leading us to accept the null hypothesis that large and small nests have an equal probability of survival within this population.

Another consideration in evaluating growth of *N. corniger* nests is that this species is facultatively polygynous. Because colonies with multiple primary queens grow faster in both population size and nest volume in the early age classes (Thorne 1984, 1985), some of the observed variance in nest growth rates might be explained by queen number. The *N. corniger* nests that survived until April 1980 were collected and all but one (Y) were fully dissected (technique described in Thorne and Noirot 1982). All but two of the nests had a single primary queen; nest "G" had two queens and nest "T" contained numerous wingless alates in the queen cell, suggesting that queen replacement was underway. In the monogynous surviving *N. corniger* nests, the net increase in volume from summer 1979 to April 1980 is highly correlated (r = 0.87) with queen wet weight at the time of nest dissection (Fig. 6). Notably, several of the nests with the highest growth rates (E, FF, C) also had large queens (> 0.35 g). However, nest EE also had a high growth rate, but only a moderately sized monogynous queen (0.22 g) at the time of dissection.

Generalizations about growth rates of *N. ephratae* nests from Frijoles, Panama are risky due to the relatively small number of nests monitored. Four of seven (57%) nests in the study survived the period of the monitoring. The highest growth rate among the survivors was a nest that increased from 1,044 cm^3 on 24 May 1979 to 4,938 cm^3 on 21 November 1979, and then remained at that size through 1 April 1980 (Fig. 7). None of the three nests that ultimately died grew during the study (Fig. 7). One of the four survivors did not increase in size during the monitoring period. The largest *N. ephratae* nest, estimated at 42,272 cm^3 on 24 May 1979, fell to the ground when its host tree, partially consumed by termites, fell over (event noted and nest dead at 13 July 1979 monitoring). The *N. ephratae* nests that began as the two largest in this study, as well as the smallest nest at the beginning of the project (373 cm^3), died during the course of the research. These trends also suggest acceptance of the original hypothesis (probability of survival is indistinguishable for small and large nests) for *N. ephratae*, although the sample size of seven nests is too small to evaluate with statistical rigor.

There was a marked seasonality to nest expansion in both *N. corniger* and *N. ephratae* (Fig. 1, 7), with growth usually being limited to the wet season. During the year of the study, the dry season lasted from early January until mid-April, 1980. The rare cases in which nest growth did occur over the dry season were in two cases of nest budding in *N. corniger.* Buds had been initiated during the wet season, but there was limited continued growth of the satellite nests during the dry season (budded nests not included in the above data; see below for further discussion of budding).

N. acajutlae nests monitored on Guana Island are obviously much larger nests, on average, than for either *N. corniger* or *N. ephratae* at the Panama site (Table 1). *N. acajutlae* characteristically builds larger nests than *N. corniger* or *N. ephratae*, and the habitat for the *N. acajutlae* study was mature vegetation while the Frijoles, Panama, site was young second-growth. Of the 17 *N. acajutlae* nests tracked on Guana Island, only four of the 17 (23.5%) survived the duration of monitoring (generally 4 to 6 years; 9 years for a single colony which was a survivor) (Fig. 8). Of the remaining 13 nests, 11 (64.7% of the total) died (Fig. 9), and two (11.8% of the original number) abandoned their original nest and relocated (see below). Including the two relocated but surviving colonies, plus the four nests that remained active during the course of the study, six of the total of 17 colonies (35%), survived the total period of the research. The simple fit using logistical regression revealed no significant linear relationship between initial nest size and survival ($\chi^2 = 2.47$). In contrast with *N. corniger*, *N. acajutlae* nests that were large at the beginning of monitoring (>150,000 cm^3) had a higher probability of survival than small nests (<100,000 cm^3) ($\chi^2 = 3.84$) (Fig. 10), although we caution that the sample size was limited, particularly among large nests.

New nests from old. There are three circumstances in which a new *Nasutitermes* nest can arise from an established nest. Nest *budding*, or active division of a *Nasutitermes* colony, involves construction of a satellite nest that remains, for at least some duration, connected to the healthy original nest by galleries and termite traffic between the two (or more) nests (Thorne 1982a, 1984; Levings and Adams 1984; Atkinson and Adams 1997; for further discussion of budding in termites, which can also be a passive process, see Nutting 1969; Thorne et al. 1999). Nest *relocation* occurs when a colony abandons its original nest and moves in entirety (including the physogastric queen) into a freshly constructed nest. From our observations the circumstances initiating such a move always involved dislocation and often substantial injury to the original nest, following a fall from its host tree or being tipped over in a mass of fallen branches during a storm. The new nest sites that we observed were all within 10 m of the downed nest, often closer. In one case on Guana Island, an *N. acajutlae* colony (G11) had previously constructed a small, satellite unit of thin carton, apparently used as a foraging hub without reproductives or brood. When the main nest was knocked down, apparently by a storm, the colony relocated into the already established satellite nest, which was rapidly expanded.

Resprouting of a colony occurs when a nest is totally destroyed or removed (as by an armadillo, anteater, or human), and the orphaned termites that remain in the colony's gallery network and foraging locations consolidate and build a new nest. If it is an opportune time of year with alates mature or in development, then alates within the nest may develop into adultoid reproductives and carry on growth of the colony. If nymphs or alates are not present, worker *Nasutitermes* may differentiate into functional ergatoid reproductives under some circumstances (Thorne and Noirot 1982; Noirot and Thorne 1988), or the resprouted nest may remain without reproductives and survive only until its cohort of workers senesce.

BLT observed all three of these rapid nest creation processes in Panamanian *N. corniger*, and documented nest relocation and resprouting in *N. ephratate* in the same habitat. Both authors witnessed relocation of two of the *N. acajutlae* nests in our Guana Island study area, and previously BLT and Margaret Collins observed relocation of a third nest and resprouting of another, also on Guana Island.

Incipient nests. Long term observation and familiarity with the sites enabled us to recognize and study newly appearing nests in both the Panama and Guana Island research plots. In Panama, during the course of two years, early in the rainy season BLT observed the appearance, virtually overnight, of four *N. corniger* nests, each 7 to 10 cm in diameter (nearly spherical, therefore approximately 180 – 524 cm^3) and containing about 10,000 to 16,000 termites (nest only; excludes individuals in foraging galleries and at food sources) (Thorne 1984). On three occasions she found small incipient colonies housed completely within wood, one of which she collected and dissected. That decaying log had no termite carton inside except around a knothole, which was later found to house the tiny royal cell, less than 1 cm x 1 cm. The primary king and queen inside weighed 0.0063 g and 0.0152 g, respectively (wet weights). Approximately 2,000 termites accompanied the royal pair in a 20 cm section of the log.

Arboreal *N. corniger* and *N. ephratae* nests frequently surround a trunk or branch which, when exposed after nest dissection, often contains a hollowed cavity or knothole that served as the original royal cell. In small nests the royal pair may still be lodged in wood; in larger nests the royal cell is generally constructed adjacent to the original copularium. We suggest that the probable ontogeny of arboreal *N. corniger* colonies is that the royal pair remains sequestered in their original copularium embedded in wood for several years as their incipient colony grows. Workers and soldiers in the young colony also remain within the wood, first eating local areas of the host tree and eventually traveling through the tree core, or perhaps building external galleries, to other food sources. Colonies may also be initiated in stumps or logs. When the colony population size approaches 10,000 termites, and when the first rains of the wet season create the right conditions, the colony blossoms into a rapidly constructed arboreal nest, normally adjacent to the royal cell, roughly 10 to 12 cm in diameter. In this proposed sequence of colony development, arboreal termites remain hidden within their host wood until their colony population size reaches a point that they can repair, maintain, defend, and ultimately expand a visible and exposed nest, although a freshly constructed, small nest remains quite vulnerable. Although some incipient colonies were found within logs, all observed new nests were on trees. This suggests that founding pairs within trees have a higher probability of survival, or that colonies that begin in wood on the ground may move to a tree prior to or during nest construction. The size of a colony, and its queen, at the time of first nest construction may influence its subsequent rate of growth.

N. acajutlae nests on Guana Island were monitored only at yearly intervals so it is impossible to precisely age new recruits or to know their size when they first appeared as carton nests. However, in 1998 we found three new nests that had not been present in 1997. Those nests had volumes of 17,981, 7,950, and 7,037 cm^3. We have never seen a *N. acajutlae* nest smaller than 7,000 cm^3 in any habitat, so if they remain cryptic within wood and then "bloom" as does *N. corniger*, a size of approximately 7,000 cm^3 may reflect their usual debut size as arboreal nests.

Discussion

There have been very few studies of long term nest growth and/or survivorship in termites. Banerjee (1975) monitored growth of five incipient colonies of *Odontotermes redemanni* (Wasmann) in India for two years, finding that the annual growth rate of individual mounds was higher for smaller mounds (<75 cm in height) than for larger mounds (>100 cm in height). All five of the mounds that he followed survived the 2-yr study. Roonwal (1977) studied the ratio of height to diameter expansion during growth of mounds of three species of *Odontotermes* in India, determining that the growth pattern was allometric. Korb and Linsenmair (1998) conducted the most detailed demographic study yet completed on termites, measuring a variety of fitness parameters (probability of survival, age of first reproduction, number of alates produced per colony, and lifelong probability of reproduction) on individual *Macrotermes bellicosus* (Smeathman) mounds in an Ivory Coast savanna. This work will be a landmark study when published.

The results of our work on three species of Neotropical, arboreal *Nasutitermes* suggest that a relatively low percentage of individual nests survive long-term, at least in the sites that we studied. Smaller nests of *N. acajutlae* had lower survivorship than larger nests within this study; the probability of survival of small and large *N. corniger* nests was indistinguishable among nests in this study. Our sample of *N. ephratae* nests was too small to evaluate the association of size and probability of survival. Both the Panama and Guana Island sites were free from human perturbation, but had other risks for termites. In Panama there were anteaters that can climb trees and swipe their sharp claws into *Nasutitermes* nests (Lubin and Montgomery 1981). Once a nest is injured, there are many species of predaceous ants that readily invade *Nasutitermes* colonies. BLT observed *Camponotus* sp. ants clean out an injured *N. corniger* nest in less than 24 h. Anteaters, ants, or armadillos may attack *Nasutitermes* nests cracked or otherwise damaged after falling from their host tree during a storm. In contrast with Panama, no vertebrate termite predators live in the British Virgin Islands other than lizards that eat termites exploring outside of their nest or galleries. During our 9-yr study, the largest cause of mortality to *N. acajutlae* nests on Guana Island appeared to be hurricanes, with drought stress as another possibly signficant factor. Hurricanes create termite food and habitat by downing trees and branches, but the storms may also dislodge and injure established nests, causing death or inducing the colony to relocate. Inter- and intraspecific competition and territorial interactions among neighboring *Nasutitermes* may also affect growth and survivorship of nests (Thorne 1982a; Levings and Adams 1984; Adams and Levings 1987; Leponce et al. 1995, 1996, 1997). In all three species, the survivorship information presented here does not include the earliest age classes of colonies, which begin sequestered within wood and are therefore invisible to scientists in this type of survey.

In this study we report on the growth and survivorship of individual *nests*, as opposed to *colonies* because some *Nasutitermes* are polydomous, meaning that a single intermingling colony may construct and occupy more than one nest (Levings and Adams 1984; Roisin and Pasteels 1986; Adams and Levings 1987; Clarke 1993; Leponce, Roisin and Pasteels 1995, 1996, 1997; Atkinson and Adams 1997; Thompson and Hebert 1998a,b). Although *N. corniger* colonies are known to form buds and occupy those satellite nests in some habitats (Thorne 1982b, 1984; Levings and Adams 1984; Adams and Levings 1987; Atkinson and Adams 1997), we feel confident that the *N. corniger* nests monitored in this study were each single colonies, not interconnected buds. None of the trails leading from *N. corniger* nests were connected to any other nest. Termites from all nests in the site were evaluated for agonistic behavior in pairwise bioassays, always resulting in aggressive interactions between neighboring nests (Thorne 1982a). The queenright condition of surviving nests, determined upon dissection, suggests that they were independent colonies. Furthermore, the habitat had been cleared of larger trees and burned 3 to 6 years previously, so while the *N. corniger* colonies in our study may have been founded prior to the habitat destruction, they bloomed into arboreal nests within a relatively few years of the beginning of the study. They were thus generally too young to bud, although two of the colonies were observed in the process of budding during the study.

N. ephratae colonies are not yet known to bud; the seven in this study were spatially dispersed and almost certainly represented individual colonies. Little is known of colony structure in *N. acajutlae*. Although the monitored nests on

Guana appear to represent independent colonies because of a scattered spatial configuration, colonies of the closely related species *N. nigriceps* (Thorne et al. 1994, 1996b) may occasionally occupy more than one nest (Levings and Adams 1984; Clarke and Garraway 1994). Further study of *N. acajutlae* is needed before we can fully interpret the association between nests and colonies.

In both *N. corniger* and *N. ephratae*, nest expansion was confined to the wet season during our study, the only exception being growth of some budded nests. Termites need rain for moisture to open existing walls and effectively masticate materials needed to build additional galleries (Thorne 1984). Colonies may be forced to repair nests during the dry season if that is when an injury occurs, but volume expansion appears to be restricted to the wet season. The occasionally enormous growth rates observed during the course of the wet season may reflect accommodation of a population increase that already occurred, and/or anticipation of growing ranks in the near future. Seasonal patterns of nest growth, particularly following rains, was also noted by Noirot and Noirot-Timothée (1962) in *Cubitermes fungifaber* (Sjöstedt) and by Bodot (1967) in *Amitermes evuncifer* Silvestri, *Cubitermes severus* Silvestri, and *Trinervitermes trinervious* (Rambur) on savannas of the Ivory Coast. Banerjee (1975) reported an inverse relationship between mound building and rainfall in the Indian termite *Odontotermes redemanni* (Wasmann), with reduced construction during heavy rains.

The ability of termite colonies to relocate to a new nest site has been documented in several species. Emerson (1929) witnessed migration of a colony of *Nasutitermes costalis* (Holmgren) including the royal couple, and Emerson

(1938) made a persuasive case that every visible arboreal *Constrictitermes cavifrons* (Holmgren) nest is the result of a colony migration because the nests are constructed on living trees with smooth bark, and there is no evidence of excavation of a royal cell into bark beneath the nests. Noirot and Noirot-Timothée (1962) describe nest relocation in *Cubitermes fungifaber* in the Ivory Coast. In the cases of nest relocation that we observed in *N. acajutlae*, *N. corniger*, and *N. ephratae*, colonies abandoned their original nest and moved to a newly built replacement following major disturbance, such as the nest falling to the ground or becoming angled at a severe tilt following storm damage or decay of the host tree. The original nest sometimes was not visibly injured, but repositioned, often in a more vulnerable site.

Growth rates and survivorship of termite nests of a particular species are almost certainly influenced by habitat, season, inter- and intraspecific competitors, and disturbance from predators, drought, storms, and humans. For example, all *N. corniger* nests monitored in this study were in an area of young second-growth, a habitat characterized by high vegetative productivity, an age distribution skewed towards young colonies, rapid succession of the young forest and therefore of nest sites, and moderate predator pressure (Thorne 1984). Nest and colony growth and survival rates in this young habitat may be quite different than in a primary forest.

Species of arboreal *Nasutitermes* appear to be remarkably adaptable and resilient, capable of colony budding, relocating, and resprouting to expand and/or adjust to changing circumstances or destruction of the original nest. Despite this flexibility, long-term survivorship of arboreal *Nasutitermes* nests and their associated colonies is low, even though these conspicuous nests appear to be abundant in many Neotropical habitats. Conservation of social insects has only recently been established as an important issue; colonies are now recognized to be more vulnerable than they appear on the basis of numbers of individuals (Pamilo and Crozier 1997). Because of their ecological importance as decomposers, and because they have a lower survival rate than previously predicted, efforts should be made to preserve active *Nasutitermes* nests in natural communities.

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Table 1. Volume (cm^3) of nests of *Nasutitermes acajutlae* on Guana Island, British Virgin Islands from 1992 to 1998

	Year [b]				
Colony	1992	1993	1994	1996	1998
G1	160,739	186,526	142,424	*relocating*	(161,432) [c]
G2 [a]	569,185	750,093	902,172		1,281,085
G3	280,730	281,103	288,500		***Dead***
G4	35,657	***Dead***			
G5	11,454	23,381	30,192	***Dead***	
G6	57,738	***Dead***			
G7	45,629	68,757	87,186	***Dead***	
G8	9,050	13,205	13,154		***Dead***
G9	82,491	91,937	***Dead***		
G10	139,409	208,578	197,072	***Dead***	
G11	199,444	---	523,421	*relocating*	(279,789) [c]
G12	85,790	134,250			287,947
G13		54,629		***Dead***	
G14			160,896		174,713
G15			66,481		251,963
G16			24,013		***Dead***
G17			7,830	10,458	***Dead***

[a] Volume of this colony was 212,171 cm^3 in 1989.

[b] Hurricane Luis damaged buildings on Guana Island in 1995 and limited access to field sites duing October, thus no measurements were taken.

[c] These measurements were taken after the colony had relocated.

FIGURE CAPTIONS

Fig. 1. Growth of *Nasutitermes corniger* nests that survived throughout the monitoring period. Note consistent lack of growth during the dry season (January through mid-April in 1980). [Figure does not show growth of budded nests.]

Fig. 2. Growth of *Nasutitermes corniger* nest FF in Frijoles, Panama over 5 mo. a. 22 June 1979. b. 7 July 1979. c. 18 October 1979. d. 14 November 1979.

Fig. 3. Growth of *Nasutitermes corniger* nests that died during the course of the study.

Fig. 4. Relationship between *Nasutitermes corniger* nest volume at the end of the growth period relative to the initial volume. Data are only from nests that survived the entire study period. The correlation was not significant (r = 0.32).

Fig. 5. Survivorship of *Nasutitermes corniger* nests based on initial size. Monitoring of individual nests began in May, June, or July of 1979.

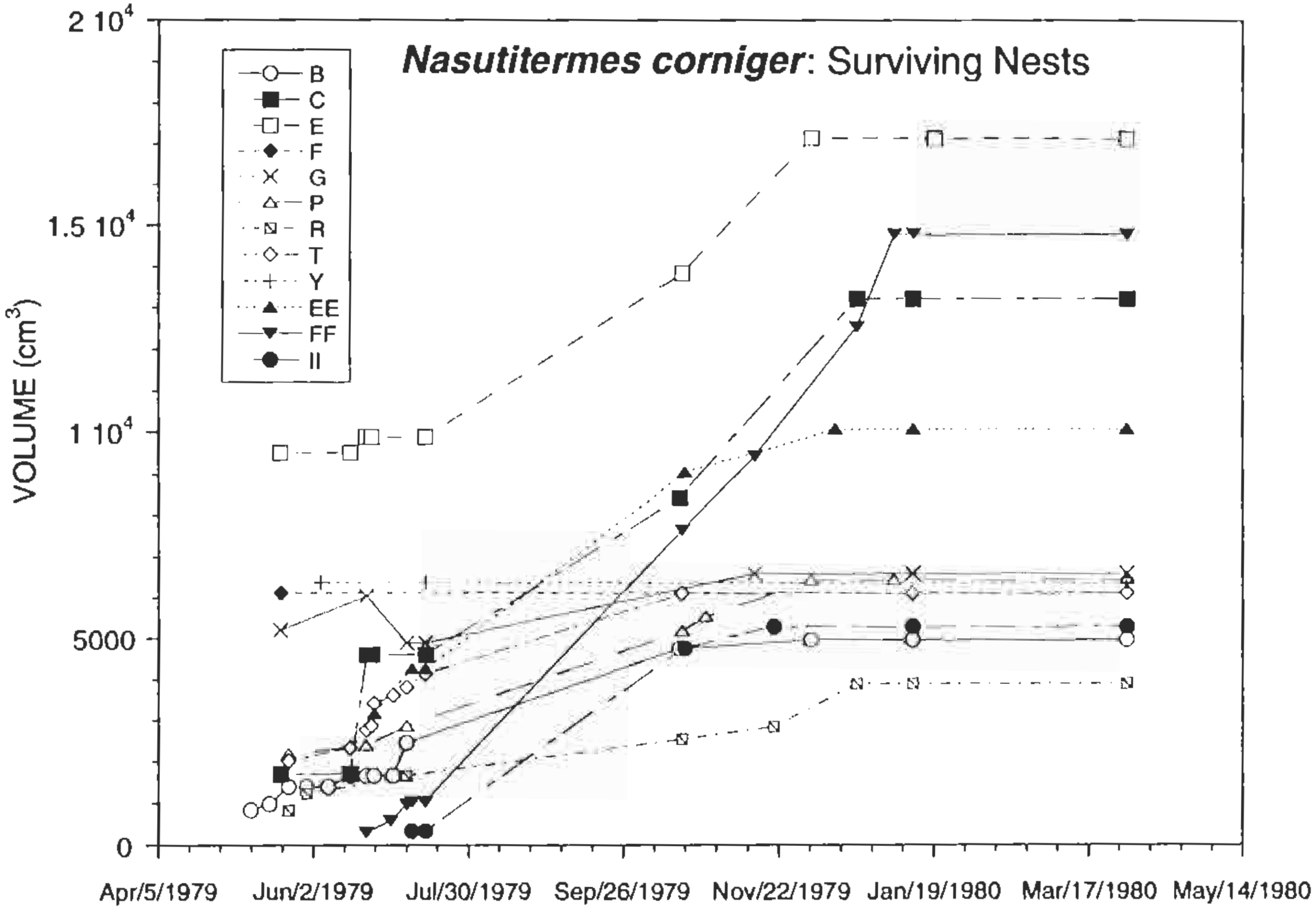
Fig. 6. Relationship between queen wet weight (*Nasutitermes corniger* colonies with monogynous queens only) and net increase in nest volume during the course of the study. The correlation was highly significant (r = 0.87). Monitoring of individual nests began in May, June, or July of 1979. Nests were collected and dissected in April 1980 to expose and measure reproductives.

Fig. 7. Growth of *Nasutitermes ephratae* nests, including survivors (open symbols) and colonies that died (dark symbols) during the course of the study. Note lack of nest expansion during the dry season (January through mid-April in 1980).

Fig. 8. Growth of *Nasutitermes acajutlae* nests on Guana Island, B.V.I. that survived until October 1998. Growth of relocated nests is not shown.

Fig. 9. Growth of *Nasutitermes acajutlae* nests on Guana Island, B.V.I. that died before October 1998.

Fig. 10. Survivorship of *Nasutitermes acajutlae* nests based on size at the beginning of monitoring.



Nasutitermes corniger: Surviving Nests
VOLUME (cm^3)
2 10^4
1.5 10^4
1 10^4
5000
0
Apr/5/1979
Jun/2/1979
Jul/30/1979
Sep/26/1979
Nov/22/1979
Jan/19/1980
Mar/17/1980
May/14/1980
B
C
E
F
G
P
R
T
Y
EE
FF
II

Fig. 1

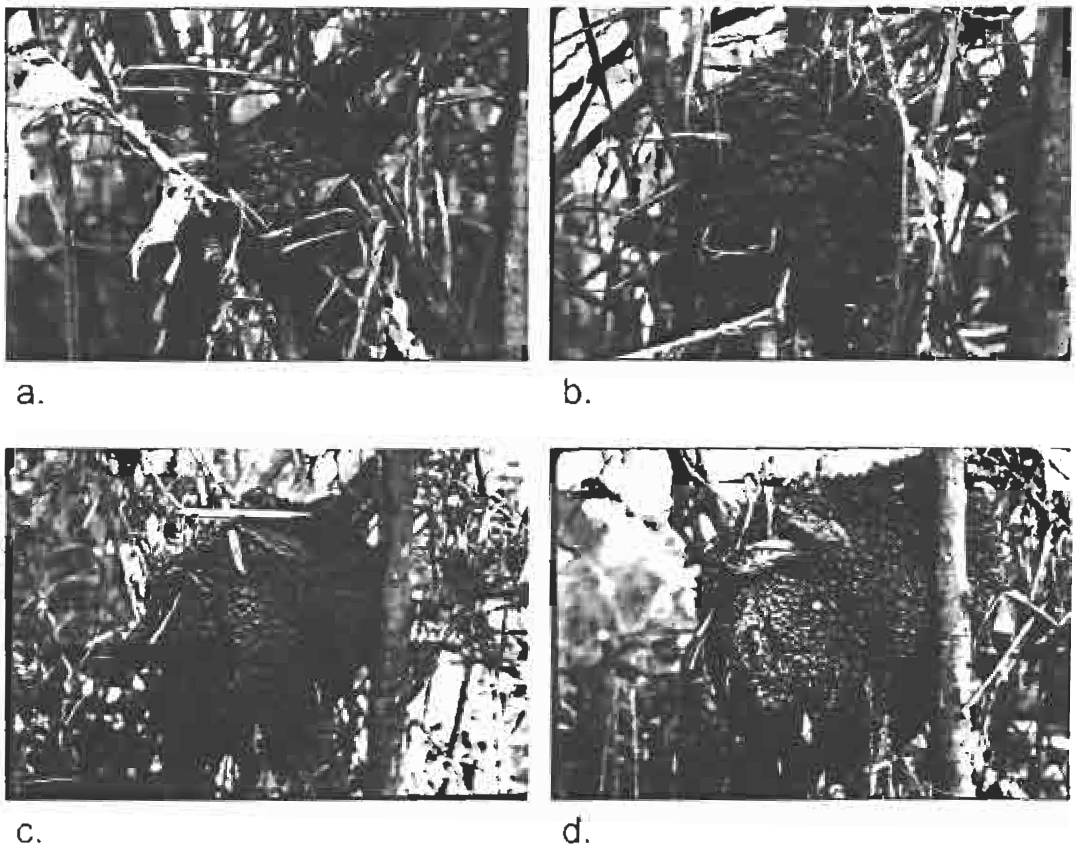


Fig. 2

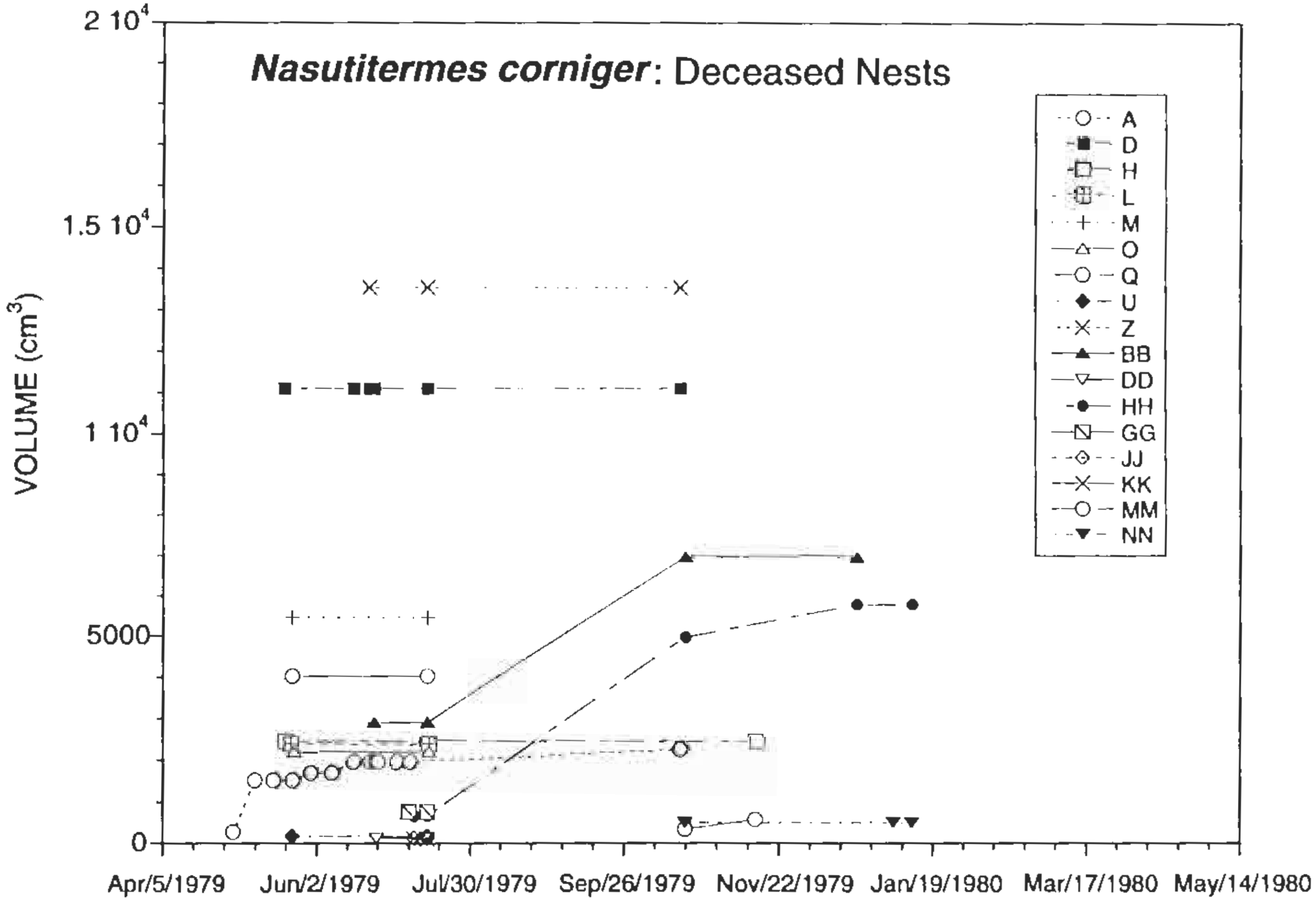

Nasutitermes corniger: Deceased Nests
VOLUME (cm³)
2 10⁴
1.5 10⁴
1 10⁴
5000
0
Apr/5/1979
Jun/2/1979
Jul/30/1979
Sep/26/1979
Nov/22/1979
Jan/19/1980
Mar/17/1980
May/14/1980
A
D
H
L
M
O
Q
U
Z
BB
DD
HH
GG
JJ
KK
MM
NN

Fig. 3

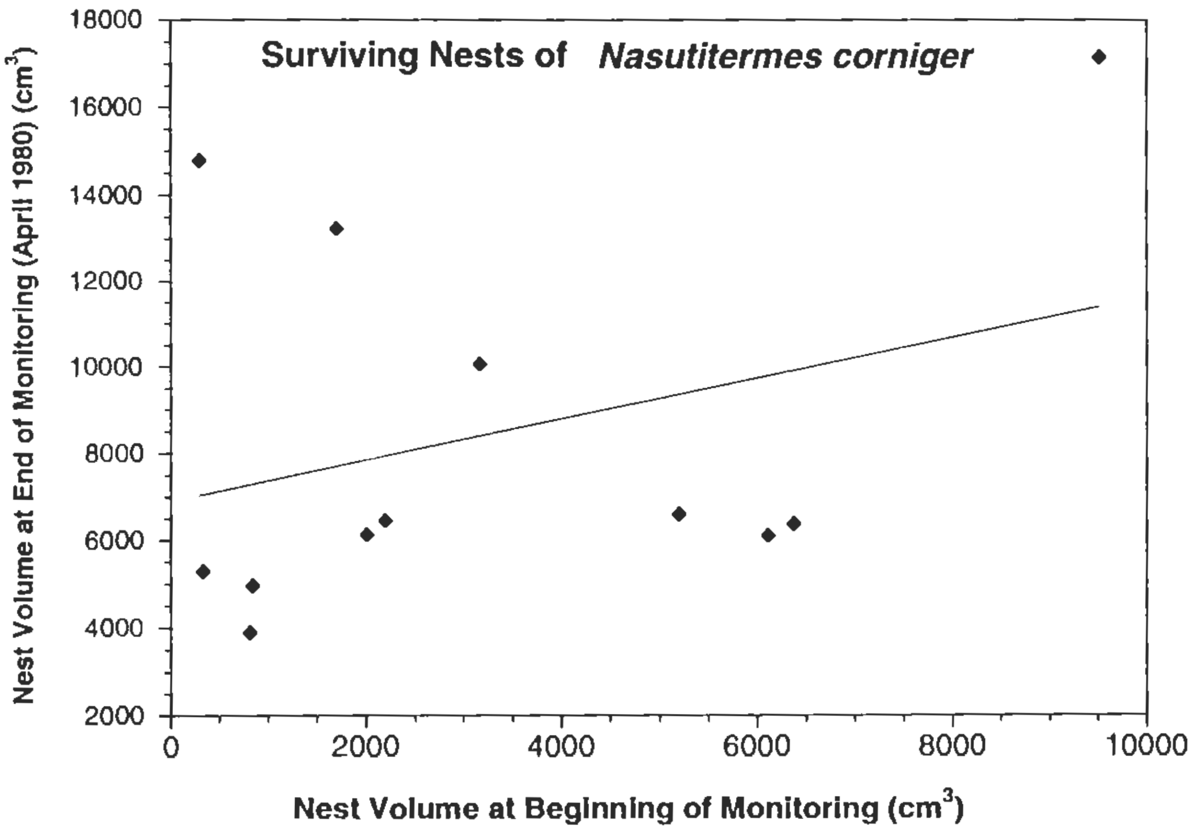

Surviving Nests of *Nasutitermes corniger*
Nest Volume at End of Monitoring (April 1980) (cm^3)
18000
16000
14000
12000
10000
8000
6000
4000
2000
0
2000
4000
6000
8000
10000
Nest Volume at Beginning of Monitoring (cm^3)

Fig. 4

Fig. 5

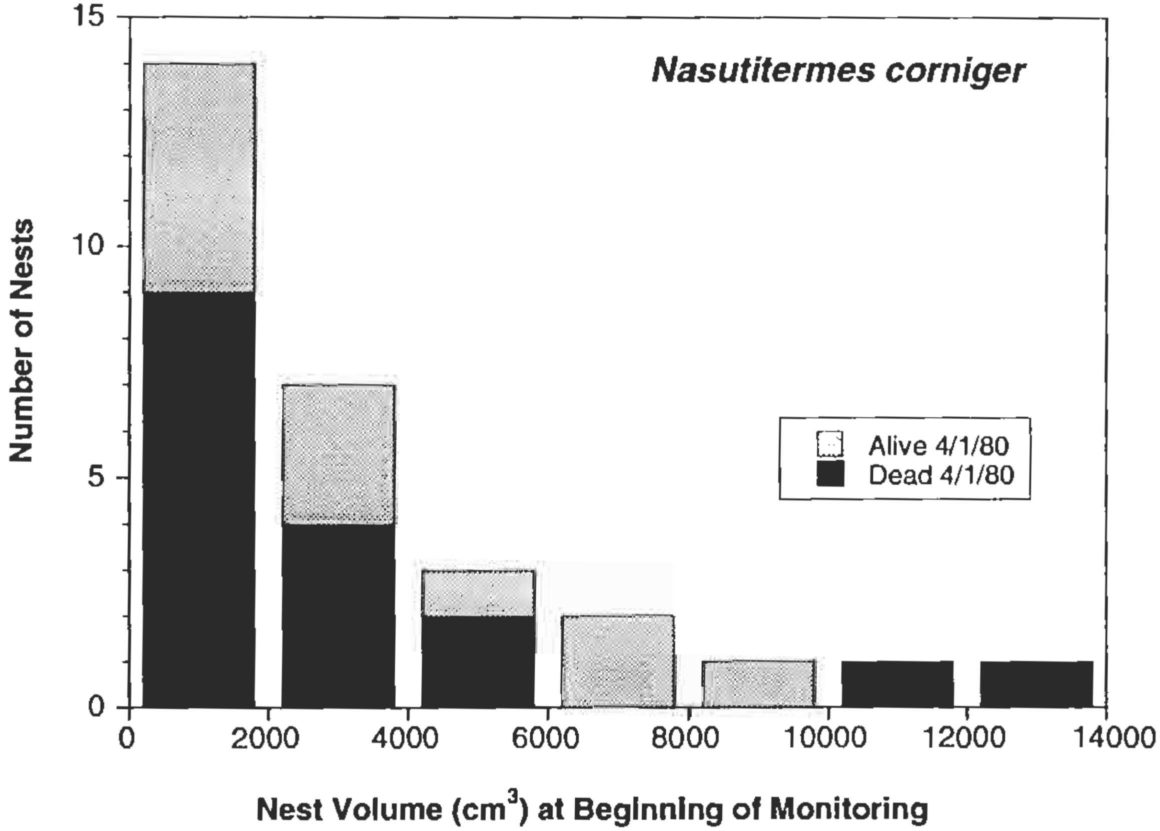

Nasutitermes corniger
Alive 4/1/80
Dead 4/1/80
Number of Nests
15
10
5
0
0
2000
4000
6000
8000
10000
12000
14000
Nest Volume (cm3) at Beginning of Monitoring

Fig. 5

Fig. 6

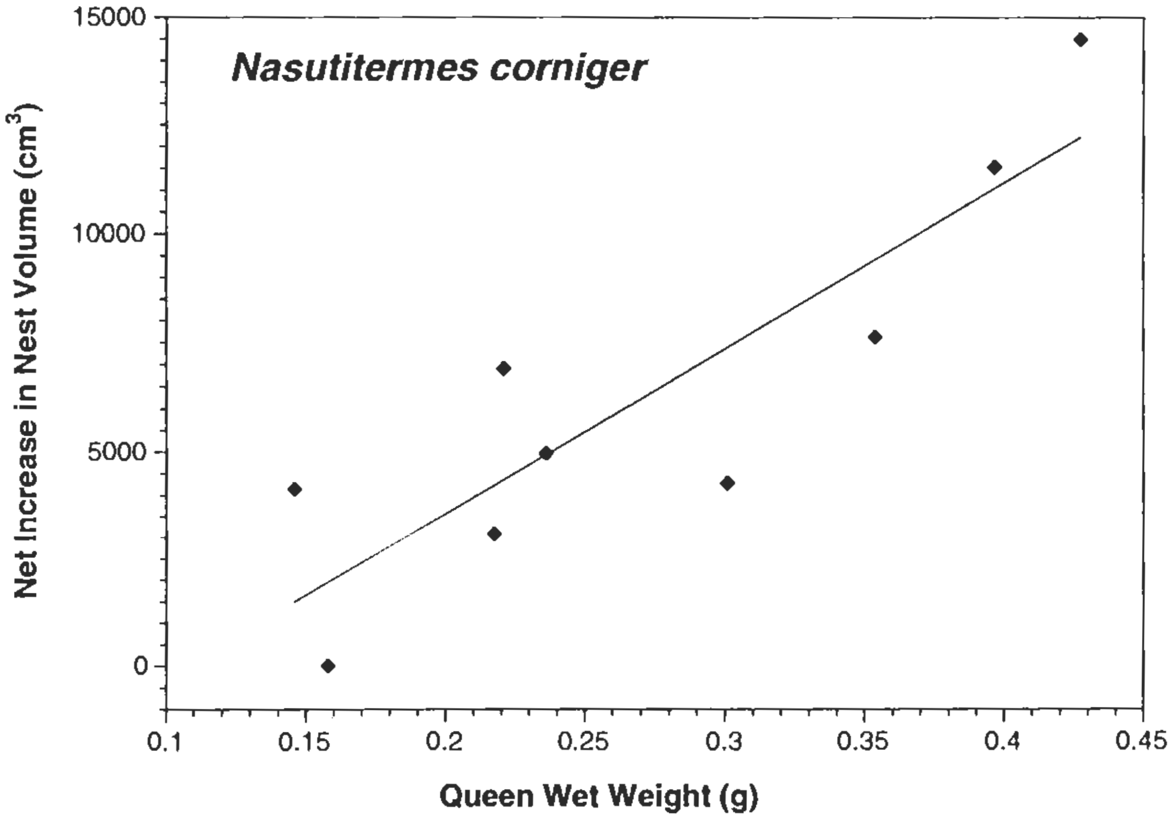

Nasutitermes corniger
Net Increase in Nest Volume (cm^3)
15000
10000
5000
0
0.1
0.15
0.2
0.25
0.3
0.35
0.4
0.45
Queen Wet Weight (g)

Fig. 6

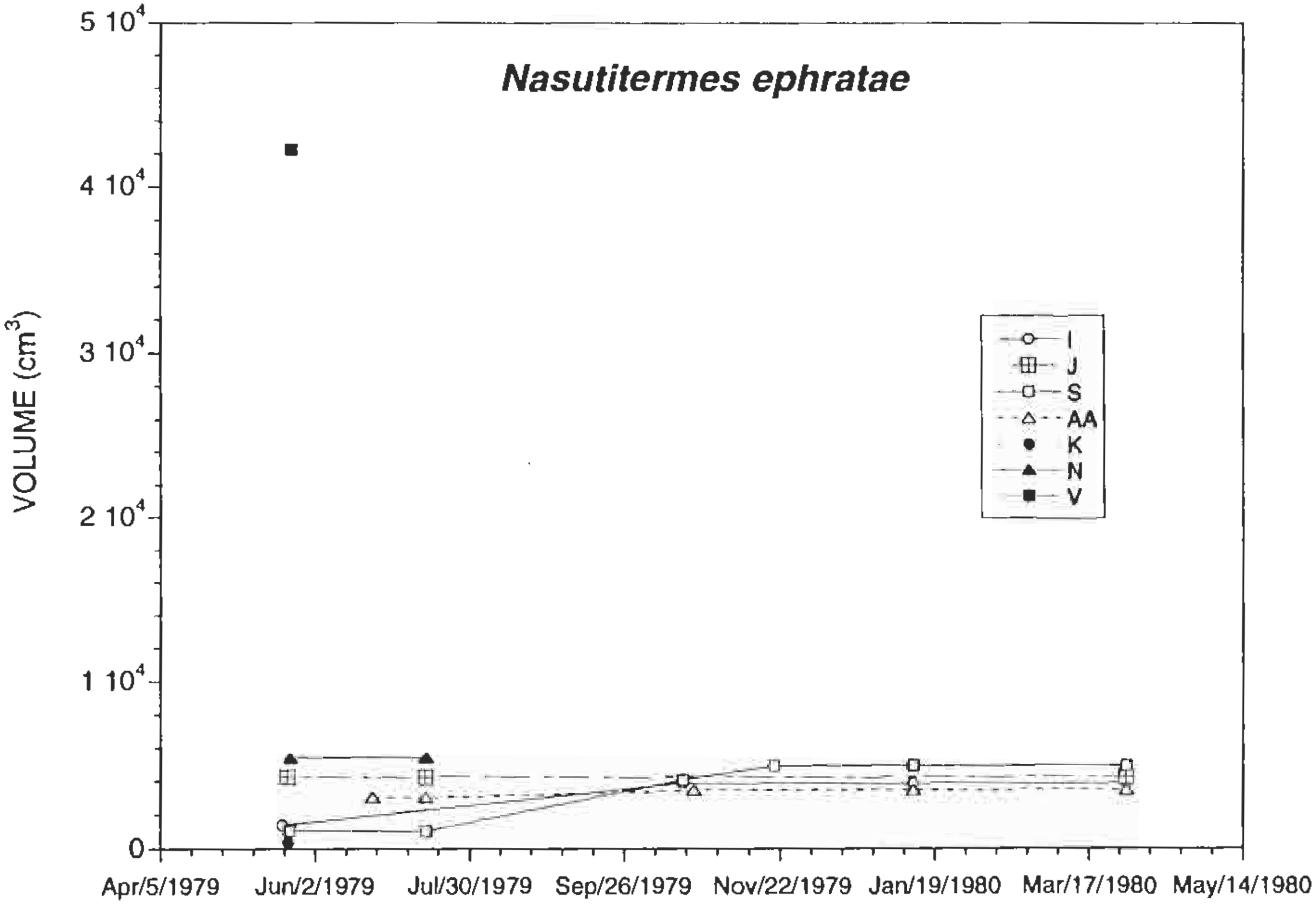

Nasutitermes ephratae
VOLUME (cm³)
5 10⁴
4 10⁴
3 10⁴
2 10⁴
1 10⁴
0
Apr/5/1979
Jun/2/1979
Jul/30/1979
Sep/26/1979
Nov/22/1979
Jan/19/1980
Mar/17/1980
May/14/1980
I
J
S
AA
K
N
V

Fig. 7

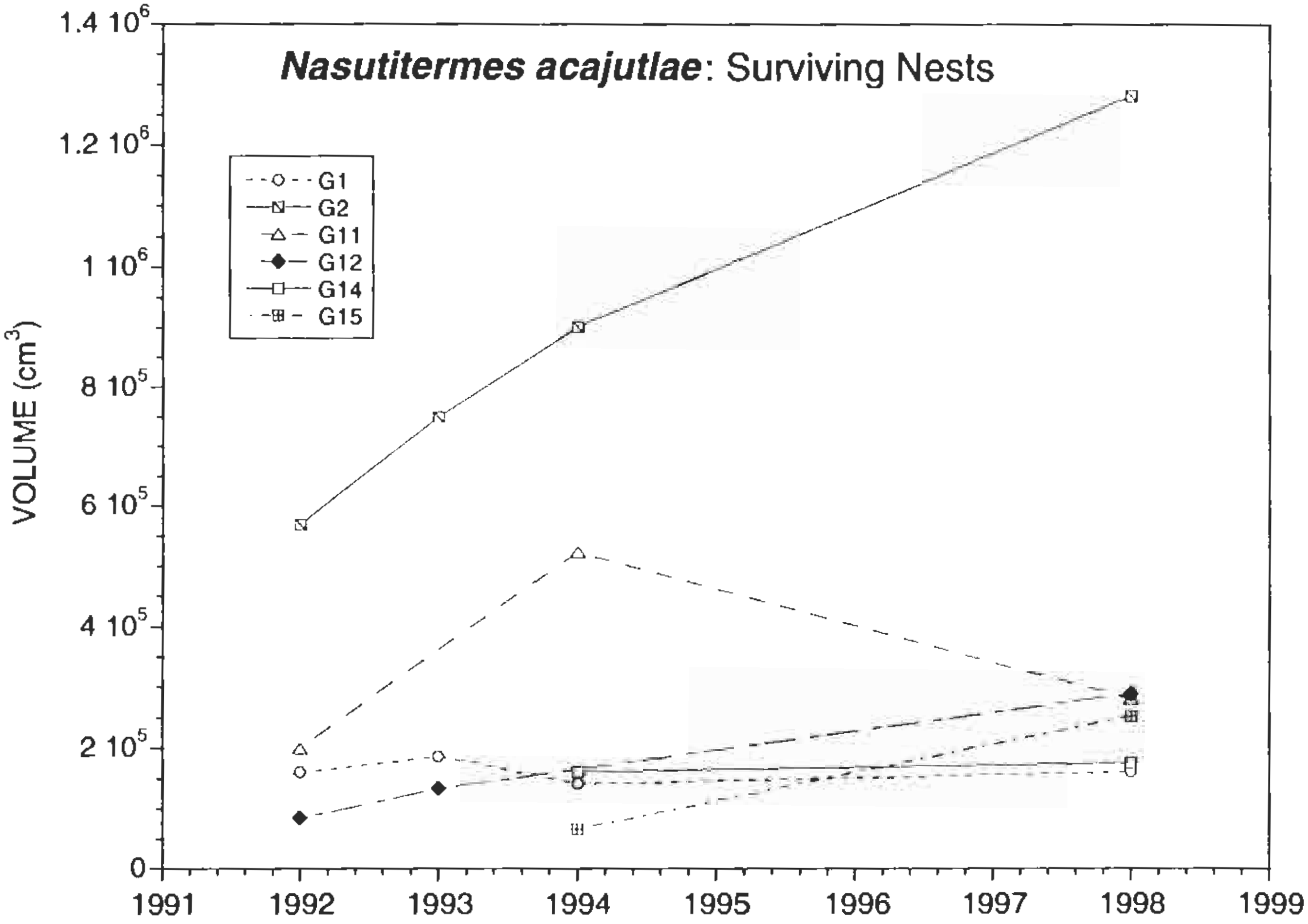
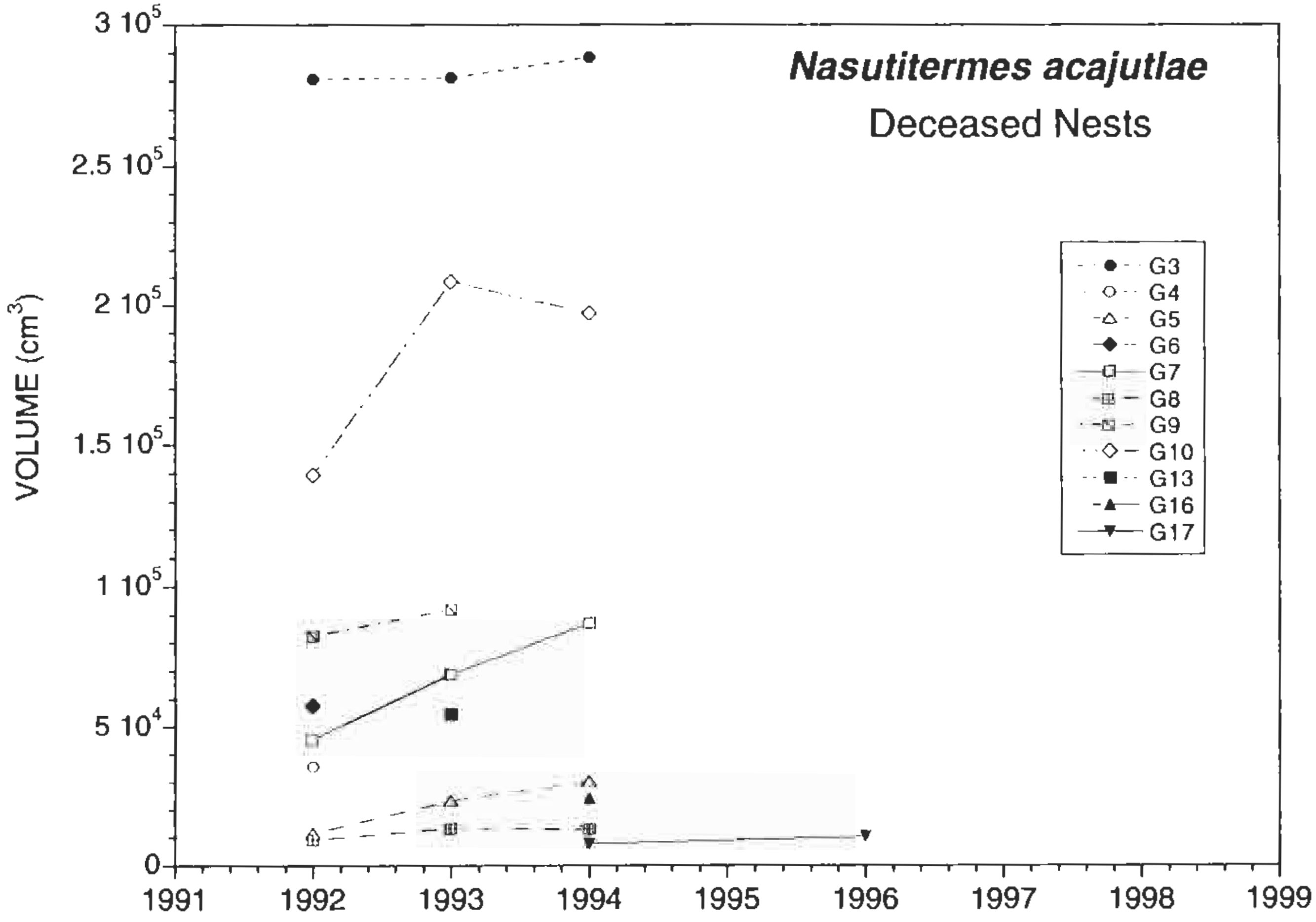

Nasutitermes acajutlae: Surviving Nests
VOLUME (cm^3)
1.4 10^6
1.2 10^6
1 10^6
8 10^5
6 10^5
4 10^5
2 10^5
0
1991
1992
1993
1994
1995
1996
1997
1998
1999
G1
G2
G11
G12
G14
G15

Fig. 8



3 10^5
2.5 10^5
2 10^5
1.5 10^5
1 10^5
5 10^4
0
VOLUME (cm^3)
1991
1992
1993
1994
1995
1996
1997
1998
1999
Nasutitermes acajutlae
Deceased Nests
G3
G4
G5
G6
G7
G8
G9
G10
G13
G16
G17

Fig. 9

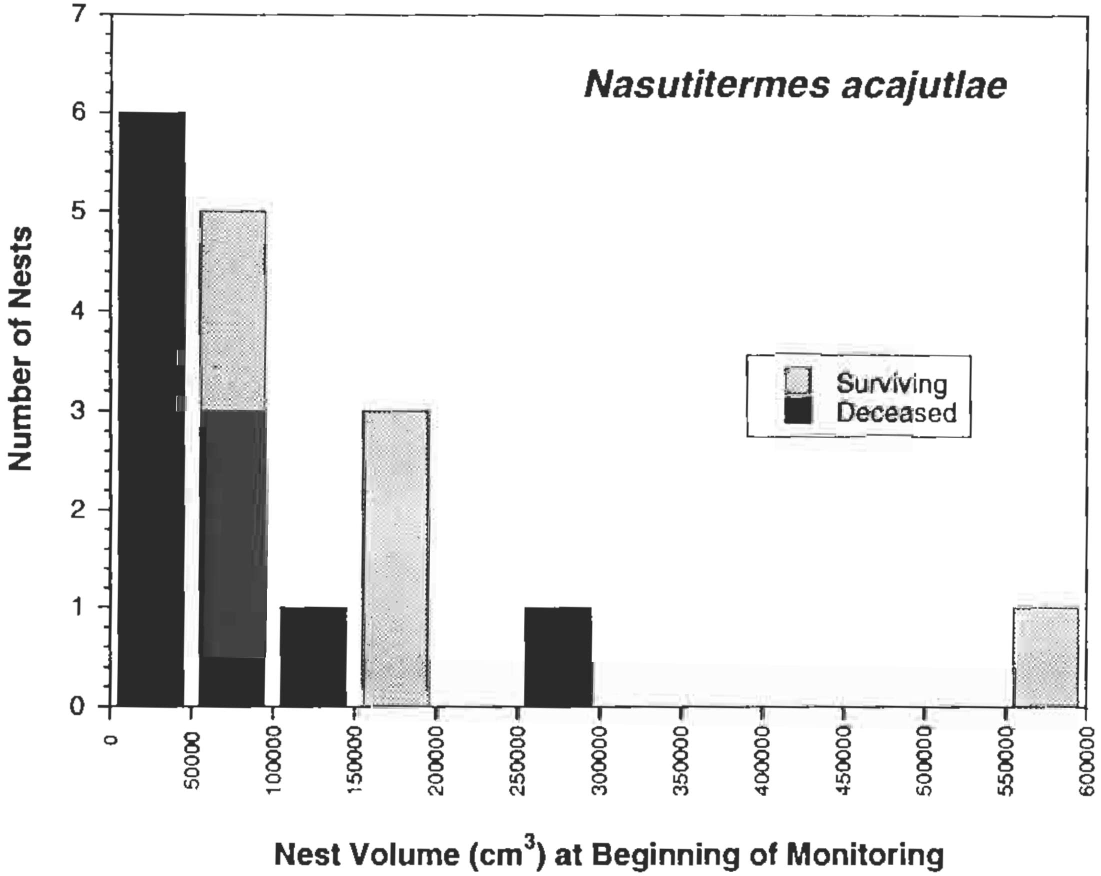

Nasutitermes acajutlae
Number of Nests
7
6
5
4
3
2
1
0
Surviving
Deceased
0
50000
100000
150000
200000
250000
300000
350000
400000
450000
500000
550000
600000
Nest Volume (cm3) at Beginning of Monitoring

Fig. 10

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RESEARCH LETTER

Munroe revisited: a survey of West Indian butterfly faunas and their species-area relationship

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Abstract. The latest butterfly species numbers for sixty-seven West Indian islands and South Florida are presented. Estimating the species richness of insular faunas is rarely straightforward and the difficulties are discussed in the context of West Indian butterflies. The data are considered minimum estimates because the number of species overlooked is still likely to exceed the number of vagrant and extinct species accidentally included. With this caveat in mind, the species-area relationship is examined. The correlation between island area and species richness was first described for West Indian butterflies by Eugene Munroe in 1948. Despite an additional fifty-seven data points, today's species-area regression (slope, $z=0.20$; intercept, $c=1.06$) is not significantly different from that observed in 1948 ($z=0.26$; $c=0.80$). To our knowledge, butterflies have the flattest species-area regression reported for any West Indian taxon. The possible implications of the species-area relationship for the biogeography of West Indian butterflies are discussed.

Key words. Island biogeography, Caribbean, South Florida, Lepidoptera, species-area relationship, survey efficiency.

INTRODUCTION

One of the oldest rules in ecology is the relationship between the number of species (species richness) and the area in which they are found (Arrhenius, 1921; Gleason, 1922). According to MacArthur and Wilson (1963, 1967) the species-area relationship is due to differences in extinction rate: smaller islands tend to support smaller populations that are more susceptible to random extinction. Variations in the form of the species-area relationship are caused by the differential isolation of islands: closer islands receive more immigrants and so have more species than expected for their size. A very similar theory was proposed by Eugene Munroe in his 1948 doctoral thesis (Gilbert, 1984; Brown & Lomolino, 1989; Wilkinson, 1993). Munroe (1948) discovered the relationship between butterfly species richness and island area in the West Indies, however, he only published his ideas in an abstract (Munroe, 1953) and did not stress their general applicability (Wilkinson, 1993). Munroe's seminal work is, therefore, rarely cited in reviews of island biogeography (e.g. Rosenzweig, 1995).

West Indian butterflies provide a useful opportunity to investigate the species-area relationship because they are unusually well described for a tropical insect fauna. Here we use West Indian butterflies to assess the stability of *observed* species-area relationships. Such information is important as many data sets (particularly those of tropical invertebrates) are still at an early stage of compilation: with what confidence can they be used in ecological and biogeographical study? The observed species-area relationship is likely to change as faunas become better known. Estimated species richness will tend to increase with time, as it is easier to record previously overlooked species than to recognize extinctions. Consequently, the intercept of the species-area regression should increase (Wilson, 1988). Estimates of species richness might not, however, increase homogeneously across an archipelago. Large islands may have been more intensively studied because,

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historically, they received more attention. Estimates of species richness might stabilise for large islands whilst continuing to rise for small islands; hence the slope of the species-area regression may lessen over time simply due to sampling considerations.

In 1948, butterfly lists for most of the West Indies were certainly incomplete. Of Munroe's eleven 'islands' (Munroe, 1948), five of the seven smallest represented pooled data (for the northern Lesser Antilles, the southern Lesser Antilles, the Cayman islands, the Virgin islands, and the entire Bahamas archipelago). Some 20 years later, small islands still had to be amalgamated for biogeographic analysis (Scott, 1972). Species records, however, continued to accumulate and based on an ever growing body of data (see Riley, 1975) the species-area relationship was again noted by Scott (1986). Many new records have been reported since Scott's list, particularly for small islands (Smith, Miller & Miller, 1994a). Here we present the latest species richness estimates. We discuss the problems associated with compiling such data and investigate the robustness of the species-area relationship.

METHODS

The islands

Historically, the West Indies have included all the Caribbean islands, the Bahamas and even parts of continental America. Faunistically, however, mainland South and Central America, together with their coastal islands, are usually excluded (Smith *et al.*, 1994a). The most notable exclusion is Trinidad, lying only 15 km off the coast of Venezuela. Although relatively small (4820 km^2), this island supports over 600 butterfly species (Barcant, 1970), compared with only some 350 in all the West Indies (Smith *et al.*, 1994a). The butterfly fauna of Trinidad is a virtually unmodified subset of the adjacent South American mainland (to which it has recently been linked); only some 10% of Trinidad's butterflies are 'West Indian'. The inclusion of south Florida is also of note. Ecologically, the southern tip of Florida (Dade and Munroe Counties, together with the Florida Keys) may be regarded as a West Indian island. This region is surrounded by either temperate land or ocean and well over half its butterflies are of Neotropical rather than Nearctic affinities (Smith *et al.*, 1994a). The areas of most West Indian islands are published, although the figures vary slightly from one source to the next. We have used the most recent figures (Evans, 1973; Hunter, 1994).

The butterflies

Nomenclature follows Smith *et al.* (1994a). Estimates of species richness were compiled from Smith *et al.* (1994a), other published sources and unpublished records. Species, once reliably recorded, were assumed to be extant even if they had not been seen for many years. All the island records supported by a museum specimen were included except for a few cases where there was doubt concerning the labelling of a specimen. A conservative approach was taken in not considering subspecies. Specific classification usually requires substantial and consistent differences, whilst subspecies are not always reliable indicators of differentiation among insular populations. Widespread polymorphisms are sometimes mistaken for evidence of separate subspecies, e.g. Ramos & Mieres (1993) reared several supposed subspecies in a single brood of *Ascia monuste*. Where butterflies were described by some authors as subspecies but by others as full species, we used the more recent revision. For example, Smith *et al.* (1994a) regarded the island populations of *Anaea troglodyta* and *Wallengrenia otho* as specifically distinct, although Riley (1975) had considered them subspecies. This does not affect the overall species number for individual islands (e.g. *W. misera* merely replaced *W. otho misera* in Cuba and *W. drury* replaced *W. otho drury* in Hispaniola). It does, however, affect the regional count because there are now two species (*W. misera* and *W. drury*), whereas previously there was just one (*W. otho*).

Occasionally species records may turn out to be synonyms of pre-described taxa (a particular problem in archipelagos where endemism is often expected). For example, Holland (1916) described the new hesperiid species *Telegonus geronae* and *Amblyscirtes insulaepinorum* from the Isle of Pines, but they were later recognized to be synonyms for *Astraptes cassander* and *Euphyes c. cornelius* respectively (Alayo & Hernández, 1987). Whilst the species richness of the Isle of Pines was unaffected by the taxonomic correction, without it the number of species in the West Indies as a whole would have been spuriously inflated by two. These taxonomic difficulties are important when faunas are poorly described and data from several islands are pooled (e.g. Munroe, 1948; Scott, 1972). We avoided this source of error, however, by treating each island individually. There are very few instances of two subspecies occurring on the same island, although eastern and western populations of the Cuban Papilionid *Parides gundlachianus* provide a rare example (Hernández, Alayón Garci & Smith, 1995).

Data analysis

The power function, $S = cA^z$, where S is species richness, A is island area, c and z are constants, describes the species-area relationship when individual abundance is distributed among species in a log-normal 'canonical' fashion (Preston, 1962). It has thus become the standard approach (and is therefore of most comparative value) to log-transform both species richness and island area: $\log S = z\log A + c$. Other transformations, however, sometimes yield higher correlation coefficients (Connor & McCoy, 1970). Munroe (1948) found it preferable to log-transform area alone, as would be expected with the exponential function: $S = z\log A + c$. We have analysed the data transformed according to both exponential and power functions. Three linear regressions were performed using the species richness data presented here, those of Munroe (1948), and of Scott (1986). Since the figures used for island area are not always consistent among the three data sets, we replaced those of Munroe (1948) and Scott (1986) with those shown in Table 1. Following Sokal & Rohlf (1995), the three regression lines thus obtained were compared for equality of slope. With no significant difference among slopes, the intercepts could then be compared using analysis of covariance (ANCOVA).

RESULTS

Species richness

Table 1 shows the number of butterfly species for each island along with citations for the island records. Several records were excluded. During the last century, major European private collections were assembled largely by purchase and, occasionally, locality data may have been manufactured to suit the market. Ramos (1982) suspects this to be the case for supposed Puerto Rican specimens of *Phocides pigmalion*, *Pyrrhocalles antiqua* and *Ephyriades zephodes*, which have been omitted accordingly. Following Brown & Heineman (1972), eight continental hesperiids (*Urbanus teleus*, *U. tanna*, *U. albimargo*, *Cogia chalcas*, *Nisoniades bessus*, *Antigonus nearchus*, *Helopetes arsalte*, and *Oileus fridericus*) were omitted from the Jamaican count. These had been attributed to the island on the basis of specimens in the British Museum (Natural History) which are not accompanied by collecting data; they have never been recorded elsewhere in the West Indies, other than an uncertain record of *O. fridericus* from Cuba (Alayo & Hernández, 1987). *O. fridericus* has been omitted from the Cuban list, together with the similarly unsubstantiated early records of *Callimormus radiola* (see Alayo and Hernández, 1987). Further exclusions included island records that were clearly unintentional errors: Riley's (1975) illustration of the Hispaniolan endemic *Heraclides machaonides* from Puerto Rico, Hall's (1925) inclusion of the Cuban *Phoebis avellaneda* on the Hispaniolan list, and Schaus' misidentification of the Puerto Rican *Choranthus borincona* as Hipaniolan *Choranthus haitensis*, recognized by Ramos (Smith *et al.*, 1994a). Although important for individual island lists, these corrections are very minor in the overall context of the statistical treatment of the area's butterflies.

Species numbers have generally risen over the three surveys. Increases have been most dramatic on smaller islands, such as the Isle of Pines (Cuba) and Mona Island (Puerto Rico) (Figs 1, 2). Holland (1916) published a list of sixty-five species from the Isle of Pines. In 1975–1976 Hernández and colleagues added twenty-five species to the list and as a result of four visits from 1993 to 1995 the species total has now reached 111 (Smith, Hernandez & Davies, 1998). For Mona, the recorded species number has risen from twenty-one (Ramos, 1946) to fifty-three (Smith, Ramos & McKenzie, 1994b). By contrast, recent work has not added greatly to the species counts of the Greater Antilles. The Cuban list, for example, has received only three additions since 1987: *Ministrymon azia* (Smith & Hernández, 1992) and the newly described *Ministrymon hernándezi* and *Leptotes hedgesi* (Schwarz & Johnson, 1992). The Hispaniolan list has grown mainly through continuing descriptions of new *Calisto* species. Only one species, *Rhinthon cubana*, has been added to the Puerto Rican count during the last few years (Smith *et al.*, 1994a). Nine species have been added to the Jamaican list (refs. 35–37, 53–55 in Table 1) since the study of Brown & Heineman (1972).

Species-area relationship

Species richness was most strongly correlated with area when both were log-transformed ($r^2 = 0.64$, $F = 118.08$, $P<0.001$; Fig. 3). The power function, however, has not always provided the best fit. Table 2 shows the

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Table 1. Butterfly species richness and island data: Munroe (1948), Scott (1986), and 1997 (this paper)

Island	Area (km²)	Species richness			References (1997 data)
		1948	1986	1997	
Acklins (Bah)	497			28	1
Andros (Bah)	5957		60	66	2,3,4,5
Anegada (B.V.I.)	39			24	6
Anguilla	91			11	7
Antigua	280			31	8,9
Barbados	430	11		25	10,11,12
Barbuda	161			16	43
Bequia (St.V.&Gr.)	18			21	13,14
Biminis (Bah)	22		20	20	8
Caille (Gr.)	1			11	13
Caja de Muertos (P.R.)	1.6			11	15
Canouan (St V.&Gr.)	7			10	13
Carriacou (Gr.)	34			23	13
Cat (Bah)	388		24	25	8,16
Cayman Brac	36		22	30	17,18
Cayo Coco (Cuba)	370			50	42
Cayo Lobo (P.R.)	0.3			8	19
Cayo Luis Pena (P.R.)	1.3			16	19
Cayo Norte (P.R.)	1.4			12	19
Crooked (Bah)	181			36	1
Cuba	108660	109	171	182	20,21,22,52
Culebra (P.R.)	26			30	19
Culebrita (P.R.)	1			18	19
Dominica	751			52	8,23
Eleuthera (Bah)	518		37	38	8,24
Florida (Dade/Munroe Co.)	8500			110	7
Grand Bahama (Bah)	1373			23	8
Grand Cayman	197		41	46	17,18,25
Grand Turk	18			28	26
Grenada	345			47	7,8,27
Gt Abaco (Bah)	1681			26	8
Gt Exuma (Bah)	210		25	33	8,24
Gt Inagua (Bah)	1500		34	37	28,29
Guadeloupe	1438			44	27
Guana Island (B.V.I.)	2.8			31	30
Hispaniola	76190	117	177	202	7,31,32
Iles des Saintes (Guad.)	13			11	27
Isle of Pines (Cuba)	2200		68	111	33
Jamaica	11424	81	126	128	34–37, 53–56
La Desirade (Guad.)	20			10	27
Lignumvitae (FL)	1			41	38,39
Little Cayman	26		24	23	17
Little Inagua (Bah)	127		19	19	28
Long (Bah)	448		31	31	8
Marie Galante (Guad.)	158			17	27
Martinique	1079			38	27
Mayaguana (Bah)	285			24	1
Mayreau (St V.&Gr.)	3			15	13
Mona (P.R.)	62		19	53	40
Montserrat	106			39	41
Mustique (St V.&Gr.)	5			16	13

continued

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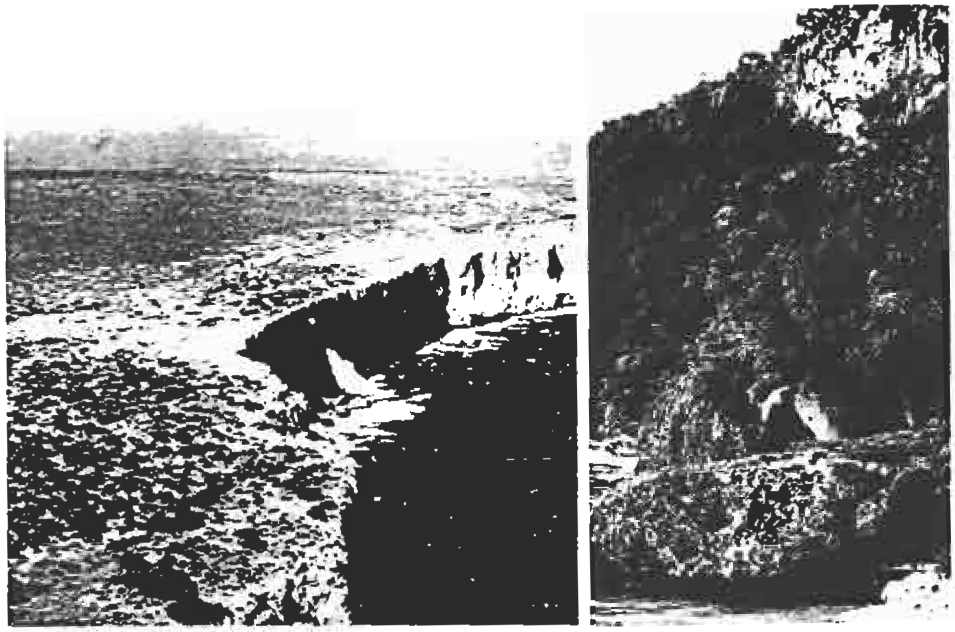
Table 1. Butterfly species richness and island data, Munroe (1948), Scott (1986), and 1997 (this paper)—*continued*

Island	Area (km^2)	Species richness			References (1997 data)
		1948	1986	1997	
Nevis	93			16	8,17
New Providence (Bah)	207		47	60	4,7,44,45
North Caicos	121			28	26
Palm (St.V.&Gr.)	0.5			9	13
Puerto Rico	8866	72	106	97	8,46
Rum Cay (Bah)	78		26	47	
Saba (D.A.)	13			22	8,17
San Salvador (Bah)	163		44	48	8,24,48
St Croix (U.S.V.I.)	212	24	41	41	49
St John (U.S.V.I.)	53		24	8	
St Kitts	168			42	7,8,50
St Lucia	617			48	51
St Thomas (U.S.V.I.)	80		33	8	
St Vincent	344			41	8
St Bartholomew (Guad.)	21			21	8,17
St Eustatius (D.A.)	21			14	8,17
Tortola (B.V.I.)	129	25			
Union (St.V.&Gr.)	11			22	13
Bahamas	777	43			
Caymans	518	32			
North Lesser Antilles	280	28			
South Lesser Antilles	984	46			
Virgin Islands	78	28			

Key to references in Table 1:

1. Miller, Simon & Harvey (1992); 2. Clench (1977); 3. Harvey & Peacock (1989); 4. Knowles & Smith (1995); 5. Smith, D.S. (unpubl. data); 6. Smith, Miller & McKenzie (1991); 7. Smith, Miller & Miller (1994a); 8. Scott (1986); 9. Miller L.D. & Miller J.Y. (pers. comm.); 10. Pearce (1969); 11. Schwarz (1990); 12. Russell (1992); 13. Davies (1989); 14. Smith D.S. & Davies, N. (unpubl. data); 15. Gaud & Martorrel (1974); 16. Clench, H.K. *In* (7) p.228. 17. Schwarz, Gonzalez & Henderson (1987); 18. Miller & Steinhauser (1992); 19. Smith, D.S. & McKenzie F. (unpubl. data); 20. Alayo & Hernandez (1987); 21. Schwarz & Johnson (1992); 22. Smith & Hernandez (1992); 23. Evans, P. (pers. comm.); 24. Knowles, D.O. (pers. comm.); 25. Askew (1988); 26. St. Leger (1991); 27. Pinchon & Enrico (1969); 28. Clench & Bjorndal (1980); 29. Simon & Miller (1986); 30. Becker & Miller (1992); 31. Schwarz (1989); 32. Smith, Classey & Ramos (1989); 33. Smith, Hernandez & Davies (1998); 34. Brown & Heineman (1972); 35. Vane-Wright, Ackery & Turner (1992); 36. Johnson & Smith (1993); 37. Iftner, Shuey & Calhoun (1993); 38. Leston, Smith & Lenczewski (1982); 39. Minno & Emmel (1993), 40. Smith, Ramus & McKenzie (1994b); 41, Schwarz & Jimenez (1982); 42. Hernandez *et al.* (in prep.); 43. Schwarz & Henderson (1990); 44. West (1966); 45. Knowles, D.O. & Smith, D.S. (unpubl. data); 46. Ramos (1982); 47. (8) pp.213; 48. Elliott, Riley & Clench (1980); 49. Miskimen & Bond (1970). 50. (7) p.116. 51. Hunt & Mitchell (1979); 52. Albelo, Hernández & Smith (1995); 53. Turner & Miller (1992); 54. Johnson & Balint (1995); 55. Vhymeister (1980); 56. Turner & Parnell (1985).

regression statistics recalculated from the two earlier surveys (Munroe, 1948; Scott, 1986). According to Munroe (1948), the exponential function (species number versus log-area) gave the strongest correlation, whilst for Scott (1986) the power and exponential functions gave very similar results. Table 2 also shows how the slope of the species-area regression (on a log-log plot) appears to have decreased somewhat over the three surveys (from $z = 0.26$ to $z = 0.20$). However, today's slope is not significantly different from that of 1948 ($F = 0.885$, $P = 0.35$), nor that of 1986 ($F = 2.37$, $P = 0.13$). Similarly, although the intercept has increased (from $c = 0.80$ to $c = 1.06$), there is no statistical difference among the three data sets (ANCOVA: $F = 1.72$, d.f. $= 2{,}99$, $P = 0.18$).



1

2

Figs 1 and 2. Mona Island, lying between Hispaniola and Puerto Rico, is only 51 km^2 in area, but has a high species count (fifty-three). A cliff defines the island's perimeter, and in the east (Fig. 1), exposed to prevailing winds, the vegetation is xeric ground cover. This merges further west into low, dry limestone forest. Along the cliff in the south-west (Fig 2) a more mesic forest is present; a very restricted area that supports several butterfly species. The richness of the island's fauna is attributed, in part, to its unusual state of ecological preservation and in part to habitat diversity. Its biogeographical importance is further stressed by the bias of its butterfly fauna towards Puerto Rico to the east as a donor source, reflecting the asymmetric prevailing wind pattern, rather than the much larger island of Hispaniola to the west (Smith *et al.*, 1994b).

Table 2. History of the species-area relationship for West Indian butterflies

	Exponential function		*Power function*	*Power function*			
Survey	N	r^2	r^2	F	P	z	c
Munroe (1948)	11	0.92	0.75	27.32	<0.001	0.26	0.80
Scott (1986)	24	0.83	0.85	124.15	<0.001	0.26	0.91
This paper	68	0.54	0.64	118.08	<0.001	0.20	1.06

DISCUSSION

Estimating species richness

Butterfly species richness in the West Indies has generally been underestimated, which probably reflects insufficient sampling. The underestimation of butterfly species richness is especially likely in the tropics where phenological patterns are poorly known. West Indian butterflies may have one, two, or several generations a year. The period when adults are flying could be short and variable as it is probably determined by local conditions. As most studies of West Indian butterflies sample only the adult population, species are easily overlooked during short surveys. Field observers often miss species that have been found previously (often at the same site and at the same time of year). It is usually impossible to determine whether colonies have gone extinct or are merely at an immature stage (eggs, larvae or pupae). Only the careful monitoring of remnant populations can demonstrate extinction, e.g. *Maculinea arion* in Britain (Thomas & Lewington, 1991). Extinction cannot even be assumed for butterflies that have not been recorded for generations. A single specimen of the skipper *Epargyreus spanna* was collected in Hispaniola in 1855 and the next in 1983

(Gali & Schwartz, 1983). The Cuban skipper *Chioides marmorosa* had not been recorded this century until its rediscovery in a relatively accessible part of the island (Albelo, Hernandez & Smith 1995). These species would certainly have been discounted if we had set a 'statute of limitations' on species records.

In addition to the problems of recognizing extinction, what should constitute immigration? If a single individual of a species is found on an island it is clearly present but should it be added to the list without evidence of a resident (i.e. breeding) population? For butterflies that could mean a single gravid female. In practice it is often difficult to establish whether a butterfly is breeding on an island, and for museum specimens it is impossible. Reliable records of butterflies in the West Indies should be counted irrespective of sex or supposed breeding status. A related difficulty is how to score species that regularly colonize islands, go extinct after a couple of generations, only to reappear a few years later as another temporary colony is established. A possible example of this is *Hamadryas amphinome mexicana* which was common in western Cuba in 1930 but disappeared until 1976. An arrival may be unsuccessful on one occasion but succeed the next; colonization may even be transient in one region of an island but long-lasting in another. Within the last three decades, butterflies reaching south Florida from Cuba and/or the Bahamas show a spectrum of colonisation success, from established breeding populations to colonies surviving only very briefly (Smith *et al.*, 1994a). In archipelagos, species may commonly range from permanent breeding populations to single-generation vagrant colonies. With long-term and detailed surveying, such metapopulations could be categorized, however, this remains a distant goal in the West Indies. At the moment, colonization success is more readily recognized than failure, hence risking an overestimation of the 'true' species number (vagrants are scored as residents and extinct species are included). This error is reduced, however, by the number of species overlooked. The latter is probably a more significant source of error and our species numbers should, therefore, be viewed as minimum estimates.

Stability of the species-area relationship

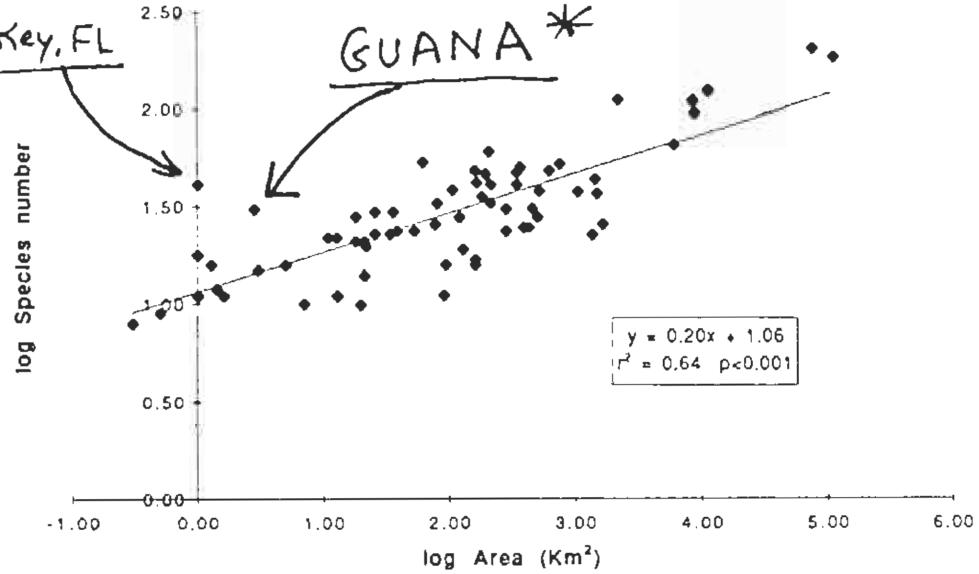
The data presented here for West Indian butterflies support Preston's (1962) prediction that species richness is related to area according to a power function (Fig. 3). However, this has not always been the case; in 1948 the exponential function yielded a higher correlation coefficient in the linear regression (Munroe, 1948). The progression from an exponential function to a power function suggests that earlier surveys were based on insufficient data to avoid sampling errors—an exponential function is expected when area is simply a measure of sample size (May, 1975). Differences in species richness among islands may reflect the number of individuals sampled as much as real differences in species number (Williams, 1964). Small islands, in particular, are likely to have been inadequately sampled; indeed many of the smallest West Indies were not even included in the earlier surveys of Munroe (1948) and Scott (1986). The inclusion of additional small islands, together with the more rapid accumulation of new records from the small islands, might explain why the slope of the species-area regression has flattened slightly. However, the change in slope is not statistically significant. Furthermore, the species-area relationship is similar if one treats only the smallest islands (Davies, 1989).

Differences in the species-area relationship probably reflect biological differences among taxa. Low z-values are often assumed to indicate high immigration rates, whilst steep regression lines suggest substantial isolation among islands (Preston, 1962; MacArthur & Wilson, 1967; but see Gilbert, 1980; Gotelli & Abele, 1982). For example, Minno & Emmel (1993) found that island area had no effect on butterfly species richness in the Florida Keys, presumably because of their extreme proximity to the mainland. Adler & Dudley (1994) reported a slope of 0.45 for the isolated butterfly faunas of the tropical Pacific. Comparisons between taxa from the same archipelago are more likely to be informative as they reduce the possible confounding effect of isolation, produced where island isolation (which is very difficult to measure in most archipelagos) is correlated with island area (Lomolino, 1989). Wilcox (1980) reported slopes for various West Indian groups: breeding land birds, $z=0.24$ (Lack, 1976), herpetofauna, $z=0.38$ (Schwarz & Thomas, 1975), recent land mammals, $z=0.48$ (Varona, 1964), and bats, $z=0.24$ (Varona, 1964). Other studies have recorded slopes of 0.34 in beetles (Darlington, 1943), 0.28 in ants (Wilson, 1988) and 0.37 in plants (Davies, Smith & Whittaker, unpubl. data).

To our knowledge, the butterfly slope of 0.20 is therefore the flattest so far recorded in the West Indies. This is relevant to the long-standing debate in West Indian biogeography: are the faunas shaped mainly through vicariance (Schubert, 1935; Rosen, 1976, 1985) or dispersal (Mathew, 1915; Simpson, 1952;

Lignumvitae Key, FL

GUANA *



Base 10!

Fig. 3. Species-area relationship for West Indian butterflies

Darlington, 1957)? One interpretation of a flat regression is that West Indian butterflies have a general propensity for dispersal and colonization. Of course, this does not mean that all West Indian butterflies are good dispersers, merely that the West Indian archipelago represents a less subdivided environment for butterflies than for many other taxa. Vicariance, however, cannot be excluded. An alternative interpretation of a low *z*-value is that West Indian butterflies have low extinction rates relative to other taxa. Changes in sea level during the Pleistocene meant that many of the smaller islands were once considerably larger. If extinction rates for butterflies are lower than for other West Indian taxa, the butterfly faunas of small islands may retain an inflated level of diversity (and hence a flatter species-area regression) simply because they are taking longer to reach equilibrium. For example, a tiny population of *Calisto anegadensis*, endemic to Anegada in the Virgin Islands, has probably survived at least 15,000 years since the Puerto Rican bank was last exposed (Smith, Miller & McKenzie, 1991; Smith *et al.*, 1994a).

In conclusion, the species-area relationship for West Indian butterflies has been stable for almost 50 years. It seems, therefore, that preliminary observations of the species-area relationship may hold-up quite well as more data are collected. Determining the species-area relationship, however, is only a first step towards understanding the processes which underlie insular biodiversity. Variables other than area are also likely to be important and future work will investigate the influence of island elevation, isolation, latitude, and habitat diversity.

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* See Note at End.

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ERRATUM

Neil Davies and David Spencer Smith: Munroe revisited: a survey of West Indian butterfly faunas and their species area relationship. *Global Ecology and Biogeography Letters*, **7**, 285–294.

We regret that some typesetting errors occurred in Table 1. These did not affect any of the calculations reported in the paper. The corrected entries are as follows:

	Area	1948	1986	1997	References (1997 data)
Rum Cay	78		26	26	47
St John	53		24	24	8
St Thomas	80		33	33	8
Tortola	129	25		31	30

Note that Tortola has the same number of species as Guana but is 46 times as large. Lignum Vitae Key, Florida, beats Guana, but it is a continental shelf island, not on an oceanic bank that has no continental connections historically.

St. Thomas beats us by 2 species but is 29½ times as large. We beat St. John by 7 species, even though it is 19 times bigger.

Area is a lousy predictor of diversity compared to ecology!

BREVIORA

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NEW RECORDS AND DISTRIBUTIONAL AND ECOLOGICAL NOTES OF LEPTODACTYLID FROGS, *LEPTODACTYLUS* AND *ELEUTHERODACTYLUS*, FROM THE BRITISH VIRGIN ISLANDS

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ABSTRACT. Information on distribution and habitat use of frogs in the British Virgin Islands is needed for assessing population trends and status and for elucidating biogeographic patterns. We discovered 10 new populations of the four known species of Leptodactylidae on five of the 17 islands visited: *Eleutherodactylus antillensis* on Great Camanoe, Great Thatch, Jost Van Dyke, and Beef Island; *E. schwartzi* on Beef Island, Frenchmans Cay, and Jost Van Dyke; *E. cochranae* on Great Thatch and Jost Van Dyke; and *Leptodactylus albilabris* on Beef Island. We confirmed all but three previous island records: *E. cochranae* and *L. albilabris* on Virgin Gorda and an unidentified *Eleutherodactylus*, known only from the stomach of a snake, on Peter Island. The earlier *E. cochranae* record is probably in error, but *L. albilabris* and *Eleutherodactylus* seem to have disappeared from Virgin Gorda and Peter Island, respectively. The mean body size of adult males of *E. antillensis* and *E. schwartzi* was smaller on Virgin Gorda than on Tortola, and males of *E. schwartzi* were relatively large on the tiny (33 ha) island of Great Dog. On all islands except Tortola, *E. schwartzi* was almost exclusively associated with bromeliads. Island elevation and area explained 61% of the variation in the number of species when all 17 islands were included in the

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model. Elevation was the most important factor (partial r^2 = 0.35), whereas area explained little of the observed variation (partial r^2 = 0.02). The availability of specific habitat features, such as aquatic breeding sites for *L. albilabris* and retreat and nesting sites for *Eleutherodactylus*, are critical for populations on small islands. The distribution patterns in the British Virgin Islands do not indicate widespread extirpations or declines of frogs comparable to those observed in Puerto Rico and other parts of the world.

> *. . . there is an urgent need to document the distribution and abundance of amphibians.*
>
> *Leonard (1997)*

INTRODUCTION

Precipitous declines in a number of anuran populations within the past few decades have led to local extirpations and even species extinctions (Mittermeier *et al.*, 1992; Pechmann and Wilbur, 1994; Phillips, 1994; Blaustein and Wake, 1995). In Puerto Rico alone, three species of frogs (genus *Eleutherodactylus*, family Leptodactylidae) have disappeared within the past 20 years, and an additional seven show serious declines (Rivero, 1991; Joglar and Burrowes, 1996). Efforts to document and understand changes in anuran population and distribution characteristics are severely constrained by the paucity of baseline data, making it difficult to distinguish between natural population fluctuations and those caused by human activities. Furthermore, in many cases, we simply do not know where populations occurred or still occur. Knowledge of habitat requirements and factors that limit the growth of populations is also incomplete for most species of frogs in neotropical areas.

The British Virgin Islands (BVI), located on the easternmost portion of the Puerto Rico Bank in the Caribbean Sea, consist of about 50 islands, some of which are mere rocks or sand bars. During the last glacial maximum, the entire bank was united as a single land mass, which subsequently fragmented into numerous islands with the rising of sea levels (Heatwole *et al.*, 1981). Most of the islands have been isolated from each other and the rest of the bank for approximately 4,000–10,000 years (reviewed by Lazell, 1983).

Four species of leptodactylid frogs occur in the BVI: *Leptodactylus albilabris, Eleutherodactylus antillensis, E. schwartzi,* and *E. cochranae* (MacLean, 1982). All but *E. schwartzi*, which is endemic to the BVI, are widespread on the islands of the Puerto Rico Bank and also occur in Puerto Rico itself (Rivero, 1978; MacLean, 1982; Schwartz and Henderson, 1991).

Leptodactylus albilabris has a biphasic life cycle with aquatic larvae, whereas *Eleutherodactylus* species are completely terrestrial and have direct development. The distribution and habitat use patterns of all four species on the islands are poorly known, although other components of the herpetofauna of the BVI have received intensive attention over the past two decades (Mayer and Lazell, 1988; Lazell, 1983, 1991, 1995; Dmi'el *et al.*, 1996). Lazell (1983) was aware of seven populations of leptodactylid frogs on four islands of the BVI. Mayer and Lazell (1988) added two new island records, including one for an islet of only 24 ha (Frenchmans Cay). Lazell (1991) reported a previously overlooked record for the 33-ha Great Dog Island (Heatwole *et al.*, 1981), bringing the total number of known populations to 11 on seven different islands. Ten additional islands that are larger than Frenchmans Cay had not been surveyed for frogs before our study. In many cases, the survey coverage of those islands known to support frogs was incomplete.

Every October from 1993 to 1997, we investigated the distribution and ecology of leptodactylid frogs in the BVI. Based on surveys of 17 islands, we report on the distribution of *Leptodactylus* and *Eleutherodactylus* species, including new island records for 10 populations. Our objectives were to (a) compile baseline data on the distribution, habitat use, and natural history of the frogs on different islands; (b) compare present distributions to historical records; and (c) examine the pattern of distribution in relation to predictions from island biogeography (MacArthur and Wilson, 1967; Lazell, 1983).

METHODS

Survey Methods

Our operations were based on Guana Island, located ca. 0.5 km north of the east end of Tortola, BVI. The survey periods were 7–30 October 1993, 2–21 October 1994, 3–19 October 1995, 8–28 October 1996, and 8–28 October 1997. During these periods, we also visited the following islands one or more times: Tortola (14–16 October 1993; 4–6, 13–15 October 1994; 6–8, 14–15 October 1995; 11–12, 15–16, 19–20 October 1997), Beef Island (3–5 October 1995, 23 October 1996), Frenchmans Cay (7 October 1995), Virgin Gorda (26–28 October 1993, 9–11 October 1994, 17–18 October 1996), Jost Van Dyke (11–12 October 1995), Great Dog (10–11, 16 October 1996; 21 October 1997), Great Camanoe (12 October 1996), Scrub (13 October 1996), Mosquito (16–17 October 1996), Anegada (20–21 October 1996), Cooper (22–23 October 1996), Peter (24–25 October 1996, 25–26 October 1997), Great Thatch (26–27 October 1996), and Great Tobago (17–18 October 1997). We also present data for Necker and Little Thatch, where residents have been listening for frogs for several years and one of us (JL) spent several rainy nights (three nights in October 1993 on Necker and one night in October 1996 on Little Thatch).

We used visual encounter surveys, auditory transect surveys, and night driving methods to locate frogs (Heyer *et al.,* 1994). We walked along trails in likely habitats after sunset listening for calls of males, and we scanned the ground and vegetation with headlamps for frogs. In 1996, we also played recorded advertisement calls of *E. antillensis* and *E. schwartzi* to induce frogs to call. In 1995 and 1996, the use of a car allowed us to cover longer distances on larger islands (Tortola, Beef Island, Anegada, Virgin Gorda); we stopped every few minutes to listen for frog calls. For each new island record, we collected at least one voucher specimen, which was deposited in the Museum of Comparative Zoology, Cambridge, Massachusetts (MCZ).

In 1993, we systematically recorded information on each *Eleutherodactylus* heard or seen during those surveys carried out on foot and noted the following for each frog captured: species, sex, calling or not (for males), gravid or not (for females), snout–vent length (SVL), weight, microhabitat (ground, tree or bush, bromeliad, agave, herbaceous vegetation), and perch height. In 1994 and 1995, we obtained comparable information only for frogs included in a separate study on vocal behavior. In 1996, we measured the body size of *E. schwartzi* on Great Dog and Virgin Gorda to examine the hypothesis suggested by initial observations that the frogs on Great Dog were relatively large. We also measured the body size of a sample of *E. antillensis* on Guana in 1996.

To obtain additional information on habitat use and dispersion of *Eleutherodactylus,* we set up auditory transects in October 1994 on three islands (Guana, Tortola, and Virgin Gorda) and in October 1996 on Guana. In 1994, there were two transects on Guana, two on Sage Mountain, Tortola, and one on Gorda Peak, Virgin Gorda. On Guana, Transect 1 was in the north of the island along a ridge where *E. antillensis* appeared to be abundant, and Transect 2 was near the southwest tip of the island where an isolated patch of the species occurred.

The transects followed the course of relatively straight sections of existing trails or paths, which marked the middle of the transect. In 1994, each transect was 150 m long and 6 m wide. In 1996 on Guana, Transect 1 was 815 m long and Transect 2 was 300 m long. We increased their width from 6 m to 10 m, because previous observations indicated that we could accurately record all calling frogs within 5 m from the center of the transect. We placed a flag every 5 m in the center of the transect to divide it into sections of 3 × 5 m (in 1994) or 5 × 5 m (in 1996) on each side of the transect.

In 1994, we recorded the presence/absence of arboreal and terrestrial bromeliads with a crown diameter >10 cm in every 5-m × 3-m section of the transect. In 1996 on Guana, we measured habitat variables only for Transect 1. The variables measured for each 5-m × 5-m section were: (a) sum of crown diameters of bromeliads (none, not present; low, <30 cm; moderate, 30–100 cm; high, >100 cm), (b) percentage of ground covered by leaf litter, (c) depth of leaf litter/humus (measured for 152 or 47% of the 5-m × 5-m sections), and percent vegetation cover at heights of (d) <1 m, (e) 1–2 m, and (f) >2 m. The depth of the leaf litter and humus in each section was the average of three randomly located measurements obtained by poking a pencil in the leaf litter and measuring the depth of penetration. We estimated the percentage of ground covered by vegetation at different vertical layers and by leaf litter visually.

To survey frogs, two observers walked along the midline of the transect after sunset and recorded the number and species of calling males in each section of the transect. We traced the exact location of frogs only when this was required to verify their presence within the transect boundaries. In 1994, we surveyed the transects for frogs on Guana on four consecutive nights (17–18, 18–19, 19–20, and 20–21 October). Transect 1 was surveyed twice each night on two nights and three times on one night to obtain information on the consistency of the number of calling frogs within nights. Transect 2 was surveyed once on 18 October. In 1996, we surveyed Transect 1 once each on 18 and 25 October and twice on 28 October. Transect 2 was surveyed once (on 18 October). We surveyed both transects on Tortola twice on 13 October 1994 and the transect on Virgin Gorda once on 10 October 1994. We checked transects only on nights when rain had fallen during the 24-hour period prior to the search, and conditions were favorable for calling.

Data Analysis

We used a multiple regression analysis to examine the effects of island size and elevation on the number of species present. We also applied multiple regression to a reduced data set that excluded both islands that contained the full complement of four species (Tortola and Jost Van Dyke) to include the distance from potential source populations in the analysis. The source for island size and elevation was Lazell (1983). The distance to the nearest potential source population was measured as the shortest distance between an island and either Tortola, Jost Van Dyke, or Virgin Gorda, whichever distance was shortest.

We used one-way ANOVA to examine differences in body size of adult male *E. antillensis* and *E. schwartzi* among years. We also used ANOVA to compare SVL of *E. antillensis* and *E. schwartzi* among years and islands.

We calculated the variance/mean ratio as an index of dispersion of calling males of *E. antillensis* in 5-m and 50-m sections of Transect 1 on Guana in 1996 and used the χ^2 test to determine whether the pattern was significantly different from random (Krebs, 1989). We performed a multiple regression analysis to examine the effects of habitat variables, measured in each 5-m × 5-m section of the transect, on the number of calling frogs on Guana on 28 October 1996, when the number of frogs was the greatest. We also performed the same analysis using the number of 5-m × 5-m sections with frogs (1) and without frogs (0) as the dependent variable. The value for each section of the transect in the second case was determined based on whether calling frogs were found within a transect section during any of the four surveys in 1996.

DISTRIBUTION

Species Diversity

The number of species per island varied from zero to four (Table 1). Only two islands, Tortola and Jost Van Dyke, contained the full complement of four species. One island had three species, three had two, and four had one. We found no frogs on the remaining seven islands.

Area and elevation explained 60.7% of the variance in the number of species among islands (multiple regression: $F_{2,14} = 10.8$, $P = 0.002$). Elevation explained most of this variance (simple $r = 0.76$, partial $r^2 = 0.35$), whereas island area contributed very little to the model (simple $r = 0.51$, partial $r^2 = 0.02$). When the two islands with the full complement of species were deleted from the analysis and the distance to nearest potential source population was added as an independent variable, the model was marginally significant ($r^2 = 0.51$, $F_{3,11} = 3.79$, $P = 0.04$). In this model, island area (simple $r = 0.22$, partial $r^2 = 0.25$) and distance to a potential source population (simple $r = -0.007$, partial $r^2 = 0.21$) explained most of the variance, whereas the contribution of elevation was small (simple $r = 0.50$, partial $r^2 = 0.001$).

Leptodactylus albilabris

We found *L. albilabris* on four of the 17 islands: Beef, Tortola, Jost Van Dyke, and Anegada (Table 2). This species had not been previously documented from Beef (372 ha), separated from Tor-

TABLE 1. NUMBER OF SPECIES OF FROGS IN RELATION TO ISLAND AREA, ELEVATION, AND DISTANCE FROM A POTENTIAL SOURCE POPULATION. ISLAND AREA AND ELEVATION ARE FROM LAZELL (1983). DISTANCES FOR EACH ISLAND WERE MEASURED EITHER FROM TORTOLA, JOST VAN DYKE, OR VIRGIN GORDA (WHICHEVER DISTANCE WAS SHORTEST).

Island	No. of Species	Area (km^2)	Elevation (m)	Distance to Potential Source Population (km)
Tortola	4	5,444	521	NA
Anegada	1	3,872	8.5	32.5 (Tortola)
Virgin Gorda	2	2,130	414	11.7 (Tortola)
Jost Van Dyke	4	840	398	NA
Peter	0	429	177	5.5 (Tortola)
Beef	3	372	244	0.1 (Tortola)
Great Camanoe	1	337	187	2.1 (Tortola)
Guana	1	297	266	0.5 (Tortola)
Cooper	0	138	155	6.8 (Tortola)
Great Thatch	2	123	187	0.7 (Tortola)
Scrub	0	97	141	3.7 (Tortola)
Great Tobago	0	87	147	4.0 (Jost Van Dyke)
Mosquito	0	50	95	17.7 (Virgin Gorda)
Great Dog	1	33	89	11.1 (Virgin Gorda)
Necker	0	30	32	22.0 (Virgin Gorda)
Frenchmans Cay	2	24	131	0.1 (Tortola)
Little Thatch	0	24	100	0.5 (Tortola)

tola by a ca. 100-m wide channel. Our attention was first called to the presence of *L. albilabris* on this island by Dr. Gregory Mayer, who reported hearing calls and locating tadpoles, which were inspected by one of us (JL), in temporary pools among rocks in scrub vegetation several years ago. We did not locate this site but found *L. albilabris* in muddy ditches around the airport (MCZ 124777–81, 125954). In 1995, we located several males calling from inside tufts of grass and from small cavities in the mud banks close to the water's edge, as well as many metamorphosed juveniles. We did not hear calls of *L. albilabris* east of the airport.

On Tortola, we heard calls of *L. albilabris* from roadside ditches throughout the island and from small pools on Sage Mountain (MCZ 107339, 110992–5, 117677). On Jost Van Dyke, we heard

L. albilabris in a riverbed by Old Hill west of White Bay and in a marshy site in the town of Great Harbour (MCZ 110990–1).

On Anegada, we found several concentrations of *L. albilabris* in an area called the Slob, ca. 1.5 km northwest of the airport (MCZ 125953). The frogs were in wet areas under dense shrubs on coral-limestone substrate covered by leaf litter and humus. Several males were calling from land crab holes, and we also saw many metamorphosed juveniles.

We did not find *L. albilabris* on any of the other islands, including Virgin Gorda, which we visited in three different years. In 1993 and 1994, our surveys were confined to Gorda Peak, but in 1996, we spent many hours driving around the island after sunset during and after rain. Extensive pools were present on Gorda Peak in 1993, but these were dry in 1994 and contained little water in 1996. Roadside ditches, where these frogs commonly occurred on Tortola, contained water, but we detected no frogs. Small, temporary freshwater puddles were present on Great Camanoe.

Eleutherodactylus antillensis

We found *E. antillensis* on eight of the 17 islands visited: Virgin Gorda, Great Camanoe, Guana, Beef, Tortola, Frenchmans Cay, Great Thatch, and Jost van Dyke (Table 2). The species has not been previously reported from Great Camanoe, Great Thatch, or Beef (MCZ 132823). In addition, we have found no previous records of *E. antillensis* from Jost Van Dyke, although MacLean (1982) reported the distribution of the species to encompass "all major islands" of the Virgin Islands. On Jost Van Dyke, calling males of *E. antillensis* were patchily distributed in areas west of White Bay toward Old Hill and east to Great Harbour, including the town site (MCZ 124786). On Great Camanoe, we located frogs in the hills on the southwest portion of the island (MCZ 125949). On Great Thatch, we found *E. antillensis* throughout the densely vegetated south slope of the island (MCZ 125950).

Eleutherodactylus schwartzi

We located *E. schwartzi* on six of the 17 islands visited: Virgin Gorda, Great Dog, Beef, Frenchmans Cay, Tortola, and Jost Van

TABLE 2. RECONFIRMED, UNCONFIRMED, AND NEW ISLAND RECORDS FOR LEPTODACTYLID FROGS IN THE BRITISH VIRGIN ISLANDS.[a]

Island	Survey Dates	Species: New Record	Species: Previous Record Confirmed	Species: Previous Record Not Confirmed	Source of Previous Records
Anegada	20–21 Oct. 1996	—	La	—	MacLean, 1982
Virgin Gorda	26–28 Oct. 1993 9–11 Oct. 1994 17–18 Oct. 1996	—	Ea, Es	Ec, La	MacLean, 1982 (all 4 spp.); Schwartz and Henderson, 1985 (Es)
Great Dog	10–11, 15 Oct. 1996 21 Oct. 1997	—	Es	—	Heatwole *et al.*, 1981
Great Camanoe	12 Oct. 1996	Ea	—	—	
Guana	7–30 Oct. 1993 2–21 Oct. 1994 9–19 Oct. 1995 8–18 Oct. 1996 8–28 Oct. 1997	—	Ea	—	Mayer and Lazell, 1988; Lazell, 1991
Beef Island	3–5 Oct. 1995 23 Oct. 1996	Es, La, Ea	—	—	
Tortola	14–16 Oct. 1993 4–6, 13–15 Oct. 1994 6–8, 14–15 Oct. 1995 11–12, 15–16, 19–20 Oct. 1997	—	Ea, Es, Ec, La	—	MacLean, 1982 (all 4 spp.); Schwartz and Henderson, 1985 (Es)

TABLE 2. CONTINUED.

Island[1]	Survey Dates	Species: New Record	Species: Previous Record Confirmed	Species: Previous Record Not Confirmed	Source of Previous Records
Peter Island	24–25 Oct. 1996 25–26 Oct. 1996		–	E. sp.	Henderson and Sadjak, 1996 (*Eleutherodactylus* in stomach of snake)
Frenchmans Cay	7 Oct. 1995	Es	Ea	–	Mayer and Lazell, 1988 (Ea)
Great Thatch	26 Oct. 1996	Ea, Ec	–	–	–
Jost Van Dyke	11–12 Oct. 1995	Ea, Es, Ec	La		Schwartz and Thomas, 1975 (La); MacLean, 1982 (La)

[1] Ea, *Eleutherodactylus antillensis*; Ec, *E. cochranae*; Es, *E. schwartzi*; La, *Leptodactylus albilabris*; E. sp, unidentified species of *Eleutherodactylus*.

Dyke (Table 2). The presence of this species on Beef, Frenchmans Cay, and Jost Van Dyke was previously undocumented. On Beef, we found *E. schwartzi* along the road that transects the island and in a patch of terrestrial bromeliads (*Bromelia pinguin*) along a path that diverges from the main road near its northern end (MCZ 124782).

On Frenchmans Cay, we heard calls of *E. schwartzi* from gardens along the road east from the bridge to Tortola (MCZ 124783). On Jost Van Dyke, we heard calls of scattered *E. schwartzi* from gardens, pastures, and gullies in and around Great Harbour (MCZ 124785).

In 1996, we confirmed the presence of *E. schwartzi* on Great Dog Island (MCZ 125946–8), an islet of 33 ha, first reported by Heatwole *et al.* (1981). Numerous frogs were present in a ca. 13-m × 16-m patch of bromeliads, *Hohenbergia antillana*, located near the peak of the ridge that extends along the length of the island. In addition, on the night of 10–11 October 1996, we heard a single male calling near the beach in dense vegetation on the south side of the island ca. 500 m from this patch. We located five egg clutches of *E. schwartzi* on 10 October within bromeliads (Ovaska *et al.*, 1998).

We observed numerous *E. schwartzi* on Sage Mountain, Tortola, and on Gorda Peak, Virgin Gorda, and we also heard calls and observed frogs in other areas of these two islands (MCZ 107340–1, 115830–8, 117567–9, 117688–92, 119247–51, 116273, 124784, and U.S. National Museum of Natural History 329482–91).

Eleutherodactylus cochranae

We located *E. cochranae* on three of the 17 islands visited: Tortola, Jost Van Dyke, and Great Thatch (Table 2). The species has not previously been reported from Jost Van Dyke or Great Thatch. Based on advertisement calls by males, *E. cochranae* was the most widely distributed and abundant frog species in the areas surveyed on Jost Van Dyke (MCZ 124787–8). These included areas west from White Bay toward Old Hill and east to Great Harbour. Calling males were perched on cacti, trees, and arboreal and terrestrial bromeliads.

On Great Thatch, we surveyed the southern slope of the densly vegetated island and captured *E. cochranae* (MCZ 125951). On Tortola, we captured *E. cochranae* on Sage Mountain (MCZ 116269–71) and also heard advertisement calls from other forested locations, including sites near sea level. We did not hear calls of *E. cochranae* on Frenchmans Cay, a 24-ha islet separated from Tortola by a channel <10 m wide, although males were calling in adjacent areas on Tortola on the same night.

We also did not find *E. cochranae* on Virgin Gorda, although we searched for it several times in 3 years (1993, 1994, and 1996). MacLean (1982) lists this species from Virgin Gorda, but we have been unable to locate a voucher specimen or any other report of its occurrence there.

BODY SIZE OF *ELEUTHERODACTYLUS*

The SVL of calling males of *E. antillensis* did not show significant differences among years on any of the islands examined, although males tended to be smaller on Tortola in 1994 than in 1993 and 1995 (Guana: $F_{3,48} = 1.67$, $P = 0.19$; Tortola: $F_{2,49} = 3.07$, $P = 0.06$; Virgin Gorda: $F_{1,57} = 0.18$, $P = 0.67$). Similarly, there were no significant differences in SVL of *E. schwartzi* among years (Tortola: $F_{1,16} = 0.01$, $P = 0.90$; Virgin Gorda: $F_{2,36} = 0.38$, $P = 0.68$). The data for all years were therefore combined for analyses of interisland differences.

The average SVL of adult male *E. antillensis* varied among Guana, Tortola, and Virgin Gorda ($F_{2,141} = 24.9$, $P < 0.001$; Fig. 2). Males on Virgin Gorda were smaller ($\bar{x} = 27.2$ mm) than those on Guana ($\bar{x} = 29.3$ mm) and Tortola ($\bar{x} = 29.2$ mm). The average SVL of calling males of *E. schwartzi* also differed among islands ($F_{2,71} = 29.4$, $P < 0.001$; Fig. 1). Males were the smallest on Virgin Gorda ($\bar{x} = 22.3$ mm), largest on Great Dog Island ($\bar{x} = 25.6$ mm), and intermediate on Tortola ($\bar{x} = 23.8$ mm).

The average weight of calling males of *E. antillensis* was 1.7 g (SD = 0.1, $n = 51$; 1993–96 combined) on Guana, 1.3 g on Virgin Gorda (SD = 0.2 g, $n = 58$; 1993–94 combined), and 1.7 g on Tortola (SD = 0.3, $n = 52$; 1993–95 combined). The average weight of calling males of *E. schwartzi* was 0.9 g (SD = 0.2 g, $n = 16$; 1993 and 1994 combined) on Tortola, 0.8 g (SD = 0.1

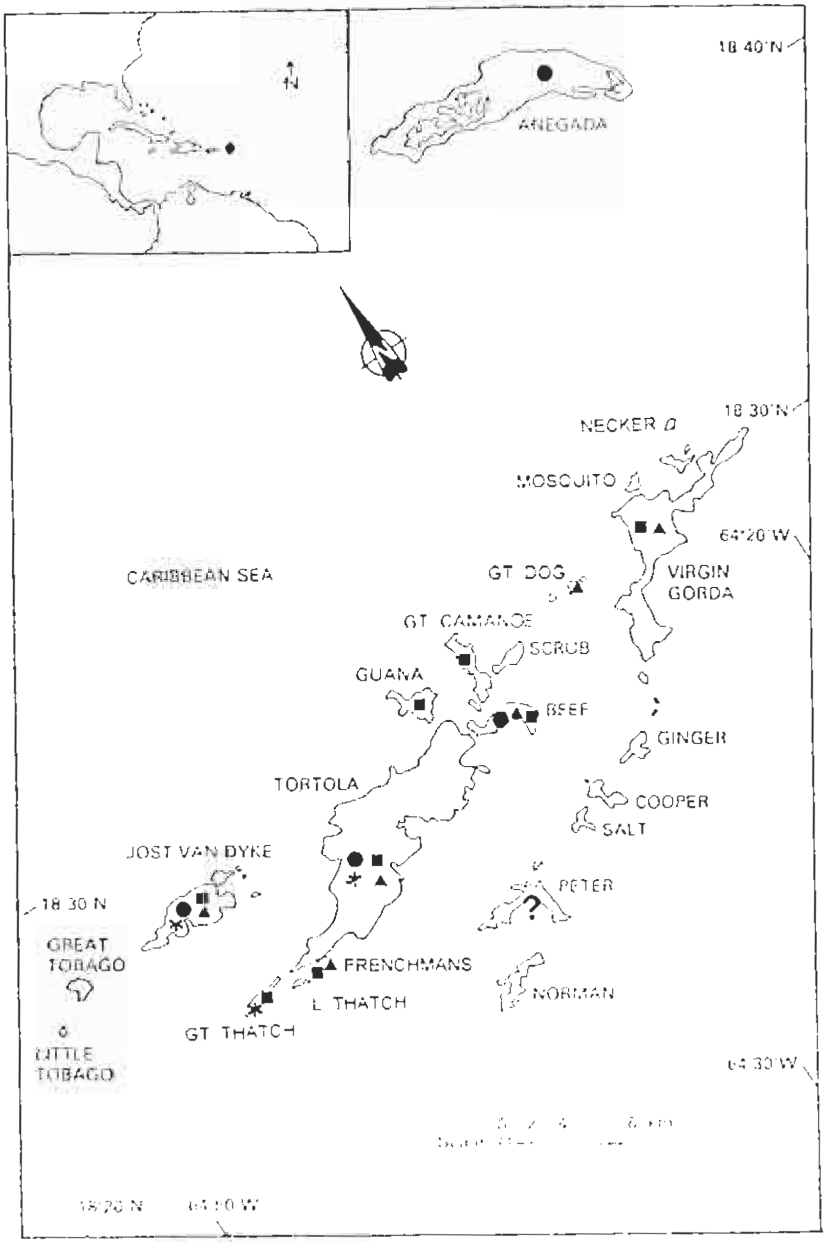

Figure 1. Map of the British Virgin Islands indicating major islands and those mentioned in the text. Insert shows the position of the these islands in the Caribbean. ● *L. albilabris*, ■ *E. antillensis*, ▲ *E. schwartzi*, ✻ *E. cochranae*.

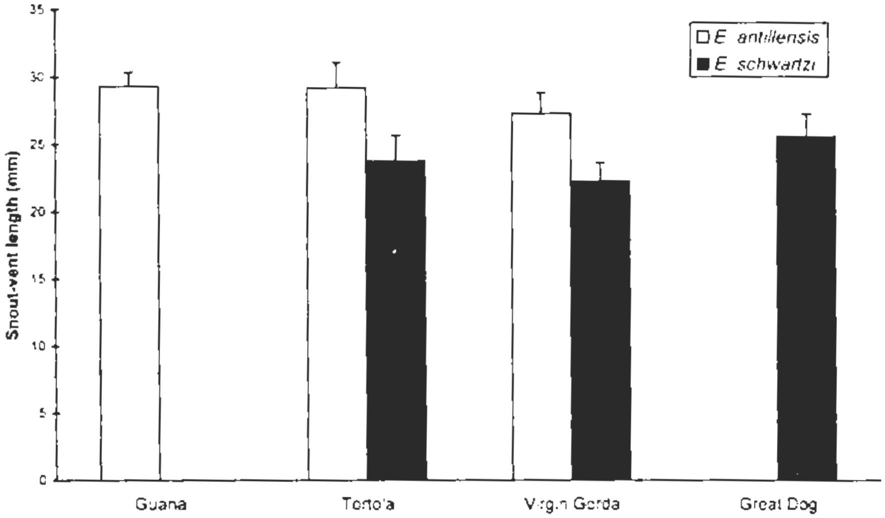

Figure 2. Snout–vent length (SVL) of calling males of *Eleutherodactylus antillensis* and *E. schwartzi* from Guana, Tortola, Virgin Gorda, and Great Dog. Mean, top of bars; 1 SD, vertical lines.

g, *n* = 39; 1993, 1994, and 1996 combined) on Virgin Gorda, and 1.2 g (SD = 0.2 g, *n* = 17; 1996) on Great Dog.

Both species were sexually dimorphic with respect to body size, females being larger than males. The SVL of 14 female *E. antillensis* measured in 1993 was 33.8 mm (SD = 4.6 mm, range = 28.0–43.2) and their weight was 2.7 g (SD = 1.2 mm, range = 1.2–4.8 g; all islands combined). Ten female *E. schwartzi* were 31.2 mm in SVL (SD = 3.0 mm, range = 25.5–35.5 mm) and weighed 1.9 g (SD = 0.4 g, range = 1.2–2.7 g).

HABITAT USE BY *ELEUTHERODACTYLUS*

Eighty-nine percent of all male *E. schwartzi* (*n* = 45) and 74% of male *E. antillensis* (*n* = 171) located in October 1993 were perched in vegetation <2.5 m high while calling (data for Tortola, Virgin Gorda, and Guana combined). The remaining 11% of calling *E. schwartzi* and 26% of *E. antillensis* were perched higher than 2.5 m and thus were out of our reach. We did not capture *E. cochranae* in 1993, although we audiotaped calls of this species on Tortola. In 1994, we captured nine *E. cochranae* (eight males and one female) at heights below 2.5 m on Sage Mountain, Tortola, but traced most calling males to perch sites well above our reach in trees. In contrast, we frequently observed *E. cochranae* (calling males, noncalling adults, and juveniles) in vegetation <2.5 m high in October 1995 after high winds associated with Hurricanes Louis and Marilyn in September had visibly altered the habitat, knocking down many trees and stripping leaves off of those left standing; however, we did not systematically record perch heights.

While calling, males of *E. antillensis* were most frequently perched on leaves or branches of trees and shrubs on Guana (60% of 94 observations), Tortola (68% of 53 observations), and Virgin Gorda (84% of 79 observations; data for 1993–95 combined for all islands). Males also called from herbaceous vegetation (Tortola: 28%; Virgin Gorda: 4%), terrestrial and arboreal bromeliads (Guana: 14%; Virgin Gorda: 4%), and agave plants (Guana: 24%). On Tortola, calling *E. schwartzi* were perched on trees or shrubs (75% of 16 recordings) and herbaceous vegetation (25%). In contrast, the majority of observations of calling *E. schwartzi* on Virgin Gorda were from bromeliads (84% of 45 recordings), followed by trees and shrubs (13%) and herbaceous vegetation (2%).

When examined in relation to the availability of bromeliads along auditory transects in 1994, the distribution of calling males of *E. antillensis* and *E. schwartzi* differed significantly from random on Virgin Gorda but not on Tortola (Table 3). On Virgin Gorda, males of *E. schwartzi* were restricted to sections of the transect that contained bromeliads. In contrast, male *E. antillensis* were not associated with bromeliads either on Virgin Gorda or Tortola (Table 3). On Guana, male *E. antillensis* were found exclusively in sections of Transect 2 containing bromeliads, but the relationship was not statistically significant based on habitat availability, due to the small sample size (Table 3). The frogs were most abundant on Transect 1, where bromeliads were present in every section, thus precluding a similar analysis.

On Guana in 1996, calling males of *E. antillensis* were aggregated among 5-m × 10-m sections of the transect during all but one check (Table 4). On a larger scale, when the transect was

TABLE 3. NUMBER OF CALLING MALES OF *ELEUTHERODACTYLUS ANTILLENSIS* AND *E. SCHWARTZI* ON VIRGIN GORDA, TORTOLA, AND GUANA IN OCTOBER 1994.[a]

Island (Transect No.)	Bromeliads Present	Bromeliads Absent	Total	X^2	*P*
Virgin Gorda (1)				23.1	<0.01
No. of *E. antillensis*	12	22	34		
No. of *E. schwartzi*	18	0	18		
No. of Sections	24	36	60		
Tortola (1 + 2)				5.2	<0.1, >0.05
No. of *E. antillensis*	11	18	29		
No. of *E. schwartzi*	19	11	30		
No. of Sections	50	70	120		
Guana (2)				3.5	<0.1, >0.05
No. of *E. antillensis*	10	0	10		
No. of Sections	44	16	60		

[a] Counted in 3- × 5-m sections of auditory transects in relation to the presence of bromeliads.

TABLE 4. DISPERSION OF CALLING MALE *E. ANTILLENSIS* ALONG A 10 × 815-M TRANSECT (TRANSECT 1 IN TEXT) ON GUANA ISLAND IN OCTOBER 1996.

	Transect Divided into 5 × 10-m Sections (no. sections = 163)			Transect Divided into 10× 50-m Sections (no. sections = 16)[1]		
Date	Variance/Mean Ratio	X^2	P	Variance/Mean Ratio	X^2	P
18 Oct.	1.2	196.4	<0.05	2.6	39.5	<0.001
25 Oct.	1.3	208.4	<0.05	2.8	42.3	<0.001
28 Oct. (Check 1)	1.7	281.2	<0.05	6.2	92.9	<0.001
28 Oct. (Check 2)	1.2	192.1	<0.05	3.1	47.0	<0.001

[1] The last 15 m was omitted from the analysis to achieve equal division of the transect.

divided into 50-m × 10-m sections, calling males were highly aggregated during each check. The habitat attributes measured explained little of this dispersion. The number of calling males was significantly correlated with the habitat variables both when only data for the night with the most calling frogs (74 frogs on first transect check on October 28; $F_{6,143} = 2.95$, $P < 0.01$) were included and when each section of the transect was scored based on whether or not it was used by frogs during any of the checks ($F_{6,143} = 5.67$, $P < 0.001$). In both cases, the correlations were weak ($r^2 = 0.11$ and 0.19 for the two models, respectively).The partial r^2 for the habitat variables in the better, second model ranged from 0.007 to 0.054 and were the highest for the sum of crown diameters of bromeliads (0.045) and percent substrate covered by leaf litter (0.054).

DISCUSSION

We found 10 previously unreported populations of leptodactylid frogs on five islands (Great Camanoe, Beef, Frenchmans Cay, Great Thatch, and Jost Van Dyke) and confirmed all but three of previous records from the BVI. Demonstrating the absence of a species is always problematic, and these small frogs are inconspicuous when not calling and could be missed easily. The month of October, however, is generally favorable for locating frogs, because, together with November, it has the highest average rainfall per month (6.44 and 6.57 inches of rain in October and November, respectively, based on weather records from 1960 to 1984 obtained from Water and Sewage Department and Planning Division, Road Town, Tortola, and compiled by A. Swain). Rainfall is probably the most important factor affecting activity by *Eleutherodactylus* species in the BVI, although activity is also likely to take place on humid, rainless nights. It was not always possible, however, to time our visits to the different islands during or immediately after rain. Our confidence that we located all species is greatest for small islands that we visited repeatedly, such as Guana. We are also highly confident that there are no native frogs on either Necker or Little Thatch, because no frogs have ever been seen or heard there either by us or by residents. The only amphibian ever found on Necker was the intro-

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duced *Hyla (Osteopilus) septentrionalis,* which was collected there on 19 October 1993 from a crack in a recently imported wooden beam (MCZ 119258).

Two of the three previous records that we failed to confirm were from Virgin Gorda (*E. cochranae* and *L. albilabris*; MacLean, 1982), and the remaining record was from Peter Island: an unidentified *Eleutherodactylus* found in the stomach of a snake, *Liophis* (*Alsophis*) *portoricensis* (Henderson and Sadjak, 1996). This snake (MCZ 37303) was collected by Chapman Grant on 14 August 1932. The frog, uncataloged, was sent to the late Albert Schwartz for identification, but R. W. Henderson (personal communication) subsequently was unable to locate it in Schwartz's materials.

On Peter Island in 1996, we walked throughout the inhabited, eastern part of the island at night, and in 1997 we spent a rainy night on the south side of the western part of the island investigating a verdant gully, which to us appeared the best site for locating frogs. *Eleutherodactylus* seems to have disappeared from Peter Island at some time since 1932. On Virgin Gorda, we covered much of the island at night in the rain in three different years, including likely habitats on Gorda Peak (but excluding the roadless, easternmost portion of the island). We have found no records other than MacLean (1982) of either *E. cochranae* or *L. albilabris,* nor have we been able to locate voucher specimens. Furthermore, MacLean *et al.* (1977) do not report *E. cochranae* or *L. albilabris* from Virgin Gorda, raising suspicions about the 1982 listings. We conclude that the record for *E. cochranae* on Virgin Gorda is in error and that there is no evidence that the range of this species extends east of Tortola. We cannot, however, conclusively dismiss the possible former presence of *L. albilabris* on the island based on accounts of residents, who remember "ditch frogs" in and around Spanish Town many years ago before the extensive ponds were drained for the construction of a marina and a hotel.

When all 17 islands visited were considered, elevation and area explained much of the variation (61%) in the number of species among islands, with elevation being the most significant factor. The importance of elevation in biogeographical patterns of small

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islands was emphasized by Lazell (1983), and our data support this hypothesis. Our data also show that even very small islands, such as Frenchmans Cay, a mere 24 ha, can support at least two species of frogs. Frenchmans Cay is relatively high, 131 m, which might allow it to support more species than expected based on area alone. Both Frenchmans Cay and Beef, however, are separated from Tortola by narrow, bridged channels. Frogs dispersing in the rain can easily cross such bridges (JL, unpublished data from New England and China). Therefore, the number of species on these islands may reflect repeated colonizations from Tortola rather than permanent populations. The reconfirmation of *E. schwartzi* from Great Dog Island, an islet of only 33 ha located at least 3 km from the nearest potential colonization source (Virgin Gorda), shows that this species can persist on very small islands, provided suitable moist microhabitats, such as bromeliads, are present.

Leptodactylus albilabris, which has an aquatic larval stage, can be expected to be absent from islands that do not have suitable water bodies for breeding. Apart from temporary pools on Gorda Peak, drainage ditches (mostly paved) in Spanish Town on Virgin Gorda, and small freshwater puddles on Great Camanoe, we did not observe potential aquatic breeding habitats on the islands where we failed to locate this species.

Stewart and Pough (1983) showed experimentally that the availability of retreat and nest sites can limit population growth of *E. coqui* in Puerto Rico. Terrestrial and arboreal bromeliads, plants that hold moisture in their leaf axils, may provide such sites for terrestrially breeding forest frogs. Of the three species of *Eleutherodactylus* that we studied, *E. schwartzi* was most closely associated with bromeliads, an association also pointed out by Schwartz and Henderson (1991). On all islands except Tortola, we found *E. schwartzi* almost exclusively in terrestrial and arboreal bromeliads. Broader habitat use on Sage Mountain, Tortola, can be explained by the relatively high rainfall and dew that this highest point in the Virgin Islands receives. On Great Dog, we found *E. schwartzi* nests with egg clutches only in a small patch of terrestrial bromeliads, which most likely facilitated the persistence of the population.

Eleutherodactylus antillensis and *E. cochranae* used a variety of microhabitats in addition to bromeliads. Most male *E. antillensis* called from perch heights <2.5 m in vegetation. Previously, Rivero (1978) and Henderson and Schwartz (1991) also noted that males often called from low vegetation. We observed *E. cochranae* using cavities in tree trunks and branches for calling, retreat, and nest sites (Ovaska and Caldbeck, 1997, and unpublished data). Most calling male *E. cochranae* were high in the trees, thus limiting our access to this species. Schwartz and Henderson (1991) stated that males call from 1 m (3 ft) above ground to high in the trees. According to Schwartz and Henderson, the species occurs primarily in xeric forests. On Tortola, however, we found *E. cochranae* together with *E. schwartzi* and *E. antillensis* in mesic forest on Sage Mountain. The habitat on Great Thatch was also mesic, and only Jost Van Dyke could be characterized as mainly xeric.

Eleutherodactylus antillensis was the most widespread of the three species. Although not associated with bromeliads on the relatively wet islands of Tortola and Virgin Gorda, the presence of bromeliads appeared to become more important with increasing aridity. On the relatively dry island of Guana, the frogs were associated with sites that contained bromeliads and abundant leaf litter, although these factors explained only a little of the spatial dispersion of frogs along transects. Abundant leaf litter might be important for breeding, as all nests of this species that we have found have been under leaf litter (Ovaska and Caldbeck, 1997, and unpublished data).

The mean body size of adult males of both *E. antillensis* and *E. schwartzi* differed among islands. Woolbright (1989) found that the growth of male *E. coqui* in the field ceased after reproductive maturity was attained. Furthermore, the period of growth could be extended in the laboratory under conditions that were unfavorable for breeding, thus resulting in greater maximum body size. Therefore, frogs that live under social or environmental conditions that favor the early attainment of reproductive maturity can be expected to be relatively small. The selective pressures responsible for the observed patterns in body size among islands cannot be resolved from our data, and studies that specifically address this question are desirable. The differences were consistent among years, indicating that the operational factors are persistent over time.

There are six islands larger than Frenchmans Cay in the BVI that have not been surveyed for frogs (Prickly Pear, Ginger, Salt, Norman, and Little Jost Van Dyke). All, however, are relatively dry and might not be suitable for frogs. Additional populations that were undetected by us may also continue to be discovered on the islands that we surveyed. Nevertheless, our study provides baseline data that may become increasingly important because of regional and global changes in climate patterns.

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Evaporative Water Loss in Insular Populations of the *Anolis cristatellus* Group (Reptilia: Sauria) in the British Virgin Islands II: The Effects of Drought[1]

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ABSTRACT

Previous work has shown that water loss in some populations of *Anolis cristatellus* from the British Virgin Islands is closely tied to the conditions available on the islands they inhabit. This manifested itself in a strong correlation between habitat aridity and several water loss rate parameters. Here we report on a similar study conducted in the same locations in 1994, a year of extreme drought.

We hypothesized that lizards caught at the height of the drought will experience lower rates of water loss than those measured during a normal year. Our findings show that in 1994, as in 1993, habitat aridity and water loss parameters were strongly correlated. Also as before, the Guana Island population of *A. cristatellus* displayed higher resistance to water loss than expected by the island's aridity. However, a striking change occurred within populations. All were at least as good at retaining water (measured as integumentary resistance to water loss, R) as in 1993, and some were over 3.5 times better. Existing evidence is insufficient to determine whether these changes were the result of phenotypic plasticity or attributable to differential mortality of nonresistant individuals.

Key words: Anolis cristatellus; Anolis ernestwilliamsi; *British Virgin Islands; differential mortality; evaporative water loss; habitat aridity; phenotypic plasticity; tropical islands.*

TERRESTRIAL ORGANISMS OFTEN RISK EXCESSIVE EVAPORATIVE WATER LOSS (EWL) to the environment. Unlike mammals, which often employ active cooling mechanisms involving water loss, reptiles mainly lose water passively. This can occur through the respiratory system or through the skin surface (cutaneous water loss, CWL), the latter generally being the more important channel in tropical species. Because excessive water loss is detrimental, natural selection should lead to physiological adaptations reducing EWL (and especially CWL). Indeed, several studies have documented an inverse interspecific correlation between habitat aridity and EWL in reptiles (Bentley & Schmidt-Nielsen 1966, Mautz 1982). Others have shown that such variation also exists at the intraspecific level (Hertz *et al.* 1979; reviewed in Garland & Adolph 1991; *cf.* Hertz 1980).

Recently, we demonstrated such intraspecific variation in *Anolis cristatellus* (Dmi'el *et al.* 1997). We also showed a strong correlation between habitat aridity and water loss rate, avoiding some perceived methodological problems with previous studies, such as allowing acclimation to occur or using small numbers of populations (Hillman & Gorman 1977, Hillman *et al.* 1979, Kattan & Lillywhite 1989, Hertz 1980, Kobayashi *et al.* 1983, Eynan & Dmi'el 1993). Our study encompassed eight populations of *Anolis cristatellus wileyae* and one population of the closely related *A. ernestwilliamsi* in the British Virgin Islands. Unfortunately, we were unable to distinguish between two possible causative agents for the correlations we found: phenotypic plasticity and natural selection leading to local physiological adaptation.

Phenotypic plasticity allows individual animals to quickly track changes in their environment and react accordingly. When conditions are dry, animals increase the resistance of their integument to water vapor loss, R (*e.g.*, Hillman *et al.* 1979). Because costly tradeoffs associated with

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such changes usually exist, R is expected to decrease when conditions become wetter. In contrast, the second possible causative agent assumes differential mortality rapidly removes from each island's population those individuals less able to withstand local conditions. When conditions allow, such selection is relaxed and the population mean water loss rate increases. This is an extreme and rapid version of a phenomenon that can also work over longer time frames. If conditions are relatively stable, or change gradually, differential reproductive success may also be involved. In a quickly changing and unpredictable environment, the conditions covered by this study, individuals suited for conditions one year are unable to "predict" what type of offspring will be favored during the next year. Though one might expect phenotypes adapted to the most extreme conditions to be favored over time, trade-offs associated with such adaptations make this an uncommon solution. In any case, because adult male *A. cristatellus* take more than a year to reach the size class we used, this mechanism is not relevant in the present context. A third major hypothesis, relating similarity in physiology to the historical sequence of population divergence (and thus phylogeny; *e.g.*, Thorpe *et al.* 1995), has been ruled out due to the lack of congruence between geographic distribution and physiological trait (Dmi'el *et al.* 1997).

An unusually severe drought that occurred on our study site in 1994 (quantified below) presented an exceptional opportunity to perform a natural experiment on the reaction of previously tested populations to radically changed environmental conditions. The drought, at its height when we arrived in October, had resulted in marked changes in the vegetation, as well as in a decrease in the number of lizards encountered on all study sites (G. Perry, pers. obs.). We therefore hypothesized that water loss rates in all populations would be lower than in the previous year. To test this hypothesis we returned to all the populations previously tested (Dmi'el *et al.* 1997) and repeated our measurements. Our goal was to document the effects of the drought on population-specific water loss parameters and elucidate causes for these changes. Our results support our prediction; its mechanistic basis and evolutionary significance are discussed.

MATERIALS AND METHODS

Study populations.—*Anolis cristatellus* are common on many of the Greater Puerto Rico Bank islands. We conducted our study in the British Virgin Islands (BVI) because a large amount of variation in environmental conditions is seen there (Dmi'el *et al.* 1997). To facilitate comparison with the results of our 1993 study, the same populations were sampled again: eight disjunct populations of *A. cristatellus* from seven islands, as well as one population of *A. ernestwilliamsi*. Again, only mature adult male lizards were used. Females are much smaller than males (thus more difficult to measure accurately), and adult-sized males are at least two to three years old (G. Perry, pers. obs.). Lizards were noosed in the field during October 1994 and transported to the laboratory on the same day. Collections were carried out during normal activity times, as were laboratory experiments. Whenever possible, individuals were released at the site of capture after the study was completed. Retained animals were euthanized and deposited in the Texas Memorial Museum at the University of Texas at Austin.

Environmental conditions.—No official rainfall records exist for any of the islands in the BVI. To quantify the extent of the drought, we used data from several privately run meteorological stations in the BVI, not all of them from islands included in our physiological study. We used a published aridity index (Dmi'el *et al.* 1997), which takes into account information not only about rainfall but also the effects of anthropogenic factors such as goat grazing, to quantify the relative aridity of different locations. This index represents a longterm estimate of habitat aridity, rather than the transitory one presented by relative humidity (RH) measurements.

Laboratory procedures.—To maximize comparability, we followed the methodology of Dmi'el *et al.* (1997). Animals were individually housed in plastic boxes (inner dimensions: 20 × 9 × 7 cm). Covering consisted of a small-mesh wire net, permitting free exchange of air between box and room. To reduce the frequency of defecation, lizards were kept in the boxes without food for 8–12 hours before the experiments commenced. They were, however, provided with moistened paper during this period to allow them to regain water lost in transit. We moved each lizard to a dry box of similar dimensions immediately before commencing experiments. Two ceiling fans continuously circulated room air to prevent the formation of a stagnant air layer around lizards or of small-scale tem-

TABLE 1. *Location, sample size (N), mean relative humidity at collection site (RH), and body dimensions of* Anolis cristatellus *from eight insular populations in 1994. Data from Carrot Rock are for* A. ernestwilliamsi *only. SD is one standard deviation. Mean values of ambient RH at collection site, lizard mass and body surface from 1993 (Dmi'el* et al. *1997) are provided for comparison purposes.*

		Mass (g)			Body surface (cm²)		
		1993	1994		1993	1994	
Location	N	$\bar{x}$	$\bar{x}$	SD	$\bar{x}$	$\bar{x}$	SD
	6						
Sage Mt., Tortola	6	5.94	6.95	0.52	40.2	45.4	2.8
Virgin Gorda		4.11	5.29	0.97	31.4	33.0	4.8
Bridge, Beef Isl.	6	7.67	6.90	1.40	47.9	45.5	8.3
Bridge, Tortola	6	7.85	6.75	1.60	45.8	48.3	6.9
Guana Isl.	6	7.63	6.28	1.86	49.3	42.9	8.7
Norman Isl.	6	5.27	5.74	1.17	42.5	46.4	9.5
Necker Isl.	6	8.27	6.23	0.88	55.3	53.4	9.6
Anegada	6	6.40	6.00	0.93	44.9	45.1	6.5
Carrot Rock	5	13.19	12.13	3.39	58.4	74.0	20.7

perature or humidity gradients within or near experimental boxes.

To obtain EWL measurements, we used a Precisa balance (model 800M) to measure the mass change of the lizards to the nearest mg over a period of 6–8 hours. Room relative humidity was measured using a Psychro-Dyne psychrometer (Environmental Tectonics Corporation). Room temperature and skin surface temperature also were measured using 36-gauge copper-constantan thermocouples connected to a Wescor TH-65 electronic thermometer. RH in the laboratory was nearly constant at 68 ± 4.0 percent (average and SD). Skin and air temperature were identical (30.3 ± 0.8°C). All measurements were taken at 30 min intervals. Animals that defecated during the study were reweighed, and the study restarted.

We revalidated the relationship between CWL and EWL previously reported for this species with the methodology used by Dmi'el *et al.* (1997) to study the Guana population. Briefly, plastic bags were used to envelope the body in the box, isolating it from the head. We assumed that any change in total mass was due to loss of water from the head. By subtracting this value from the total value obtained for the same animal under similar conditions the previous day, we could isolate body Ec. We also evaluated the porosity of the bag by measuring the mass change in boxes stocked with Drierite and enclosed in similar plastic bags. Control (bagged box without lizard) mass change was small (2–4% of lizard mass change) over the experimental period but was nonetheless factored into the calculation of EWL. The measured ratio of CWL/EWL in the Guana Island lizards was the same as that found in 1993 (CWL = 72% of EWL). To avoid an unnecessary stress to the experimental lizards, we therefore decided to derive CWL values for each of the eight populations using its 1993 CWL/EWL value. Integumentary resistance (R) was then calculated using the equation:

$$\text{CWL} = (\text{eTs} - \text{eTa})/\text{R}$$

where eTs is the water vapor density of the skin, assuming saturation at skin temperature; eTa is the actual water vapor density of the room air; and R incorporates the resistances of the skin and the boundary layer surrounding it (Lillywhite & Sanmartino 1993). R is an especially useful parameter because it factors out immediate environmental conditions (Eynan & Dmi'el 1993). Whereas CWL changes rapidly as a result of proximate RH or temperature, making comparisons difficult, R remains relatively constant.

Data on sample size and body dimensions for each population are given in Table 1. Surface area was measured using the methods of Dmi'el *et al.* (1997), judged superior to alternative methods.

RESULTS

MAGNITUDE OF THE DROUGHT.—Though covering only a few sites in the BVI, rainfall data overwhelmingly showed the extreme nature of the 1994 drought (Table 2). Rainfall in 1994 was less than half the average rainfall accumulated by early October in previous years at sites for which we could obtain data. Moreover, cumulative 1994 rainfall

TABLE 2. *Rainfall data (mm) for several sites in the BVI. Data for each year are cumulative rainfall (mm) for 1 January–30 September, one day prior to the beginning of our 1994 study. Data from G. Perry* (pers. obs.).

Site	Years spanned	$\bar{x}$	SD	Min	Max	1994
Anegada	1980–1994	493	126	269	668	204
Guana Isl.	1979–1984 & 1990–1995	634	273	500	851	459
Great Camanoe	1992–1993	571	?	521	621	259
Tortola site 1	1974–1993	607	178	368	1063	324
Tortola site 2	1991–1993	675	?	618	752	459
Tortola site 3	1901–1977	1326	318	779	2394	—
Tortola site 4	1960–1991	1206	257	787	1842	—

was, without exception, less than that previously recorded for that site. RH measurements obtained over the entire experimental period in the Guana lab differed between 1993 (RH = 75.8 ± 12.20%, $\bar{x}$ and SD) and 1994 (68.0 ± 4.0%). This difference was highly statistically significant ($P < 0.01$, two-sided t-test).

Concordant with the low rainfall, we observed a marked decrease in lushness at all locations. Few plant species flowered in 1994 that flowered at the same time the year before. Of the local vegetation at each site, only succulents appeared unaffected, for the most part. Sizes of study lizards were not significantly different between the years ($t = 1.22$, df = 8, $P > 0.3$, paired t-test). For the best studied population, that found on Guana, fewer adult individuals were noted in 1994 than in 1993 (G. Perry, R. Dmi'el, & J. Lazell, pers. obs.). Similar trends were noted on all other islands, where collection of the necessary number of specimens was more difficult and time consuming in 1994 than in 1993 (G. Perry, R. Dmiél, & J. Lazell, pers. obs.).

WATER LOSS PARAMETERS.—As in 1993, both EWL and CWL were significantly correlated with habitat aridity. Losses were lower in lizards from drier habitats (Table 3; $r = -0.7$ and -0.75 for EWL and CWL, respectively; two-tailed $P = 0.04$ and 0.02, respectively). Values for R were higher in 1994 than in 1993 (Fig. 1. Excluding *A. ernestwilliamsi*, $P = 0.0078$ one-tailed sign test. Including *A. ernestwilliamsi* and treating 1994 R as lower than the 1993 value [for worst-case scenario], $P = 0.035$; one-tailed sign test; all species and localities included: $t = 3.826$, df = 7, one-sided $P = 0.003$, paired t-test).

Interestingly, the magnitude of the change in R between the years differed between dry island populations and moist island populations (Table 1). For the former, it was small (20.75 ± 14.41 s/cm) and not statistically significant ($t = 1.571$, df = 3, one-tailed $P = 0.17$, paired t-test), while for the latter it was large (76.75 ± 27.06) and significant ($t = 5.672$, df = 3, one-tailed $P = 0.003$, paired t-test). The relative magnitude of the difference between years, expressed by the percent change, was significantly different between the two island types ($t = 3.653$, df = 4.6 (equal variances not assumed), one-tailed $P = 0.009$, t-test).

Variation in R, as measured by SD, was significantly higher in 1994 than in 1993 ($P < 0.025$, one-tailed sign test) if *A. ernestwilliamsi* were excluded from the analysis and almost significantly higher when it was included. *A. cristatellus* from Guana were more resistant to water loss than expected from the island's aridity index, but data for *A. ernestwilliamsi* could be accurately predicted from the relationship between aridity and water loss in *A. cristatellus* (Fig. 1).

DISCUSSION

As in our previous study (Dmi'el *et al.* 1997), EWL and CWL were negatively correlated with habitat aridity, and R was positively correlated with it. Also as in our 1993 study, Guana lizards showed inexplicably higher R values than the aridity index for that island would suggest. However, in the 12 months between our 1993 study (Dmi'el *et al.* 1997) and the present investigation, *Anolis cristatellus* over the entire BVI showed a striking increase in their integumentary resistance to water loss. Such change is consistent with our prediction for a time of such unusual drought. This difference was greater in animals from normally wet islands, suggesting the impact on them was greater. Perhaps animals from relatively dry islands were already conserving water to a degree that could not be surpassed. Interestingly, animals of similar mass from different populations (and even within a population) can have markedly different surface areas, due to the great differences in crest size found both within and among populations (Rivero 1978). Such differences can affect water loss rates (Hertz

TABLE 3. *Total evaporative water loss (EWL, mg/g/h), cutaneous water loss (CWL, mg/cm²/h), and integumentary resistance (R, s/cm) of* Anolis cristatellus *and* A. ernestwilliamsi *from the BVI in 1994. The change in R values compared to 1993 (Dmi'el* et al. *1997) is given for comparison purposes. The aridity index goes from 1 (= wet) to 10 (= dry).*

		EWL		CWL		R		
Location	Aridity index	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	1994 SD	Change (%)
Sage Mt., Tortola	1.0	3.8	1.4	0.5	0.2	100	49	+69
Virgin Gorda	2.3	3.5	1.0	0.4	0.1	100	34	+245
Beef Isl.	5.0	2.0	0.6	0.2	0.1	148	22	+174
Bridge, Tortola	5.0	2.3	0.7	0.3	0.1	156	42	+184
Guana Isl.	5.0	1.7	0.5	0.2	0.1	229	62	+15
Norman Isl.	6.3	2.5	0.5	0.2	0.04	114	22	0
Necker Isl.	6.9	2.1	0.4	0.2	0.05	186	40	+20
Anegada	8.3	2.6	0.8	0.3	0.1	150	61	+17
Carrot Rock	9.3	2.0	0.5	0.2	0.1	167	56	0

1980), and a thorough survey of morphological differences among these populations could prove instructive.

Traditionally, R is considered relatively insensitive to rapid environmental changes (Eynan & Dmi'el 1993), yet genetically isolated populations of *A. cristatellus* clearly were able to respond to the drought by modifying R within relatively short periods (months or less). What was the basis for these rapid changes? The animals were all born before the drought began, and changes could not have resulted from the differential reproductive success of dry-adapted phenotypes. This leaves two possible main mechanisms. First, natural selection could have been the main mechanism by which these lizard populations changed their EWL. If so, then severe drought should have caused mortality in high-EWL individuals, resulting in short-term decreases in population size. Such mortality should have been differential in nature, since high water-loss individuals would have been less likely to survive. This should have resulted in reduced intrapopulational variability in R (Fig. 2a). Since small individuals are more highly susceptible to water loss (Hertz 1980), average body size also was predicted to increase. Second, phenotypic plasticity may have been responsible. Under this scenario, study populations also were predicted to show greater resistance to water loss as a result of drought conditions. Mortality and reduced variability, however, are not predicted (Fig. 2b).

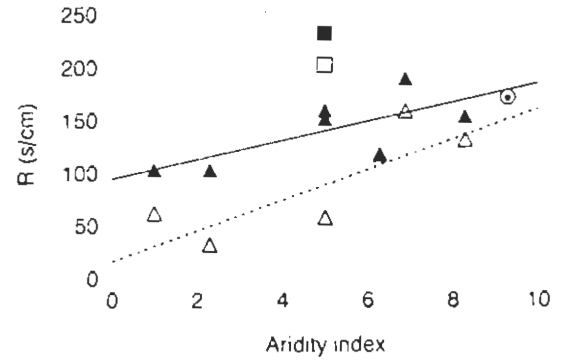

FIGURE 1. The relationship between habitat aridity and mean integumentary resistance in eight populations of *Anolis cristatellus* (triangles; except for Guana which is represented by squares) and one population of *A. ernestwilliamsi* (circles). Full symbols are from 1994, empty symbols from 1993. Regression lines (dashed for 1993, full for 1994) are based on data for *A. cristatellus* only. R values were significantly higher in 1994, both when *A. ernestwilliamsi* was included and when it was excluded from the analysis.

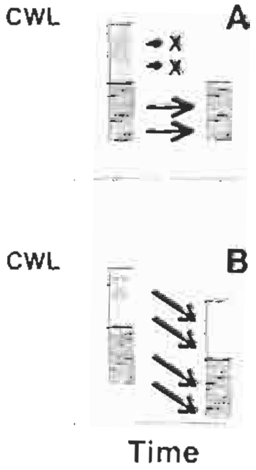

FIGURE 2. Two hypothetical models that could cause a decrease in CWL following drought: (A) differential mortality; (B) phenotypic plasticity. Vertically striped bar: high water-loss individuals; horizontal bars: low water-loss lizards. Note that mean values in A and B are the same.

Both models presented in Figure 2 predict the pattern we observed. The difference in change between wet and dry island populations and similarity in the slope of the correlation between R and aridity between the years are also consistent with both differential mortality and phenotypic plasticity hypotheses. Two lines of evidence lead to two contrasting conclusions. First, the amount of intrapopulation variance in R, predicted to decrease if differential mortality was the cause, actually increased from 1993 to 1994. This leads us to prefer phenotypic plasticity (Hillman *et al.* 1979, Kobayashi *et al.* 1983) as the main mechanism responsible, and this view is supported by lack of increase in the average size of individuals in various populations as predicted by the differential mortality hypothesis.

On the other hand, population estimates from Guana show a considerable decrease in adult numbers from 1993 to 1994 (G. C. Mayer & J. D. Lazell, pers. obs.), as does our subjective evaluation of population densities elsewhere. This suggests differential mortality could have played a major role. This conclusion is concordant with finding that changes were much greater on relatively wet islands than on dry ones, where longer exposure to selection would be expected to have resulted in drought-resistant individuals. It also agrees with published reports that *A. cristatellus* cannot change their metabolism to conform to different thermal regimes (Rogowitz 1996). Studies on a closely related species have shown that strong responses can be obtained (even over a few months) as environmental conditions changed, and that selection was the primary cause for these changes (Malhotra & Thorpe 1996). Thus, there is reason to expect that selection is an active mechanism in our system.

The two hypotheses, however, are not necessarily mutually exclusive. An evolutionarily established difference among island populations (a reasonable interpretation of Dmi'el *et al.* 1997) can be strengthened or concealed by phenotypic plasticity (arguably responsible for differences between our 1993 and 1994 results). Indeed, we believe that both evolutionary changes and phenotypically plastic traits were involved at different levels. It would appear that much of the change observed in R within populations between years was due to phenotypic plasticity, since the time scale seems insufficient to support an evolutionary explanation. Evolutionary processes, however, may well set the limits for such changes at the interpopulation level and be responsible for the similarity in relationship of R and aridity between the years. Possibly, a greater change would have been even more beneficial in some populations; yet genetically determined limitations prevented such shifts. The continued abnormality of Guana lizards strengthens our previous suggestion that this population may represent a genetically divergent lineage deserving special attention and conservation. Since the exact mechanism(s) responsible for this rapid adjustment remain unclear, we now are planning a common garden experiment to answer this question more decisively.

ACKNOWLEDGMENTS

We thank P. E. Hertz for providing insightful comments that improved the manuscript considerably. This project was funded by the Conservation Agency through a grant from the Falconwood Foundation. GP was financially assisted by a grant from the Institute of Latin American Studies at the University of Texas. We thank H. Jarecki for access to Guana Island, R. Branson for permission to work on Necker Island, and R. Rusher, K. R. LeVering and the entire Guana staff for technical assistance.

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Subj: **Guana Island**
Date: 11/17/1999 9:35:47 AM Eastern Standard Time
From: fcsibley@snet.net (fcSibley)
To: JCINJTOWN@aol.com (JCINJTOWN@aol.com)

Dear Jim or Skip:

Didn't pay attention to your schedule. Is Skip still in town and reachable by phone? Will be curious as to how Guana Island survives hurricane.

Also like to discuss trail maintenance on Guana Island. Numi seemed distressed in October that the island staff would not maintain scientist trails and I've always been bothered by the difficult of traveling on trails.

Had some messages back and forth with Clive at community college concerning dragonflies and banding. Turns out he knows all the ponds on Tortola and Virgin Gorda so will milk his dragonfly knowledge next year. Perhaps more important is banding. He agreed that banding was frowned on but suggested we consider doing a project on Anegada as a college project with some students involved. Felt that would avoid the political problems. Still thinking about that. May even see if Doug McNair at Tall Timber Research Station could help out.

Of possible interest is a new initiative by Fish and Wildlife Service and Caribbean Ornithological Society to have popular bird identification guides for all the islands - not all birds just a selection of the common or more interesting ones. A natural for the National Parks Trust of Community College but perhaps a tie in for Guana Island as well. Not clear what sort of financial support USF&WS is willing to provide.

Sent Black Kite note to Judy for comments and will send it to a couple good birders before submitting it. Probably American Birds. Positively a Black Kite and at least West African if not Cape Verde Island bird [skins so variable that people have even put them as a subspecies of the Red Kite].

We are off mid-day tomorrow for week at Ithaca and then back here Friday after Thanksgiving.

Very nice weekend on the Outer Banks 5-8th, but couldn't find your book Ribbon of Sand at any of the stores. Has it gone out of print again?
Fred C. Sibley
Home phone 203-729-3582
25 Shirley Street, Naugatuck, CT 06770

Jan. 6, 1999

Dear Skip:

Hope you're enjoying your travels. Sure Jim will get this to you one way or another.

Making progress on migrant paper with McNair - supposed to be submitted by first week January, but already accepted so presumably the last polishing will get done in time. Also have another short note on dragonflies of Guana off to journal - should come out in June. Still talking with Wayne about joint article on rarities and suddenly having some extra time so may actually get that started. Black Kite paper finalized. Sent copy to Rob Norton for suggestions on submission but no reply.

Lot of discussion with the Guana Island crowd about 1. banding on Anegada and 2. trail work on Guana.

BANDING ON ANEGADA

Asked Clive Petrovich how one might get around the objection to banding and he suggested a joint operation with the Community College. That sounded great to me and asked him for some more input - nothing to date.

Flew the idea by Numi - mainly to get suggestion on the difficulty and expense of carrying out such an operation. She thought it would be easy to set up - said she didn't think Henry would support it. That had not been the original idea but maybe there is an opening there with the community college involvement.

INITIAL [PIE IN THE SKY] THOUGHTS:
Run a banding station on Anegada for all of October with possible start in late September and end early November.

THEORY:
Anegada gets greater numbers of neotropical migrants, they would be more easily netted, the fall outs might be more reliable/predictable [i.e. they don't have a choice of Virgin Gorda, Tortola, Guana, etc. they have to land on Anegada or keep flying].

STAFFING:
2-4 people. volunteers from states. ? students from community college.

ROOM AND BOARD:
Rent a house do cooking, laundry, etc. there. Some sort of arrangement with Guana Island so people could spend a night there to or from Anegada or spend part of their time banding on Guana.

LOGISTICS:

Volunteers arrive from states and either match schedule to air service to Anegada or lay over at Guana. Return trip same way - might require, if going to Guana, arriving on morning flight so there is no special boat run.

College student catch flights to and from Anegada and arrange own ground transportation.

On Anegada try to set nets so they can be checked on foot from house. Taxi pickup to and from airport.

SCHEDULE:

Large number of nets run all suitable days and all day during period of operation.

Individuals work out some rotation of duties during slow periods so there is time to swim, fish or sightsee.

Students would be trained in netting, identification and banding techniques and whenever possible put in charge of operations.

The goal would be to reduce number of volunteers or increase staffing by having a self perpetuating group of students who could do the whole operation on their own including training new students.

FUNDING:

Volunteers provide own transportation down and some if not all food expenses on island. i.e. project pays for house and taxi.

Students get free or heavily subsidized transportation and food cost.

Major project costs covered by donations, Henry, CT Audubon, Manomet Bird Observatory.

This is where I need major input from you.

Any approach to Henry should be through you or preferably by you.

What toes are we stepping on, yours included, if we start asking for support from other individuals or other organizations?

For an example: Lets assume Manomet Bird Observatory becomes interested in funding this project or even taking over this project. Is that going to bother you or Henry that another organization is getting a foothold in the BVI.? Would it be difficult to establish a joint venture with an outside organization and Guana Island? - i.e. potential mentioned above of switching people from Anegada project to a Guana Island project or giving them time on Guana Island.

Don't need to use a lot of words here. I don't want to start something that is disagreeable to you and Henry. You know the political mine fields here far better than I ever care to. The intentions are all noble and idealistic. Your job is to figure out how we can avoid major friction and misunderstandings. Perhaps even the inevitable tendency of government agencies to play one party against another.

TRAIL WORK ON GUANA

This seems like a far simpler operation. Numi says great, volunteers seems to be numerous.

Basic idea as I discussed on phone is to maintain and upgrade science trails - first emphasis on lost trails but eventually assume crew would work on tourist trails heavily used by scientist [Quail Dove Ghut and Monkey Point]. A certain amount of widening, marking and straightening with more extensive use of switch backs on the steep slopes. Most trails are now just made passable not maintained.

Funding for tools would seem to be rather minimal. An initial $1000 should provide an abundance of hand tools, wheel barrows, etc. Assuming it is adequately stored the replacement cost each session should be a fraction of that.

Major problems I see are bed-nights and Henry's reaction to improving trails.

QUESTIONS - NO ANSWERS

1. Does Henry like the trails the way they are?

Some people don't like improved trails - we will keep small tree clearing to a minimum but in a lot of places you turn sideways to get between trees. One or both have to go. There's going to be considerable rock moving to level or mark trails.

If you think Henry will be upset by any of this activity would suggest doing one of the lesser trails and then seeing what he thinks. Other choice is to make the tree removal and rock moving less obvious and just not mention it unless he has questions.

On the off chance that you feel he's enthusiastic about trail improvement but not wasting time and money on the science trail you might suggest that we do a partial upgrade on Monkey Point while doing the Science Trails.

1A. Paint marking.

Does Henry have an objection to marking trails with paint? This would certainly be a lot easier than the rope markings or flagging tape and a lot longer lasting.

2. Bed Nights

You had, I think, suggested July as the month with already available bed nights. This seems to be a more difficult month to line up volunteers although perhaps I'm just hearing from the wrong crowd - have discussed idea with Eric, Judy and Alison. Should be lots of potential volunteers in the college student crowd if we ever settle on a plan.

An October crew has already attracted interest from Larry Gall and Tim White - sure I could fill in a couple people from Birdcraft. The idea of going to Guana Island and not having to do any taxing mental work seems to have great appeal.

Since you're always full up in October assume you're not enthusiastic about losing bed nights to trail crew. Maybe if think of it as putting a 10 percent surcharge on scientist for trail work it would go down better. Ideal solution would be to put on extra bed nights and enough extra the first year to really make a dent in the trail work.

This July is bad for me, but tentatively toying with idea of going to Dominica in late June and then back to BVI for early July to hopefully check out Anegada for fall banding, Tortola with Clive for some dragonfly localities and then Guana for trail work. Would not be able to put together and work with a trail crew this July.

3. Options.

July survey - equipment needs, purchase, feasibility survey - couple days. **or same in October.**

October field crew - 3-4 people for whole period - 100 bed nights? **or minimal field crew - 40 bed nights.**

July 2001 - full field crew - 100 bed nights

4. Accomplishments.

Can't really predict how much work the crew can accomplish. Logistic will always be the hardest problem. Monkey Point would be an easy trail to work. Anything requiring getting to top of Quail Dove Ghut or back side of Guana Peak will be difficult.

Still a 4 man crew should get in 4x4 hrs of real work a day and that can trim a lot of brush and move a lot of rocks. Also a difference between someone moving rock and quitting to sleep and someone doing some trail work and then back to struggle with science. [Point? - a trail worker is going to accomplish more in a day than Numi or I trying to work it in around other commitments]. Translating 40 bed nights into 160 hours of work is unrealistic unless it's 2 people for 20 days.

Would be confident that all the trails would be opened to travel and at least one major science trail - Palm Point and branch down to mouth of Great Ghut could be completed. [the main trail down to Great Ghut and then following Great Ghut would be much more difficult and I think is already labeled a tourist trail]

Lets just say 40 bed nights would significantly improve trail travel for scientist.

OTHER NEWS

Have sent a few messages to Nancy Woodfield and Bettyanne Schreiber. Not much feed back from Nancy yet. Betty had a lot of questions about Norman - nesting Pelicans?, protecting tern nesting areas, etc. - couldn't answer any of them. Interested in seeing banding and censusing efforts moved along. Think [always the optimist] that Nancy might actually get Park Trust to initiate censusing of seabird colonies. Not just let someone else do it but do it and invite someone else to participate. I keep hinting that she should move in that direction - see if the tropical inertia sets in or youthful enthusiasm carries the day.

How did thin~~k~~gs go with our Austrian friend on Dominica? Interested in any information on arrangements there. Have to start the permit process soon now that I've freed up some schedule time.

Too much for one letter. More when you reply or get back or whatever.

Fred.

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THE CONSERVATION STATUS OF BIRDS IN BRITISH VIRGIN ISLANDS NATIONAL PARKS

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THE BRITISH VIRGIN ISLANDS National Parks Trust currently manages 18 National Parks and Protected Areas, five of which are bird sanctuaries: Deadmans Chest, Fallen Jerusalem, Great Tobago, Little Tobago, and Prickly Pear. One of the main objectives of the Trust is to manage selected natural areas that are vital to the protection of endangered species and the life patterns of other critical species, such as seabirds. The Trust is able to carry out this objective through legislation that supports effective management. The Wild Birds Protection Ordinance (1980) fully protects approximately 21 species of rare or endangered wild birds within the British Virgin Islands (BVI), as well as their nests, eggs, and young. The Bird Sanctuaries Order (1977) provides complete protection of all species of wild birds in 20 designated bird sanctuaries, some of which are existing National Parks and others are proposed protected areas.

Seabirds in the BVI are particularly threatened by mangrove destruction, coastal development, and land reclamation. Additional pressure is increasing from intrusion by tourists and developers in search of isolated beaches and cays for recreation or developmental pursuits. Feral animals pose still another threat for increased nesting and colonization on many of the outlying islands. Unfortunately, some of these visitation and feral animals problems occur within the Parks, but the major habitat destruction is beyond the control of the National Parks Trust because it occurs on private land. In response to these pressures, the Trust is updating its System Plan, which outlines its objectives and plans for management. This will refocus attention to the areas that were originally recommended for inclusion into the Parks system, many of which are bird sanctuaries. Ideally, these proposed areas will be reviewed in terms of their environmental importance and then be declared National Parks by the BVI Government. The urgency of the situation is evident in the increasing number of small offshore islands within the BVI that are for sale within exclusive markets that focus on private island resorts. Whereas this is preferable to large-scale development, these small island resorts still affect previously undisturbed bird colonies, which will inevitably reduce the number of seabirds colonizing these islands.

The finest example of protection is the Tobagos National Park, which includes Great Tobago, Little Tobago, and Watsons Rock. These islands are reputed to be the most important seabird nesting sites in the BVI, and the entire Eastern Caribbean for the endangered Magnificent Frigatebird (*Fregata magnificens*) and Brown Booby (*Sula leucogaster*), whose nests are found in the hundreds. Access to the islands is geographically restricted by the harsh north swell and rocky shorelines, in addition to the steep cliffs and cactus scrub. Consequently, the islands are undisturbed by humans, although historical intrusion has resulted in the presence of approximately 20 feral goats. The vegetation is predominantly cactus scrub, as foraging feral goats restrict tree growth to the extent that the bird colonies may be limited in their ability to expand. Several attempts have been made by the National Parks Trust to remove these animals, but a small number were not captured and they have been able to reproduce. The complete removal of these animals is being planned in conjunction with the Department of Agriculture. This is considered to be an important project that should be completed by the year 2000. Fortunately, no goats occur on Little Tobago and the difference in vegetative cover is immediately noticeable. Visiting scientist Dr. Betty Anne Schreiber, Executive Director of the Ornithological Council, began research on Great Tobago in 1997 and it is her intention to study the taxonomic status of certain pelecaniform birds, in relation to their conservation status (Schreiber 1997). With further research such as this, the National Parks Trust will be able to make more informed management decisions to protect these species within the BVI.

One important site for inclusion in the National Parks system is the group of islands called The Dogs. At present only West Dog is a National Park, but the original proposal included George Dog, Great Dog, East Seal Dog, West Seal Dog, and Cockroach Island; all of these islands are bird sanctuaries, but they are predominantly privately owned. In addition, their landscape is less severe, thereby allowing easy shore access to the many sailors who visit the islands. As a bird sanctuary, West Dog is an important nesting site for seabirds such as the Bridled Tern (*Sterna anaethetus*), Sooty Tern (*Sterna fuscata*), Roseate Tern (*Sterna dougallii*), and Red-billed Tropicbird (*Phaethon aethereus*).

Another proposed protected area includes the archipelago of Sandy Cay, Green Cay, Sandy Spit, and the eastern point of Little Jost Van Dyke. These islands are home to the endangered Brown Pelican (*Pelecanus occidentalis*), White-tailed Tropicbird (*Phaethon lepturus*), and Roseate Tern. However, because all three cays are privately owned, the extent to which the National Parks Trust is able to manage these areas is restricted. These islands are another example of how the impact of tourism and development can affect the future of nesting seabirds in the BVI.

On Anegada, the proposed protected area includes all of the western ponds, all coastal mangroves, and the eastern ponds. The island is currently home to 51 Greater Flamingos (*Phoenicopterus ruber*), 20 of which were reintroduced in 1992 and 4 are wild flamingos that joined the flock in 1994. Terrestrial wardens of the National Parks Trust are monitoring the flamingos by conducting weekly bird counts, stating location, activity, and age. These records show that the population has increased by successful undisturbed nesting, mainly in Red Pond. Presently no encroachment threats exist, since all of the western ponds, Red Pond, and Flamingo Pond (an existing bird sanctuary) have been declared Ramsar sites and are now protected under the International Ramsar Convention on Wetlands.

Within the inland terrestrial parks, the protection of forests along the peaks and ridges of Tortola and Virgin Gorda has resulted in a safe habitat for local avifauna, such as the rare Bridled Quail-Dove (*Geotrygon mystacea*) at Gorda Peak National Park. The importance of buffer zones around the Parks to ensure that these habitats are not eventually isolated refugia, however, is an urgent matter on small islands where available land is scarce. The National Parks Trust is developing management plans for each of its parks, as part of the training received through the Darwin Initiative Project, Integrating National Parks, Education and Community Development. Within these plans are recommendations for effective management within and surrounding the Parks, since boundaries cannot be placed on flora and fauna.

The newest National Park is Shark Bay on the northern coast of Tortola, declared in April 1999. This Park includes 18.4 acres of forest and extends along the cliffs to the bay below, which is a popular feeding zone for Magnificent Frigatebirds, Brown Pelicans, and Brown Boobies. The bay is mainly inaccessible because of the north shore swells and is not a likely visitor location because of its rocky beach, but from the cliffs there is the most amazing view of these seabirds in their natural environment. This Park will provide the best educational tool for visitors, so that they will understand why it is imperative to protect nesting areas such as Great Tobago and The Dogs.

In addition to the resident avifauna, the diverse habitats within the British Virgin Islands also support many migratory and pelagic species. These seasonal visitors include the summer pelagic seabirds that nest on the outlying cays and islets, such as those in the family Procellariidae, notably Audubon's Shearwater (*Puffinus lherminieri*) on the Tobago islands. The winter months are dominated by migratory species, predominantly from North America, and include the Double-crested (*Phalacrocorax auritus*) and Neotropic (*P. brasilianus*) coromorants, and Black-bellied Plover (*Pluvialis squatarola*) and American Golden-Plover (*P. dominica*). Therefore, the conservation of these habitats has repercussions beyond the resident avifauna, to the extent that these habitats provide important corridors for migratory species. Hence, these islands are one link in a much greater chain that determines their survival.

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CONSERVATION PARTNERSHIPS IN THE UK OVERSEAS TERRITORIES

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The UK Overseas Territories in the Caribbean region comprise Anguilla, Bermuda, the British Virgin Isles, the Cayman Islands, Montserrat, and the Turks and Caicos Islands. Political links with the UK remain strong but, until recently, links with conservation agencies in the UK have been relatively weak. Two partnerships have recently increased their activity in the region. These are BirdLife International and the UK Overseas Territories Conservation Forum. BirdLife International has become a world-wide partnership of conservation organizations with a common agenda. One of BirdLife's prime objectives is to identify and conserve the world's most important areas for birds (IBAs). This programme is well underway in Europe, Asia, and Africa, and is now starting in the Americas. The UK Overseas Territories Conservation Forum is a partnership of voluntary conservation agencies in the UK and the Territories and meets regularly with Government. A new UK Government policy document has been produced on "good governance," including environmental protection, in the Territories. Each island will be expected to produce an "Environmental Charter" and a "Biodiversity Action Plan."

COMPAÑEROS DE CONSERVACIÓN EN LOS TERRITORIOS DE ULTRAMAR DEL REINO UNIDO.—Los territories de ultramar del R.U. en la region del Caribe comprenden: Anguilla, Bermuda, Islas Virgenes Británicas, Islas Caymán, Montserrat y las Islas Turcas y Caicos. Los vinculos politicos de estas con el R. U. permanecen fuertes, pero, hasta hace poco sus vinculos con las agencies de conservación en el R. U. han sido relativamente débiles. Dos compañeras han incrementado recientemente su acitividad en la region. Estos son: BirdLife International y el UK Overseas Territories Conservation Forum. BirdLife se ha convertido en compañera mundial de organizaciones conservacionistas con una agenda común. Uno de los principales objetivos de BirdLife es identificar y conservar las areas más importantes para las aves a nivel mundial (IBAs). Este programa marchabien en Europa, Asia y Africa, y ahora empieza en América. El UK Overseas Territories Conservation Forum es compañia de agencies voluntaries de conservation en el R. U. y sus territories y se reune regularmente con el gobierno. Un Nuevo documento sobre politica del R. U. se ha producido en "good governance," incluyendo la protección ambiental en los territories, se espera que cada isla produzca una "Carta Ambiental" y un "Plan de Acción sobre Biodiversidad."

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STATUS AND CONSERVATION OF WEST INDIAN SEABIRDS

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West Indian Seabirds: a disappearing natural resource

* * *

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Introduction

The Caribbean Islands are considered one of the world's "Biodiversity Hotspots", defined as an area of the planet that is critical to preserving the diversity of life on earth (Madre 1999). Twenty-five threatened regions were designated as Hotspots by Conservation International, representing only 1.4% of the land surface of the world, but containing over 60% of all plant and animal species. These 25 areas also contain 81.6% of the world's endangered bird species and high concentrations of endangered mammals and plants. All 25 areas have already lost 75% or more of their original vegetation. Five of the listed Hotspots are tropical archipelagos: the Caribbean, Madagascar and the Indian Ocean Islands, Polynesia-Micronesia complex, New Caledonia, and Wallacea (Indonesia). This points out the severe conservation problems suffered in the islands today and the continuing loss of biodiversity. We hope in this publication, by presenting the status and conservation needs of West Indian seabirds, to draw attention to the ongoing declines in these populations and the need for immediate conservation action to preserve these species.

In the early 1980s van Halewyn and Norton (1984) and Sprunt (1984) summarized the status of and conservation issues for seabirds of the Caribbean region. Since then, more detailed inventories have revealed that, for a number of species, population estimates made at that time were too high, and in a few cases where population monitoring has occurred, dramatic declines in the number of nesting pairs have been recorded. The original problems identified by van Halewyn and Norton (1984) have not been resolved (egg collecting, exotic predators, pollution, habitat destruction and disturbance) and several of them have become increasingly more severe over the last 15 years. Primarily because of the growing tourism industry, development of coastal habitats has increased and isolated cays and rocks, which were formerly relatively safe nesting sites, are now being developed or are visited by tourists seeking remote island experiences. Ironically, the seabird colonies themselves are becoming attractions for the ecotourism industry. Presently most of the species of seabirds nesting in the region are represented by tremendously reduced populations with aggregate numbers totaling only a few thousand pairs.

In August 1997, an International Seabird Workshop was held at the Society of Caribbean Ornithology's annual meeting in Aruba. Participants addressed conservation issues related to seabirds in the West Indies region (Fig. 1) and discussed steps needed to preserve seabird populations. All in attendance agreed that research and standardized monitoring had been largely neglected throughout the region, and that programs addressing these issues were vital to the long range survival of a number of locally breeding seabirds. Furthermore, with the general lack of biology, distribution, conservation status and management needs was greatly needed. This publication is a direct result of these concerns. It represents the combined efforts of not only the authors of the chapters presented herein but also of a large number of biologists residing in the greater West Indies region.

The Bahama archipelago, Greater and Lesser Antilles, and Trinidad and Tobago (hereafter the West Indies region; Fig. 1) support an important assemblage of breeding seabirds. In former times, the relatively predator-free islands of the region sustained much more abundant seabird populations which were probably ten times or more greater than those of today (Pregill et. al 1994). Human habitation of the islands started about 7,000 years before the present and evidence suggests that the initial impact on nesting seabirds was devastating. With the arrival of man, seabirds became a common, easily obtained source of food, as evidenced by middens on St. Croix, the Bahamas, and elsewhere (Palmer 1962, Steadman et al. 1984, Pregill et al. 1994, Steadman 1997, Wetmore 1938). This exploitation was followed by a period of European contact where human predation on seabirds and their eggs continued, and continues today, but to a lesser degree. A variety of introduced mammals compounded the problem. This not only includes mammalian predators but over grazing by feral goats and sheep which is causing major erosion problems on some islands. Generally, seabirds were driven from nesting on the primary islands where human habitation and exotic mammal associates had taken over. For the most part, seabird colonies are now restricted to off shore rocks and cays, and inaccessible cliff faces.

It is difficult in modern times to fully appreciate the extent of pre-European contact, human reliance on seabird populations as a source of food in the West Indies. They provided an excellent, easily obtainable source of protein that was extensively exploited. The loss of seabirds from tropical islands is estimated to be about 90 to 99% (Pregill et al. 1994, Steadman 1985, 1989, 1995). In some cases, single species became a primary source for subsistence hunters and continual collecting over many years greatly depleated them. The following quotes from the 1600-1700s illustrate the extensive hunting of the Black-capped Petrel (*Pterodroma hasitata*), formerly an abundant species, but now in danger of extinction.

> "It may be said that these birds are a manna that sends every year for Negroes and for the lowly inhabitants, who do not live on any thing else during the season.
>
> After two or three hours of hunting I returned with my Negro to rest to cook some birds for dinner. I began finally to hunt alone. We reassembled at midday. The four Negroes had 138 diablotins. Albert had 43, and I had 17. Each of us ate two, and we left carrying the rest of our game.
>
> "Those who read these memoirs will doubtless be surprised that we should eat birds in Lent; but the missionaries who are in these islands, and who in many matters exercise the power of bishops, after serious deliberation and consultation of a medical man, have declared that lizards and diablotins are vegetable food, and that consequently they may be eaten at all times (Labat 1724)."

> "Its flesh is so delicate that no hunter ever returns from the mountain who does not ardently desire to have a dozen of these "devils" hanging from his neck (du Tertre 1654)."

Status and Conservation Priorities for White-tailed and Red-billed Tropicbirds in the West Indies

* * *

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Introduction

Populations of both the White-tailed *(Phaethon lepturus catesbyi)* and Red-billed Tropicbirds (*P. aethereus mesonauta*) in the West Indies were undoubtedly much higher prior to human contact. This contact resulted in a loss of suitable nesting sites in the West Indies, the introduction of alien predators, and the taking of eggs and young for food. Present populations are primarily confined to predator-free cliffs on remote cays, and the number of nesting pairs is limited by the availability of suitable nest sites. There have been few surveys of tropicbirds in the West Indies, and most were incomplete and unreliable. The last published report on population estimates was in 1984 (van Halewyn and Norton 1984) and much of the data used in this report were from 20 to 100 years previous to its publication. Using recently published reports (post 1995) and information obtained from resident experts, a reassessment has been made for these species in the West Indies (D. Lee and M. Walsh-McGehee, unpubl. data). This reassessment indicates a dramatic decline in the numbers of White-tailed Tropicbirds in the past fifteen years. While the numbers for Red-billed Tropicbirds appear to have increased, the populations may actually be in decline since a disproportionately large extant colony was discovered on Saba and the number of known sites with confirmed breeding was more than quadrupled, yet the actual increase in the total number of pairs is slight.

Species Accounts

White-tailed Tropicbird *(Phaethon lepturus catesbyi)*

The White-tailed Tropicbird is the smaller and more common of the two tropicbird species in the West Indies (Lee and Walsh-McGehee1998). Tropicbirds occur on islands in the tropical Pacific, Indian, and tropical Atlantic Oceans. The Western Atlantic White-tailed birds occur on Bermuda, the Bahamas, and the Antilles, and are an endemic subspecies, *P.l. catesbyi*. Tropicbirds are highly pelagic and are seldom seen within sight of land except during courtship and nesting. They lay one egg on a cliff ledge, in a rock crevice or under vegetation. Most nests are inaccessible and thus censuses are difficult to carryout.

Van Halewyn and Norton (1984) estimated the total population of West Indies birds in the 1980s at over 10,000 pairs breeding at more than 30 sites. A review of recently published reports and consultation with people on most of the islands in the West Indies has resulted in a current estimate of a maximum number between 2,500 and 3,500 pairs (Table 1; Lee and Walsh-McGehee, unpubl. data), and actual population numbers may be 15-20% lower. Bermuda (not part of the West Indies) has the largest colony in the Western Atlantic: estimated at 3,000 pairs in

1950. The current population is down to 2,500 pairs and may be as low as 2,000 (Wingate pers. comm., Table 1).

The Dominican Republic and the Bahaman Islands have an estimated 500 and 1,000 pairs respectively. Combined colonies on Puerto Rico and Mona Island number 200-300 pairs. The remaining islands in the West Indies typically have colonies of 10 to 100 pairs, the majority

Table 1. Extant and extirpated colonies of White-tailed Tropicbirds and estimated number of nesting pairs in the West Indies. Bermuda is not considered part of West Indies.

Location		Number of Pairs
Bermuda		fewer than 2500
Bahamas		fewer than 500
Turks & Caicos Islands		82
Cuba		fewer than 50
Cayman Islands		60
Jamaica		80-162
Hispaniola		1000
Puerto Rico		200-300
U.S. Virgin Islands, total		40-80
Cas Cay		
Han Lollick Cay		
Water Island		
Congo Cay		
Brass Cays		
Misc. other cays		
British Virgin Islands, total		40-100
Fallen Jerusalem, Great Tobago	B	
Guana Isl., Norman Isl.	B	
Peter Isl., Round Rock, Virgin Gorda	?	
Dog Islands	?	
Anguilla		E
Redonda		5-15
Antigua		E
Barbuda		10-50
St. Martin		15
Saba		50-100
St. Eustatius		fewer than 10
Guadeloupe		68
Dominica		10-30
Martinique		fewer than 50
St. Vincent		?
Grenadines		?
TOTAL		**2,500-3,500**

E - extirpated

? - bred historically, no recent data to confirm present breeding

B = Breeds but no count of pairs

having fewer than 50. There have been documented declines in Bermuda, Cuba, Cayman Islands, Puerto Rico, U. S. Virgin Islands and Jamaica. While the colony on Saba was estimated to be only a few pairs in 1984, there was a large population estimated at 300-400 pairs present in 1990. Local residents indicated that the birds were present in those numbers since the 1950s when they ceased to be taken for food. These numbers dramatically declined to between 50 and 100 pairs in 1998. It is believed that this decline is due primarily to nest site competition with the larger and more aggressive Red-billed Tropicbird, which breeds on Saba throughout the year (pers. obser.). There are fossil records from Anguilla where the species has been extirpated. Additional colonies throughout the area have historic records, but no recent information that confirms current breeding.

White-tailed Tropicbirds are not currently designated as globally threatened. The population on Christmas Island in the Indian Ocean (*P. l. fulvus*) has declined slightly, but is estimated at between 6,000 and 12,000 pairs. There are an additional 5,000 pairs in the remainder of the Indian Ocean (*P. l. lepturus*). The Pacific (*P. l. dorotheae*) is thought to have several thousand pairs and the South Atlantic (*P. l. ascensionis*) fewer than 3,000 (del Hoyo et al. 1992). The Western Atlantic subspecies (*P. l. catesbyi*) was classified as a species of no immediate concern with regard to conservation priority by van Halewyn and Norton (1984). A more detailed census and a documented continuing decline in the number of nesting pairs in the West Indian population has led us to designate this population as "Vulnerable" in the West Indies (see Chapter entitled Action Plan for Conservation of West Indian Seabirds).

Red-billed Tropicbird (*Phaethon aethereus mesonauta*)

The Red-billed Tropicbird is the largest and least numerous of the three tropicbird species. It occurs in the tropical eastern Pacific, Caribbean Sea, Atlantic Ocean, Red Sea, Persian Gulf, and Indian Ocean to the Straits of Malacca, ranging north to the Bay of California and Bermuda and North Carolina, and south to Chile. Birds found in the West Indies are *P. a. mesonauta*. Those breeding on Fernando Noronha, St. Helena, and Ascension Island are *P. a. aethereus* and those found in the Red Sea, Indian Ocean, and Persian Gulf are *P. a. indicus* (del Hoyo et al. 1992). Their nesting habits are similar to those of the White-tailed Tropicbird above. Because Red-bills are larger than white-tails, they can out-compete them for nest sites and this may be part of the reason the number of White-tails is declining in the Caribbean.

The endemic West Indian subspecies ranges from Puerto Rico east and south through the Lesser Antilles to islands off Venezuela and Panama (Table 2, Fig. 2). Its range overlaps that of the White-tailed Tropicbird from Puerto Rico to St. Vincent. They are absent from the rest of the Greater Antilles. Compared to the White-tailed Tropicbird, the Red-billed appears to be limited to more productive water (van Halewyn and Norton 1984).

Van Halewyn and Norton (1984) estimated the West Indian population at 1,600 pairs at 22 sites in the 1980s. After a review of recently published reports (post 1995) and consultation with resident experts in most of the West Indies, a revised estimate of 1,800 - 2,500 pairs was made. Populations and breeding locations for Red-billed Tropicbirds have been less well documented than those of the White-tailed because many of their breeding sites are not frequented by biologists. Inaccuracy in earlier estimates makes direct comparison with the data in van Halewyn and Norton (1984) and later publications difficult. For example, Voous (1982) estimated Saba's population to number no more than twenty pairs. D. Lee and Walsh-McGehee (pers. obs.) estimated its population at 750-1,000 in 1996. Local inhabitants indicated that the numbers of birds had not increased substantially in that fourteen-year period. Given the disparity of Saba's estimate and the quadrupling of sites, the 1998 estimate should have been dramatically higher if populations at other sites were not declining. Furthermore, islands with Red-billed Tropicbirds have experienced the same loss of habitat, introduction of alien predators, and human disturbance as those with White-tailed Tropicbirds, and can be expected to have suffered the same deleterious effects. A breeding colony on Little Flat in the U. S. Virgin Islands

Table 2. Extant and extirpated colonies of Red-billed Tropicbirds and estimated number of breeding pairs in the West Indies.

Location	**Number of Pairs**
Puerto Rico, total	30±
U. S. Virgin Islands, total	225-300
Cockroach Cay	
Cricket Cay	
Hans Lollick Cay	
Mingo Cay	
Capella Cay	
Buck Cay	
Congo Cay	
Grass Cay	
Carval Rock	
Brass Cays	
Savannah Island	
Water Island	
Kalkun Cay	
Little Flat Cay	E
British Virgin Islands, total	fewer then 50
Great Tobago, Guana Island, misc. other isls.	
Sombrero	?
Antigua	50
Barbuda	50-100
Redonda	100
Anguilla	?
St. Martin	15
St. Bartholomew	?
Saba	750-1000
St. Eustatius	30
Montserrat	?/E
Guadeloupe	69
Dominica	10±
Martinique	50±
St. Vincent	?
Grenadines	?
Tobago	400
TOTAL	**1,800-2,500±**

E Extirpated,
? Bred historically, no recent data to confirm present breeding

was extirpated and a historic colony on Montserrat is also thought to be extirpated (D. Lee and Walsh-McGehee unpubl.).

Red-Billed Tropicbirds are not classified as globally threatened at present. However, the global population may be under 10,000 pairs (D Lee and Walsh-McGehee unpubl.). Van Halewyn and Norton (1984) did list the West Indian population under "status to be monitored." I suggest that the status of this species be listed as "Vulnerable" in the West Indies (see Chapter entitled Action Plan for Conservation of West Indian Seabirds). It occurs in the West Indies, the Gulf of California, the Galapagos Islands and the Cape Verde Islands (persecution by fisherman in the Cape Verde Islands has reduced a population of fewer than 1,000 birds in 1969 to no more than 100 pairs in 1990) with a total maximum population estimated to be 3,200 to 3,700 pairs. Other subspecies have experienced similar declines around the world (del Hoyo et al. 1992). I believe that this species deserves global conservation consideration and that the West Indies supports a substantial portion of the world's population.

Research and Conservation Needs

Because tropicbirds in the West Indies nest primarily on inaccessible cliffs and remote cays, possibly to avoid predators and human disturbance, monitoring and research on these species is difficult. Apart from a study of the breeding biology and energetics on the White-tailed Tropicbird on Culebra, Puerto Rico done by Fred Schaffner (1988), there has been little other research done. A breeding biology study of Red-billed Tropicbirds is currently underway on Saba. Populations of White- tailed Tropicbirds on Bermuda have been well monitored by David Wingate, and Judy Pierce has monitored both White-tailed and Red-billed Tropicbird populations in the U.S. Virgin Islands. All tropicbird colonies, extant and extirpated (Table 1 and Table 2) should be surveyed during the breeding season and problems experienced by individual colonies should be noted (nest site competition, habitat degradation, predators, human disturbance, etc.).

Monitoring schedules should be established to determine fluctuations in population numbers and to determine rates of breeding success. Long term banding projects throughout the West Indies would yield valuable information on the age structure of colonies and on fidelity to colonies, specific nest sites, and mates. To date, there is little information on any of the breeding biology and ecology of these two species. DNA studies are needed to determine the degree of reproductive isolation between colonies at different locations.

The construction and placement of artificial nest sites could provide much useful information on nest requirements, and could attract pairs to sites where various aspects of their reproductive biology could be easily monitored. These nests could also be used as an environmental education tool. In more remote areas, artificial nests could be used to provide additional sites where natural nest sites are limited. Further conservation needs and monitoring plans are discussed in the Chapter entitled Action Plan for the Conservation of West Indian Seabirds.

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Conservation of the Brown Pelican in the West Indies

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Introduction

Brown Pelicans (*Pelecanus occidentalis occidentalis*) occur throughout the Caribbean and are often seen near shore, feeding. This subspecies is endemic to the Caribbean. Unfortunately, information on their status, population ecology, and conservation needs is scant. In recent decades the population was thought to be in trouble owing to the same factors affecting United States populations (e.g., contaminants, human disturbance; Schreiber and Risebrough 1972). Available data for the U.S. West Indies (i.e., Puerto Rico, U.S. Virgin Islands) and elsewhere in the Caribbean suggest that contaminants (e.g., DDT and metabolites, Hg) are not affecting their reproductive performance in the Caribbean (van Halewyn and Norton 1984, Collazo et al. 1998). Environmental contaminants, particularly DDT and its metabolites, induced eggshell thinning with concomitant reproductive failures in other areas of their range (Anderson and Hickey 1970, Blus et al. 1971, Blus et al. 1974a, 1974b).

Human disturbance and loss or degradation of roosting and nesting habitat is adversely affecting populations throughout the West Indian region (Collazo et al. 1998). Also of great concern in these islands is coastal degradation and how it may affect feeding habitats (Collazo and Klaas 1986). Pelicans are long-lived, hence, a long-term monitoring program is needed to better understand their population dynamics, and to identify and protect essential habitats.

Status in the West Indies

The Caribbean Brown Pelican is the smaller of two subspecies recorded in the Caribbean (Wetmore 1945, Blake 1977). *P. o. occidentalis* (Caribbean) is similar to *P. o. carolinensis* (mainland U.S.) but breeding plumage is usually darker on the undersurface and nonbreeding plumage is usually darker above (Blake 1977). The Caribbean Brown Pelican occurs along the Caribbean coast and offshore islands of Central America, and south from Venezuela to northern Brazil at the mouth of the Amazon (Blake 1977, van Halewyn and Norton 1984). In the Greater and Lesser Antilles, its range includes Bahamas, Cuba, Jamaica, Haiti, Dominican Republic, Puerto Rico, Virgin Islands, St. Martin, and Barbuda (Fig. 1, Table 1). This account adds Trinidad (G. Alleng, pers. comm.) to the range reported by van Halewyn and Norton (1984) and updates counts of nesting pairs of birds. An estimated 1500 pairs (Table 1, Fig. 1) nest within this area, and the species is considered Threatened in the West Indies.

Pelicans are long-lived (25-30 yrs) with deferred maturity, usually not breeding until they are at least three years of age (Schreiber 1980). Breeding in the West Indies has been recorded

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throughout the year; peak nesting activity varies across its range (Collazo and Klaas 1986). In eastern Puerto Rico and the Virgin Islands they nest throughout the year and have two peaks of laying, September-October and March-April. In the other parts of Puerto Rico laying peaks in June-July. Clutch size is usually three eggs but can vary from one to three (Schreiber 1979). Productivity varies from year to year, depending on food availability and amount of human disturbance (Schreiber 1980), but averages about one young per nest (Collazo et al. 1998).

Concerns that factors affecting continental populations were also affecting populations in Puerto Rico and the U.S. Virgin Islands led to the designation of the species as endangered in this part of its range (DNR 1973, Philibosian and Yntema 1977). This designation prompted various research and monitoring efforts, generating perhaps the most extensive and detailed data base on their ecology outside the conterminous United States (Schreiber et al. 1981, Agardy et al. 1982, Collazo and Klaas 1986, Collazo et al. 1998). The mean number of individuals recorded during winter counts in Puerto Rico in 1992-95 (593) were 74% lower than in 1980-82 (2,289). Mean young per successful nest in the region was lower in 1992-93 (1.14) than 1980-82 (1.65). DDE, PCBs and mercury levels in egg samples, however, were low and did not adversely affect the species in either study period. The decrease in winter population counts from the 1980's to 1990's in Puerto Rico could be cause for concern because the 1990s counts were 32% (593/1840) of the expected mean winter count (Collazo and Klaas 1986). There was no obvious evidence that human disturbance was adversely affecting breeding or roosting birds during either study period but the birds are not well monitored and it could be a factor (Collazo et al. 1995). It is likely that roosting birds are often disturbed from beaches and this could cause them to leave an area.

The status of the species outside Puerto Rico and the U.S. Virgin Islands is hard to establish because data are scant, comprised mostly of notes or short-term surveys most of which were not done in recent years. Van Halewyn and Norton (1984) and Crivelli and Schreiber (1984) summarized this information and provided benchmark assessments of Brown Pelican status and conservation needs throughout the West Indies. Van Halewyn and Norton (1984) suggested that it was doubtful the species was in a precarious state outside of the U.S. West Indies, yet there are no real data on the number of nests. Brown Pelicans are considered common in Dominican Republic (Stockton de Dod 1981) and in Trinidad (5-100 seen daily, G. Alleng pers. comm.), but these could be roosting and wintering birds that are non-breeders. Data on number of nesting pairs and nesting success is lacking for the Dominican Republic. There are about 100 pairs nesting in Trinidad (Table 1) but we do not have data on their nest success.

Breeding populations in Mexico and Panamá (on both Caribbean and Pacific coasts) are believed to be large (i.e., 50,000+ birds Panamá and 40,000 pairs Mexico; Crivelli and Schreiber 1984) although there are no recent surveys. The number of individuals along coastal Venezuela and adjacent islands was estimated at 17,500 in 25 colonies (Guzmán and Schreiber 1987) but these data were not taken from recent surveys and the number of nests may be a fraction of this (2,000 pairs±). It is not known if there is genetic mixing of the birds through the Caribbean region or if there are separate sub-populations. There may be little to no interbreeding between West Indian and Mexican colonies, for instance.

Conservation Needs

Effective implementation of conservation measures depends on the availability of sound baseline information. These data do not exist for most colonies in the Caribbean basin. Pelicans are long-lived, and as such, reliable assessments about their demography and habitat requirements

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will only emerge from the implementation of long-term monitoring and research programs (i.e., 6-8 years; Schreiber and Schreiber 1983, Collazo and Klaas 1986). Basic data on population numbers, movement patterns, roost and nest site locations, and breeding productivity are needed to better understand the status of the species throughout its range (Schreiber and Risebrough 1972, Crivelli and Schreiber 1984, Collazo and Klaas 1986, Collazo et al. 1998). Conservation efforts should ensure the availability and integrity of essential habitats (i.e., foraging, roosting, and nesting), including restricting human visitation to colonies. Recommendations outlined by Anderson and Keith (1980) and Schreiber (1979) with regard to human disturbance and to promote pelican breeding productivity should be followed or used as initial guidelines. Organochlorines (e.g., DDT, PCBs) and other contaminants (e.g., Hg) known to have affected pelicans should be banned throughout the Caribbean basin. Mercury is suspected to be a problem in Venezuela (Guzmán and Schreiber 1987). Events such as oil spills need to be monitored. Mortality is not only recorded at the spill site, but due to its teratogenic effects, oiled adults can also cause embryo mortality.

Research Priorities

To determine the status of Brown Pelicans across its West Indian range basic information on their demography and factors that may affect their population health are needed. Particular attention should be given to estimating population numbers, survival and quantifying movement patterns. Mark-resight approaches were used in Puerto Rico and the U.S. Virgin Islands to document movement patterns (Collazo and Klaas 1986). Recent analytical advances provide an opportunity to obtain reliable estimates of population numbers and survival from mark and resight data (e.g., Pollock et al. 1990). Reliable estimates of population numbers, survival and breeding productivity, collected over 6-8 years, are needed to define a range of acceptable population parameter fluctuations for Caribbean Brown Pelicans. If such a research program cannot be implemented, Schreiber and Schreiber (1983) outlined procedures to assess the status of the species through a combination of minimum colony visits and population counts, albeit these data also need to be collected over 6-8 years. Contaminant evaluations should be conducted when available evidence suggest their presence (e.g., eggshell thinning, die-offs) or as part of a long-term monitoring program (e.g., every 10 years in the U.S. West Indies; Collazo et al. 1998).

The importance of understanding food availability patterns cannot be overemphasized. The population dynamics of this species is intimately related with this factor (Schreiber 1979, Anderson et al. 1982). Where possible, research efforts should focus on trying to understand factors such as prey species spawning patterns, habitat requirements and quality (see Murphy 1978, Yoshioka et al. 1985). Research efforts should ultimately provide an ecological basis to define what constitutes essential and high quality habitats for pelicans, and what factors undermine that quality.

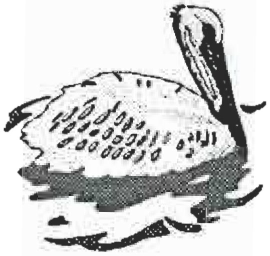

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Table 1. Extant and extirpated colonies of Caribbean Brown Pelicans in the Greater West Indian area, and minimum estimated number of nesting pairs:

Location	Number of Pairs
Bahamas, Turks and Caicos Islands	10±
Inagua	50-100
Cuba	B
Jamaica, St. Elizabeth	1-5
Portland Bight	?
Port Royal	15-25
Haiti	?
Dominican Republic	500±
Beata Island	?
Parque Nacional del Este	?
Puerto Rico (120-200 pairs)	
Montalva Bay	40±
Añasco Bay	E
Crash Boats, Aguadilla	25±
Conejo Cay, Vieques	100±
U. S. Virgin Islands (300-350 pairs)	
Dutchcap	100-120
Congo Key	100-120
Whistling Point, St. John	35±
Mary's Point, St. John	35±
Buck Island, St. Croix	35±
British Virgin Islands (160-180 pairs)	
Little Tobago	50-70
Guana Island	50-75
Norman Island	50 +
Lesser Antilles (150± pairs)	
St. Martin	B
St. Kitts, SE peninsula	B
Barbuda	2-10
Antigua	B
Trinidad	100
TOTAL	**1,500±**

? = bred historically but no recent observations
B = breeds but number of pairs and exact colony location is not available
E = extirpated.

Sources: van Halewyn and Norton (1984), Crivelli and Schreiber (1984), Collazo and Klaas (1986), Guzmán and Schreiber (1987), Collazo et al. (1998), A. Haynes-Sutton (Jamaica) J. Pierce (USVI, BVI), E. A. Schreiber (BVI), John Wilson (St. Kitts) pers. comm.

Status of Red-footed, Brown and Masked Boobies in the West Indies

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Introduction

There is little information on the status of the three nesting booby species (Red-footed Booby, *Sula sula*; Brown Booby *S. leucogaster*; Masked Booby, *S. dactylatra*) in the West Indies. Visits to Caribbean islands by naturalists during the 1800s and early 1900s record the presence of these species on various islands but few to no data are given on the numbers of nests present or even if birds were nesting. Frequently large roosting groups of boobies were assumed to be at nesting colonies and these areas were reported as colonies, when in fact no nests were present. Some recorded visits were during the non-breeding season when no data on numbers of nests could be obtained. Thus it is difficult at this point to accurately assess what the status of these species was in most of its historical colonies. In recent years, few of the colonies have been visited by scientists. We do know that several colonies have been extirpated and others are often disturbed. Current existing colonies are shown in Figure 1 and numbers of nesting pairs in Tables 1-3.

Species Accounts

Red-footed Booby (*S. s. sula*)

This pantropical species (found in the Caribbean, and tropical Atlantic, Pacific, Indian Ocean and in the seas north of Australia) and is the smallest of the six booby species (Schreiber et al. 1996). They feed by plunge diving, eating mainly flying fish and squid (Schreiber and Hensley 1976) but little is known about where they feed. They probably feed at oceanographic features such as down-island eddies and current shears which produce an upwelling or downwelling and thus food concentrations (Schreiber et al. 1996).

They nest in trees in most cases, but will nest on the ground if trees are not available. Incubation lasts 43-49 days (mean 46; Nelson 1978) and chicks fledge at 91-110 days (Verner 1961, Amerson and Shelton 1975), taking longer in years of poor food supply. The fledgling continues to return to its nest each night for several weeks after first flying to be fed by it parents. The length of this period varies extensively: 78-103 days (mean 90) in the Galapagos (Nelson 1978) to about 1 month in Belize (Verner 1961). This points out the flexibility of chicks to adapt growth rate to food availability and thus survive bad years (Schreiber et al. 1996). The main nesting season in the northern Caribbean lasts from October through May (Nelson 1978).

Currently, I estimate there are a maximum of 8,200-10,000 pairs of Red-footed Boobies nesting on Caribbean islands (Table 1). Fourteen colonies are thought to exist (Fig. 1), although some of these may have been extirpated since the last visit by a scientist. There are only three

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appears to be the one place where the nesting population increased in recent years: from 2600 pairs in 1986 (Clapp 1987) to 5,000 pairs in 1997 (E. A. Schreiber unpubl.). This colony is a Ramsar Site and the fact that access is very difficult has helped to protect the birds over the years. Data for other colonies indicates that they are declining in size. On Desecheo Island, Puerto Rico, Wetmore (field notes, June 1912) counted 2,000 birds (no number of nests given). There are about 150 nests on Desecheo today, probably a decrease from what was present during Wetmore's visit. The number of nests in the U. S. Virgin Islands declined from 300 in three sites just 15 years ago (van Halewyn and Norton 1984) to fewer than 200 in 2 sites in 1996 (J. Pierce pers. comm.). Clark (1905) said it was reported to nest commonly on Battowia and Kick-em-Jenny in the Grenadines where recent reports of nesting indicate only a few pairs. All indications are that the population in the Caribbean is continuing to decline.

In the greater Caribbean area, colonies are reported on the Campeche Banks, off Mexico (1,400 pairs), on Half Moon Key, Belize (1,300 pairs), on several islands off Venezuela (Aves Islets 1,200 pairs, Los Hermanos Isles 100's of pairs, Los Roques Isles 2,000 pairs, and Los Testigos 100's of pairs), and on Little Swan Island off Honduras (a few). Other colonies may exist off Colombia (Albuquerque Cays, Ron Cador Cays, Serrana Bank, Seranilla Bank) but there are no data on the number of nests. Data are badly needed for colonies off Colombia and Venezuela some of which may be extirpated.

Brown Booby (*S. l. leucogaster*)

Brown Boobies are pan-tropical in distribution, occurring commonly with other booby species: this subspecies ranges through the Caribbean and tropical Atlantic. They feed by plunge diving and eat primarily flying fish and squid (Dorward 1962). They are thought to feed closer to shore than other boobies (Norton et al. in press). The nest is built on the ground and colonies are either on flat coral atolls or rock ledges and hillsides of high islands. Two eggs (1-3) are generally laid, and incubation lasts 42-47 days (Nelson 1978). Adults generally raise only one chick and the second egg is often considered to be an insurance policy in case the first chick dies. On Johnston Atoll (Pacific Ocean) about 0.5% of pairs raise 2 chicks (Schreiber 1997). Chicks fledge at 85-119 days (Dorward 1962, Nelson 1978) probably taking longer during bad food years, such as occur during El Niño events. They return to the nest to be fed by their parents for 1-2 more months (Nelson 1978) and have been known to do so for up to six months (Simmons 1967; study conducted during 1963-65 El Niño). Some nesting birds can be found in all months of the year on Great Tobago in the BVI but this may be due to nests failing and adults re-nesting. Goats destroy many nests so that adults probably relay quite often (Schreiber, unpubl.). Wetmore (1918) reports large young present on Desecheo, Puerto Rico during June 1912 which means the nesting season probably began in October-November. In the southern islands the nesting season is said to be from February through May (Clark 1905), but must be much more extended than that.

I estimate there are 5,500-7,800 pairs of Brown Boobies nesting on the Caribbean islands (Table 2). They are known to be extirpated from 6-8 colonies and the existence of another 11 is questionable (Fig. 2). Large colonies have been destroyed, such as the one on Desecheo Is., Puerto Rico which was reported to have 4,000-5,000 nests in 1912 (Gochfeld et al. 1994). There are only 15 current known colonies with more than 50 pairs and only one colony with more than 1,000 pairs (Southwest Cay, Pedro Cays, Jamaica, A. Sutton & C. Levy pers. comm.). Most colonies of this species are small (1-100 pairs) and could easily be destroyed. For instance, Great Tobago, British Virgin Islands (80-120 pairs) has feral goats on it which trample nests, directly destroying some, and causing severe erosion. The total number of nests in the U.S. Virgin Islands has been declining over the past 10 years from about 950 in 1987 to fewer than 200 in 1996 (J. Pierce, pers. comm.). Clark (1905) was told hundreds nest on Battowia and Kick-em-Jenny in the Grenadines and Grenada where they are suspected to be extirpated today. In the Bahamas, Cay Verde had 550 pairs and the Mira Por Vos group had 600 during a visit by S. Sprunt in 1979. Chapman (1908) reported 1,500 pairs on Cay Verde in 1907 so the population appears to have declined in recent years. Cay Santo Domingo, for which I can find no bird data for the past 100 years, had a large colony of Brown Boobies in 1859 (Bryant 1859). Van Halewyn and Norton (1984) estimated that about 2300 pairs nested in Puerto Rico and the Virgin Islands as recently as 15 years ago, and today only an estimated 1500 pairs nest there (J. Saliva and J. Pierce pers. comm.).

Another 4,500 to 7,000 pairs of Brown Boobies nest to the south and west of the West Indian islands on islands off Venezuela, Colombia, Honduras, Costa Rica, Belize and Mexico. The largest colonies are those on Albuquerque Cays, Columbia (1,000's of pairs), Seranilla Bank, Colombia (1,000's of pairs; van Halewyn and Norton 1984), and Las Aves Isles, Venezuela (1,000's of pairs; Phelps and Phelps 1959). There are essentially no recent data from these islands to indicate the current status of the birds. Most accounts of sightings of Brown Boobies do not include data on nesting. Paynter (1955) counted about 800 on Alacran Reef off the Yucatan with no notes on nesting. At the time, local lighthouse keepers said 1000's nested on two nearby islands (Islas Desterrada and Parajos), however, these reports are difficult to interpret. In 1986 only 20-50 pairs nested in the area, and only on Isla Desterrada (B. Chapman pers. comm.).

Masked Booby (*S. d. dactylatra*)

This species is also called White Booby and Blue-faced Booby. They are the largest booby species, weighing up to 2300 g (Anderson 1993, Schreiber unpubl.). They are pantropical occurring in tropical oceans throughout the world, frequently in colonies near or with other booby species; this subspecies is found in the Caribbean and tropical Atlantic. Masked Boobies eat mainly sardines (Galapagos), flying fish, jacks and squid (Anderson 1993, Schreiber 1997), in sizes which often overlap with those eaten by Red-footed and Brown Boobies. They feed in offshore, pelagic waters and are known to feed 65 km from the colony in the Galapagos (Anderson 1993) but feeding areas in the Caribbean are unknown. Masked Boobies nest on the ground and build no nest to hold the eggs. Two eggs are generally laid (only one chick is raised) and incubation lasts 38-49 days (Nelson 1978, Anderson 1993). Chicks first fly at 109-151 days of age and return to the nest to be fed by their parents until 139-180 ± days of age (Nelson 1978).

There are an estimated 550 – 650 pairs of Masked Boobies nesting in 8 known and 3-5 suspected colonies on Caribbean islands (Table 3, Fig. 3). Three colonies have been extirpated and five more may be. It is most likely that more colonies were extirpated prior to known written records. Masked Booby bones are found in pre-Columbian middens on St. Croix (Palmer 1962) indicating that they were eaten by early Indian inhabitants of the Caribbean. No boobies nest on St. Croix today. Owing to the small current size of most colonies (2 to 25) they could easily be extirpated by introduced predators or other anthropogenic factors. Only one colony has more than 60 pairs; about 250-350 pairs nest on Southwest Cay in the Pedro cays off Jamaica (A. Haynes-Sutton and C. Levy, pers. comm.). They have been extirpated from Middle Cay of the Pedro Cays in Jamaica where 440 pairs were reported as recently as 1986. The number of nests in the U. S. Virgin Islands has declined from 60 pairs in 1987 to 25 pairs in 1996 (J. Pierce, pers. comm.). In the Grenadines and on Grenada, Clark (1905) reported that a few were said to nest on

Table 2. Extant and extirpated colonies of Brown Boobies and estimated number of nesting pairs in the West Indies.

Location	Nmbr. of Pairs	Reference
Bahamas, White Cay	100+	D. Lee pers. comm. 1999
Cay Verde	550	Sprunt 1984
North Rock	600	Sprunt 1984
Booby Rocks, off Mayaguana	70-80	A. White pers. comm.
Turks and Caicos	B	Walsh-McGehee et al. 1987
4 other sites	E	A. Sprunt pers. comm.
Cayman Is., Cayman Brac	10-20	E.A. Schreiber unpubl.
Cuba: Cayo Piedras	?	Palmer 1962
Is. off north and one off south shore	?	Palmer 1962
Dominican Republic: offshore N	B	van Halewyn & Norton 1984
offshore NE	B	van Halewyn & Norton 1984
Beata	100s	van Halewyn & Norton 1984
Alta Vela	100s	van Halewyn & Norton 1984
Jamaica, Pedro Cays, Southwest Cay	1,000-1,500	A. Haynes-Sutton pers. comm.
Pedro Cays, Middle Cay & NE Cay	E	A. Haynes-Sutton pers. comm.
Navassa	?	Wetmore and Swales 1931
Puerto Rico, Mona	100	J. Saliva pers. comm.
Monito	500	J. Saliva pers. comm.
Culebra, Cayos Geniqui	75-200	J. Saliva pers. comm.
Desecheo	E	J. Saliva pers. comm.
Cordillera	?	J. Saliva pers. comm.
U.S. Virgin Isl., Cockroach & Sula Keys	150	J. Pierce pers. comm.
Cricket	B	J. Pierce pers comm.
Dutchcap	170	J. Pierce pers. comm.
Frenchcap Key	280	J. Pierce pers. comm.
Kalkun	70	J. Pierce pers comm.
British Virgin Islands: Great Tobago	80-120	E. A. Schreiber 1997 ✳ —?
Little Tobago	20-75	J. Pierce pers. comm.
Redonda	B	van Halewyn and Norton 1984
Anguilla, Dog Island	690±	ICF Kaiser 1999
Prickley Pear Cay East	a few	ICF Kaiser 1999
Prickley Pear Cay West	100±	ICF Kaiser 1999
Sombrero	350-400	J. Pierce & RSPB pers. comm.
St. Barts	?	van Halewyn & Norton 1984
Saba	?	van Halewyn & Norton 1984
Dominica, Bird Isles	?	Nelson 1978
Guadeloupe, outlying islands	?	Noble 1916
Grand Islet	200-300	Feldmann et al. 1999
Martinique, Little Tobago	B	Nelson 1978

continued........

✳ I have tried to find out why Guana is not listed. They do nest. No reply yet. Skip 22.v.00

Conservation Priorities for Roseate Terns in the West Indies

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Introduction

The West Indian population of the Roseate Tern (*Sterna dougallii*) breeds from Florida through the West Indies to islands off Central America and northern South America. Roseate Terns also breed in North America, the Palearctic, Indian Ocean, southern Africa, and Australasia. In addition to the North American population, the European and southern African populations are endangered (Nisbet 1980, Randall and Randall 1980, Gochfeld 1983). The history and status of the Caribbean colonies are little known. Much of our knowledge of the status and distribution of birds in the West Indies was compiled by Bond (1958), who originally misidentified Caribbean Roseate Terns as Common Terns (*Sterna hirundo*) because of the similarity in their bill coloration (Furniss 1983). Failure to distinguish between the two species makes it difficult to reconstruct the history of Roseate Terns in the Caribbean. Reliable information on the distribution of these two species in the Caribbean first became available in 1984 (van Halewyn and Norton 1984). This report updates that account.

The Roseate Tern has a black crown, pale grey upper surface and immaculate white underparts. Both the upper and under surfaces are paler than in the very similar Common Tern. The long tail streamers are pure white and extend past the folded wing tips; whereas those of Common Terns are grayish with a black outer margin and do not extend past the wing tips. Male and female Roseate Terns are essentially identical in size and color. In non-breeding plumage, both Common and Roseate Terns have a dark carpal bar over the bend of the wing, although it is slightly lighter in Roseate Terns. During the breeding season only the tip of the bill of the Caribbean birds is black; the basal three-quarters is reddish orange, unlike the northeastern Roseate Terns (Shealer and Saliva 1992).

When Roseate Terns arrive at their colonies in the Caribbean their bills are mostly black, with the basal quarter reddish orange. By the time egg-laying begins, the basal three-fourths of the bill is reddish-orange, and this condition remains until after the chicks fledge and adults leave their breeding colonies (Saliva, pers. obs.). At this time, the red on the bill starts fading and the forehead begins to lose its black color. After the breeding season, most adults lose the tail streamers and the forehead becomes whitish.

In the Caribbean, Roseate Terns breed primarily on small offshore islands, or marine rocks, cays, and islets (Burger and Gochfeld 1988, Norton 1988, Shealer 1995: Table 1, Fig. 1). Rarely do they breed on large islands (e.g., Punta Soldado, Culebra in 1989 and 1991, Saliva, pers. obs.). On Culebra and the Virgin Islands the birds constantly shift locations from year to year moving from one small islet to another, possibly as a result of human disturbance. Nisbet (1980, 1989) reviewed accounts of Roseate Tern habitat use in the northeast United States where

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they typically nest under vegetation or other shelter (Spendelow 1982). This is not characteristic of the Caribbean birds where they nest near vegetation or jagged limestone rock (Robertson 1976, Voous 1983, Burger and Gochfeld 1988), on open sandy beaches (Robertson 1976), close to the water line on narrow ledges of emerging rocks (R. Norton and J. Pierce, pers. comm.), or among coral rubble (Saliva, pers. obs.). Although they may nest on slopes up to 70 degree angle, they generally seek flat or even back-sloping ledges for their nests. Most of them add little or no material to the nest but lay their eggs directly on the ground, rock, or vegetation.

Roseate Terns in the Caribbean usually begin egg laying in mid May, and hatching occurs from mid-June through early July. However, they may abandon a nesting area, re-lay on the same island, or move to up to three different islands in one breeding period. Sometimes laying may be reinitiated as late as mid-July, after the terns have attempted to nest on several islands (Saliva, pers. obs.). Reasons for failing on one island and moving to another are not always known since colonies are not monitored, but most likely are related to human disturbance.

Population Status

In the West Indies, there are very few published data on Roseate Tern colony sizes so that historical and current estimates of the population for the area are speculative (Table 1, Fig. 1). The only long documented history is that of the Dry Tortugas population (Robertson 1964). The history of the northeastern U. S. population has been summarized (Nisbet 1980, 1989; Gochfeld 1983; Kirkham and Nettleship 1987) and these accounts document the dramatic reduction of all species of terns in the late 19th century owing to market hunting, egging and, particularly, the millinery trade. In the U. S., nearly universal bird protection was instituted in 1913 with the passage of the Migratory Bird Treaty Act, significantly curtailing the exploitation of the past century. Following protection, Roseate Tern populations slowly recovered until the 1950's and 1960's when, somewhat erratically, they began to decline again. In the 1970's the decline became alarming, particularly in the face of a general increase in the population of Common Terns with which the Roseate Terns nest in the northeast (Buckley and Buckley 1981).

Potential predators on Roseate Tern in the West Indies include Magnificent Frigatebirds (*Fregata magnificens*), Laughing Gulls (*Larus atricilla*), Red-tailed Hawks (*Buteo jamaicensis*), Peregrine Falcons (*Falco peregrinus*), American Kestrels (*Falco sparverius*), Short-eared Owls (*Asio flammeus*), Cattle Egrets (*Bubulcus ibis*), Night Herons (*Nycticorax nycticorax*), Ruddy Turnstones (*Arenaria interpres*), American Oystercatchers (*Haematopus palliatus*), mockingbirds (*Mimus gilvus*), hermit crabs (*Coenobita clypeatus*), land crabs (*Gecarcinus ruricola*), marine or sally lightfoot crabs (*Grapsus grapsus*), feral cats, and rats (Saliva and Burger 1989). Mostly eggs and small chicks are taken by these predators.

Nisbet (1989) reported that Roseate Terns tend to shift colonies quickly in response to predation or reproductive failure. The number of potential predators found in or near some of the Caribbean Roseate Tern colonies (Saliva and Burger 1989, Shealer and Burger 1992) may be an important factor explaining the poor colony-site fidelity, aggressive behavior, and lower reproductive success of this species in some of those areas.

In the Caribbean, humans take eggs for food or linger on nesting islands causing fatal disturbance (J. Pierce and D. Shealer, pers. comm.). Egging is perhaps the major factor threatening many of the Caribbean colonies (van Halewyn and Norton 1984, J. Pierce pers. comm.). Human residential, commercial, and recreational activities in proximity to Roseate Tern colonies is a significant source of disturbance to breeding terns. Although terns can habituate to some human disturbance, it does nonetheless cause chicks to run from nesting ledges or may keep adults off their nests, allowing predators to steal eggs.

According to Nisbet (1980), the Virgin Islands population ranged from 750 to 1,500 pairs, Culebra Island held 325, Florida up to 200, the Exumas up to 200 pairs, and Antigua 50 pairs. Formerly, Roseate Tern colonies were reported in the Grenadines in 1902, Grenada in 1935, Dominica from 1941 to 1951, and Islas Las Aves in 1956 (Table 1). Many potential breeding sites have rarely been visited. Nisbet (1980) estimated the West Indian population to be 1,500 to 2,000 pairs. Van Halewyn and Norton (1984) argued that there was no evidence of a decreasing population and estimated the Puerto Rico-Virgin Islands population at 2,500 pairs. They concluded that the regional West Indian population was greater than 2,500 pairs and put the maximum at about 4,000 pairs but many areas were not surveyed at that point. Based on monitoring of Roseate Tern colonies in Puerto Rico and the Virgin Islands since 1990 and reports from biologists in other Caribbean countries, the estimated number of breeding pairs in the West Indies today is between 4,000 and 6,000 pairs (Table 1, Fig. 1).

Conservation Needs

The greatest challenge in the conservation of the Roseate Tern in the West Indies is the monitoring of colonies to determine population size and breeding success to assess the stability of the Caribbean metapopulation. Most countries in the West Indies have limited manpower and economic resources to study, manage, and protect the Roseate Tern. The fact that the Caribbean has large areas of potential Roseate Tern breeding habitat (e.g., the Bahamas), and Roseate Terns have low philopatry, monitoring of all potential sites becomes impractical for many countries. The protection of currently known Roseate Tern breeding areas, therefore, should be given the highest priority.

Conservation programs that promote the protection of Roseate Tern colonies should be developed. Posting of breeding areas, regular patrolling of these areas during the breeding season, limiting recreational use, and developing techniques for predator control are examples of programs necessary to achieve protection of breeding terns. The recovery of this species will depend on the development of these programs and on coordinating efforts with all the different countries involved (USFWS 1993).

Ownership of sites used by Roseate Terns should be determined to effect protective measures. Landowners in these areas should be appraised of the importance of their land for breeding terns, and appropriate guidance should be provided to them as to how to avoid disturbance to nesting terns. Government agencies and entities with jurisdiction over Roseate Tern colonies should become involved in the education of the public on general conservation values, as well as on the importance of protecting this species and adhering to government regulations. One step could be the preparation of an illustrated brochure to be distributed to local groups, schools, and organizations.

Management of breeding habitat may be necessary to increase Roseate Tern reproductive success, particularly when coupled with predator control programs. Based on the available information on Roseate Tern habitat selection in Caribbean colonies, it appears as if the preferred nesting areas have little or no vegetation cover. However, the terns seem to like some type of shelter near the nests. Therefore, a vegetation control program should be developed with guidance from knowledgeable biologists to prevent vegetation encroachment into nesting areas.

In otherwise suitable areas where Roseate Terns breed, sometimes nearby shelters such as rocks, boulders, or logs are not available. This situation renders eggs and younger chicks vulnerable to predators. Artificial shelters (e.g., nest boxes, tires, logs, coral crevices) should be provided were natural shelters are scarce. Roseate Terns usually select areas where a depression can be excavated in soft terrain to receive the eggs, or where a natural cavity or shelter exists. In cases where these are not available, artificial shelters may be provided.

The presence of predators at Roseate Tern colonies may result in nest abandonment or direct predation on eggs, young, or adult terns (Shealer and Burger 1992). Therefore, the effect of potential predators on breeding Roseate Terns should be evaluated and appropriate management techniques to prevent or deter predators should be implemented. Individual avian predators may specialize in preying on terns, and may regularly visit tern nesting areas to feed. Whenever possible, these nuisance birds should be scared off or trapped and relocated away from Roseate Tern colonies. Hermit and land crabs prey upon hatchlings and very young terns. However, it seems as if chicks are vulnerable to these predators only when adult terns are disturbed off the nests by people. Otherwise, adult terns usually prevent crabs from getting close to the nests. Some species of ants (e.g., *Solenopsis invicta*) may kill young terns when eggs are pipping or soon after hatching. The use of ant poisons or traps in areas of high incidence of these insects may be necessary.

Poaching of eggs is an important human factor affecting Roseate Terns. In some areas egging is legal, but there is no control on the number of eggs collected. For endangered or threatened species, such as the Roseate Tern, egging should be illegal. In areas where egging is illegal, governments may not have the facilities or manpower to patrol tern colonies to prevent it. Patrolling colonies during incubation, coupled with education of nearby communities may be the best tools to prevent poaching.

Although studies on the biology of the Roseate Tern in some parts of the Caribbean have been conducted (Burger and Gochfeld 1988, Shealer and Burger 1992, Shealer and Saliva 1992, Shealer 1995), these have been limited to very few colonies. Additional research is needed on the genetics of the West Indies metapopulation, as well as colony-site fidelity, to determine the degree of intermixing between sub colonies. Preliminary information from banded birds suggests that some populations may not intermix, whereas others do (Saliva, unpub. data). Banded Roseate Terns from Culebra and the Virgin Islands, for example, have been recorded breeding at either location, whereas no exchange has been observed between Roseate Terns from these two areas and western Puerto Rico (Saliva, unpub. data).

The implementation of conservation measures to maintain, protect, and enhance populations of the Roseate Tern, with the contribution and coordination of all Caribbean countries where this species breeds and winters, will ensure a self-sustaining Roseate Tern metapopulation in the West Indies.

Table 1. Known breeding sites and estimated number of breeding pairs of Roseate Terns in the West Indies (Netherlands Antilles and South American colonies are not considered part of the West Indies).

Location	Historical Colony Size	Current Colony Size
Bahamas	100-200	?
Cuba	A	C
Jamaica, Pedro Cays	B	3-5
Portland Bight	A	?
Haiti	B	?
Dominican Republic, Beata Island	12-20	C
Puerto Rico, Culebra cays	5-325	5-30
La Parguera	A	300-650
Guayanilla	A	2-350
Barceloneta/Manatí	A	75-200
U. S. Virgin Islands, Booby Rock	A	E
Carval Rock	A	E
Dog Island	A	E
Flanagan Island	A	200-1000 sporadically
Flat Cays	A	20-200
Kalkun Cay	A	50-350 sporadically
Le Duck Island	A	500-800
Pelican Cay	A	100-400 sporadically
Saba Island	A	20-400
Shark Island	A	100-800
British Virgin Islands, Carrot Rock	A	0-20
Cockroach	A	0-600
Dog Islands	A	C
Fallen Jerusalem	A	0-20
Green Cay	A	C
Guana Island	A	E ← *
Indian Rocks	A	C
Round Rock	A	C
Anguilla, Sombrero Island	A	30-40
Antigua	50	50 ?
Dominica	A	C
St. Kitts	A	100-200
St. Martin	24+	?
St. Lucia	A	?
Grenada	A	?
Grenadines	A	?
Guadeloupe	A	C

continued -

* This is claim that our colony on Guana is extirpated. I do not believe it. I think the still nest on Bigelow Beach in May. We should check!

Table 1 continued –

Location	Historical Colony Size	Current Colony Size
Martinique	B	C
Nevis	B	?
Tobago	500-1,000	?
Aruba	A	C
Bonaire	A	?
Curaçao	20-40	?
Venezuela	A	?
Honduras	A	?
TOTAL	**5,000-10,000**	**4,000-6,000**

A= Breeding reported before 1984, but number of pairs not known.
B= Breeding suspected, but not confirmed.
C= Breeding reported after 1984, but number of pairs not known.
?= Used to breed but no recent reports.
E – extirpated.

?

Cory 1891a, Cory 1891b, Noble 1916, Wetmore 1927, Wetmore and Swales 1931, Danforth 1936, Bond 1941, Devas 1942, Bond 1950, Phelps and Phelps 1955, Voous 1957, Bond 1958, Van der Werf et al. 1958, Pinchon 1963, Montaña and Garrido 1965, Pelzl 1969, Bond 1970, Dinsmore 1972, Garrido and Montaña 1975, LeCroy 1976, Robertson 1976, Holland and Williams 1978, Buckley and Buckley 1981, Prys-Jones 1982, Spendelow 1982, Gochfeld 1983, Voous 1983, van Halewyn and Norton 1984, Sprunt 1984, Ogden et al.1985, van Halewyn 1987, Norton 1987, Nisbet 1989, Saliva and Burger 1989, Shealer and Burger 1992, Shealer and Saliva 1992, Shealer 1995.

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The Vital Role of Research and Museum Collections in the Conservation of Seabirds

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Introduction

A thorough knowledge of the breeding biology and ecology of a species is necessary in order to develop conservation plans. All too often attempts to save species have been made with little knowledge about the species habits, needs or even a knowledge of what is causing its demise. Without research wrong assumptions are made and when acted upon may, in fact, harm the species in spite of good intentions. We must have good, scientific information on birds in order to preserve them.

Until recently, ornithology in the West Indies has focused on land bird studies, particularly on zoogeography and conservation. Unfortunately, research on seabirds has been neglected over the years. This may be because seabirds often nest in remote areas where it is difficult or expensive to conduct research. In many cases, the birds have been driven to nest in inaccessible areas because their original colony sites have been developed. What this means in the Caribbean is that we have little knowledge about the current status of most seabirds, and even less knowledge about their local natural history. This makes developing conservation criteria for them very difficult. If we are to preserve seabirds in the Caribbean, we must develop and implement some basic research and monitoring plans in a consistent, long-term format.

We know that many seabird species suffered egg shell thinning from the use of DDT before it and other pesticides were banned from use in the United States (Hickey and Anderson 1968, Risebrough et al.1968, Anderson and Hickey 1976). Since that time there has been a heightened awareness of the problems caused to birds by various sources of pollution: pesticides, heavy metals, PCBs, and oil (Ohlendorf et al.1978, Batty 1989, Koskimies 1989, Root 1990). We have essentially no data from the Caribbean area on various pollutant levels in fish or birds and yet we know that many substances are dumped into the water. There is a great need for a basin wide assessment of current pollutant levels in birds.

Specimens exist for so few areas in the Caribbean that no detailed historic record of population ranges and sizes can be reconstructed, and no record of geographic variation exists. Museum collections are an integral part of our knowledge about species and often play a significant role in understanding the conservation needs of species. Having collections is imperative for research on species identification, species diversity (biodiversity), species distributions, documenting changes in species distribution, and documenting effects of anthropogenic changes in our environment that affect bird species (such as historic levels of heavy metals in bird feathers and changes in this over time).

Perhaps more than any other organism, seabirds are symbolic of the land-water interface of Caribbean Islands. They can serve as indicators of the health of the land based environment as well as the sea because they depend on both. Setting up well designed research and monitoring programs for seabirds will enable us to use them as a means of monitoring the environment, as well as enabling us to preserve them. Seabirds can also provide a source of income to countries that do preserve them as eco-tours become more and more popular.

The Need for Research In The West Indies

Basic research on the breeding biology and ecology of birds is necessary in order to make well-informed decisions about conservation of those birds. The Caribbean is a unique ecosystem and the fact that a petrel or tern has been well-studied on a Pacific Ocean island does not necessarily mean that those data will be particularly relevant to the same species in the Caribbean. While the needs of each country may vary somewhat, there are some basic research needs that apply to all seabird colonies in the Caribbean. There are few historic data on colonies and in most cases we do not even know the size of colonies historically or today (Croxall et al. 1984 and papers therein, this publication). The current populations of seabirds present in the Caribbean probably represent about 10% of levels before human exploitation (Steadman et al. 1984, Kirch et al. 1992, Pregill et al.1994). Since the first humans arrived (about 7,000 BP), seabirds have been exploited as a food source and still are today on some Caribbean Islands (van Halewyn and Norton 1984). In addition to the fact that there are few historic data on seabirds, the little data we have are often inadequate. People frequently reported only the number of seabirds present in an area. Did this represent total birds or number of nests or just the number of birds seen? Were the birds even nesting? Because seabirds often travel hundreds of miles from colonies when they are not breeding, the presence of birds in an area does not mean that they nest there.

For many Caribbean countries there are no good data on what seabird species nest there currently, partly because nesting sites are often on uninhabited islands. Yet, the successful conservation of biodiversity depends greatly on an accurate assessment of the status of the animals to be preserved (Winker 1996). This basic research (quantitative listing) needs to be carried out on a Caribbean wide basis in order to determine the current status of seabirds in the Caribbean. Then current data need to be compared to any existing historic counts and to any available data from museum collections to examine trends in population levels and loss of former nesting colonies. The lack of this source of information (collections) for the Caribbean makes it more difficult to determine and defend populations goals for species.

The number of nests is probably the single most important piece of data that can be collected. The next step in monitoring is to make an estimate of nest success: proportion of nests that fledge a chick. These data are not always easy to collect. If a nesting season is extended, with adults laying eggs over 2-4 months, it is more difficult and labor intensive to determine the total number of nests for the colony since a census cannot be conducted in a single visit. Added to this difficulty is that getting to specific colonies may be difficult and expensive. Bad weather can prevent scheduled boat trips to colonies and boats are expensive to maintain and run. Many colonies are in sites that are dangerous to access: on steep cliffs where landing must be made on rocks with surging surf. It is easy to see why we do not know more about the status of many colonies. Yet, this inaccessibility is exactly what has protected these colonies. Once surveys of seabird colonies are completed, action plans can be formulated for preservation of important colony sites. Top priority sites for preservation are listed in individual chapters on each species.

the last chapter by Schreiber and Lee lists criteria for determining important sites. Each site should have legal protection and fines for trespassers.

Another problem that needs to be addressed is that the taxonomic status of seabirds in the Caribbean is poorly determined in many cases. In general, the decision to describe the complete population of a species in the Caribbean as a subspecies was based merely on the fact that the Caribbean was considered to be one continuous region. It was assumed that seabirds from one island move freely between islands, interbreeding with other island populations. The decision was not based on actual data about the birds. A recent analysis of Magnificent Frigatebird (*Fregata magnificens*) sizes in the Caribbean determined that there are significant size and mass differences of adults between colonies on Barbuda, the British Virgin Islands and the Cayman Islands (E. A. Schreiber, unpubl.). This indicates that even among the northern Caribbean islands there is little to no movement of birds between colonies, as found in the central Pacific with Great Frigatebirds (*Fregata minor*; Schreiber and Schreiber 1988). Further analyses may, in fact, determine that northern and southern Caribbean colonies of frigatebirds are different subspecies. Pitman and Jehl (1998) suggest that size and soft-part color differences in Masked Boobies (*Sula dactylatra*) nesting in separate areas on one island in the Pacific indicate that they should be considered separate species. Analyses such as this, combined with DNA analyses are needed for all Caribbean seabird species to determine accurate taxonomy. If some species have two or more subspecies in the Caribbean basin this has tremendous ramifications for conservation, by reducing, even further, the size of subspecific populations.

Ideally, a collection should be made of each seabird species from 3-4 areas in its range through the Caribbean. These specimens should be archived in a museum where they would be available to scientists to study. Specimens not only document colony locations today and current phenotypic variation in the species, they also will be available to scientists in the future as we develop other study needs (such as documentation of heavy metal levels in birds at that time) and techniques. If some seabird species are divided into new subspecies as a result of this study these collections will represent type specimens and be a necessary part of the documentation for taxonomic description (Banks et al. 1993).

The research recommended below may be difficult for some Caribbean countries to carry out since not every country has trained ornithologists on their staff. However, there are organizations available to assist in such studies (see last chapter). Another method for getting assistance with the needed research is to encourage researchers to come from elsewhere to study seabirds. These scientists can then provide a report on their findings and recommendations for conservation. Visiting researchers often provide important collaborative opportunities or training for local staff. The expertise and knowledge provided by visiting researchers can be very helpful and provide the information needed for management and conservation of seabird colonies.

Recommended Research

1) Locate and map nesting colonies of seabirds within each country. Surveys of all potential nesting sites should be undertaken and colony sites mapped. Timing of surveys will have to be determined for each species as the length and timing of the nesting season varies for different species. Seabirds in the Caribbean have two basic nesting seasons so that surveys of potential colony areas may need to take place monthly to determine a baseline for what species are nesting and where. Unfortunately the exact nesting phenology of most Caribbean seabirds is poorly known and, annual and regional variation in this has not been determined. Most tern species lay eggs in the Spring; April to June. Most boobies, frigatebirds and petrels lay in the late fall to

winter: October through January. Burrow and hole nesting birds such as petrels and tropicbirds will be more difficult to locate and often birds flying around a cliff side is the first indication of nesting activity in the area.

2) Determine the status of birds present and set up a monitoring program. Part of determining if a species is in trouble is knowing the number of nesting birds each year and monitoring for annual variation in this. A drastic decline in the nesting population in one year or a slow decline over several years can both be indications of a problem occurring to the birds.

Colonies should be surveyed (meaning that the number of nests is counted and their contents noted) at least three times during a breeding season: 1) near the end of the egg laying period, 2) during the small chick stage and 3) during the stage when larger chicks are present. The first survey records an approximate number of nests with eggs. The second survey records approximate hatching success. The third survey indicates an approximate number of young that will fledge from that colony in that year (reproductive success). The ideal survey plan would be to survey colonies monthly during the active nesting season. Colony sites that only had terns nesting from May through August only need to be surveyed each month through that time period. However, if Fall and Spring nesting species are present, the colony really needs to be surveyed monthly year-round.

3) Determine what if any perturbations are occurring to seabirds and their habitat. Each seabird colony should be specifically surveyed for any potential problems. Do boaters visit the island? Are there predators present on the island? Are goats present on the island, destroying nesting vegetation and causing erosion? Is the area protected by law so that it will not be developed?

If boaters visiting an island are a problem the island should probably be posted with signs. Legal protection for colonies is the most preferable situation but in lieu of this, people will often respect signs that ask them to stay away and explain that nesting seabirds need to be left undisturbed. Goats, sheep, rats, cats and other introduced mammals on nesting colonies should be removed. Cats and rats will eat seabird eggs and cats will take young chicks. Goats and sheep grazing an island trample ground nests and cause erosion that causes nests to be washed away in rains. They also destroy vegetation that is used for nesting habitat by many species.

During monitoring surveys, when nests are counted, observations should be made and recorded on other aspects of nesting and vegetation. Recorded observations often turn out to be very important in interpreting data. Any changes to vegetation should be noted. Any dead birds found should be recorded, along with age of bird (adult or chick) and reason for death (if this can be determined: broken wing, eaten by mammal, etc.). Annual changes can be monitored when notes are taken throughout the year and can be helpful in determining if anything is happening to the birds. For instance, an increase in the number of dead young found during surveys would be cause for concern and further investigation.

4) Determine and protect important roosting and feeding sites. Roosting and feeding sites are almost as important to seabirds as nesting sites and these areas should also be protected when possible. Roost sites are places where birds sit, rest and preen when they are not feeding.

Birds need to be able to rest, preen, sleep and feed safely to survive. If they are disturbed every time they sit down to roost on a sandbar, beach or rocky outcropping, they will not remain in an area. Protected wetlands serve as feeding areas for many birds, and as nursery grounds of the fish that many seabird species need for food. Protecting wetlands is vital not only to seabirds, but to the fishing industry. Sites such as these are often ignored when areas are considered for protection for seabirds, yet they are vital to the birds.

5) Band representative samples of nesting adult and young seabirds each year. We currently have almost no knowledge of the movements of seabirds in the Caribbean (except for a couple studies being carried out in Puerto Rico and the U.S. Virgin Islands). Banded birds are needed in order to determine movements of birds and to study demographics. The proposal to build a rocket launching facility on Sombrero Island will destroy the nesting area for Brown (*Sula leucogaster*) and Masked Boobies (*Sula dactylatra*); species considered "Threatened" and "Endangered" (respectively) in the Caribbean (see final chapter). It has been proposed that other islands could be set aside and protected for these birds to use. Data from banded birds of these species in the Pacific indicate that they do not readily change nesting islands (Schreiber et al. 1993, 1996), thus expecting them to move is probably untenable. Without banded birds, we have no way of knowing this type of information for Caribbean seabirds and it has severe ramifications for conservation efforts.

6) Encourage research projects on seabirds. Research by qualified scientists can often provide an inexpensive way for governments to obtain valuable information about their birds. Most researchers have funding to pay for their research and are not asking the local government to support their work. Full advantage should be taken of the findings of these studies. Most scientists are willing to advise on conservation issues that will help preserve the birds they want to study and they should be asked to do so.

7) Establish a series of museum specimens for research and reference. See below.

The Need For Specimens

A series of specimens of local seabirds can be very important to conservation efforts. Part of the reason for the lack of recent specimens in collections has been the reluctance of governments to give permits to collect birds. This is in some part owing to the environmental movement which works to protect species and habitat. Yet, one of the most important aspects of any conservation program is to ensure that voucher specimens exist for that area in that time. Vouchers are vital to documenting basic life history information, morphology, genetics, geographic variation, zoogeography, heavy metal levels and other pollutants, and the presence of genetic aberrations. For instance, if it were suspected that the deposition of heavy metals were increasing in Caribbean seabirds for some reason a set of samples could be taken to test for heavy metal levels but that would tell us little without historic data for comparison. Some heavy metals are naturally occurring in the environment and all seabirds will have them in their tissues naturally. To determine if levels are increasing we need a data set from a previous time-period for comparison. Currently this does not exist. A 14 year study, designed to analyze seabird diets and study molt by collecting specimens, has produced the only available evidence for increased consumption of plastic debris by seabirds (Moser and Lee 1992). This study also provided data on the importance of a specific ocean area to feeding seabirds and helped stop oil-drilling in the area (Lee and Socci 1989).

Today there are few specimens of seabirds from the Caribbean in any collection in the world. For instance, the National Museum of Natural History in Washington, D.C. (one of the largest collections in the world) has 13 round skin specimens of Red-billed Tropicbirds (*Phaethon aetherus*) from 5 islands, and has no skeletons or tissues. They have 19 round skin specimens and 2 unsexed skeletons of Magnificent Frigatebirds from 7 islands. Given the already documented variability in frigatebirds on the northern Caribbean islands (above), we would need 20 skeletons (10 of each sex) from each of four sites through the Caribbean (80 total skeletons) in order to examine the differences in their morphology throughout their Caribbean range and to determine their taxonomic status. Remsen (1995) suggests it is likely that many island populations of birds of widespread species should be classified as separate biological species. But these studies require specimens and genetic material. Collections also have many other uses which involve conservation and documentation of the effects on birds of anthropogenic changes in our environment.

Uses of museum specimens which aid in conservation.

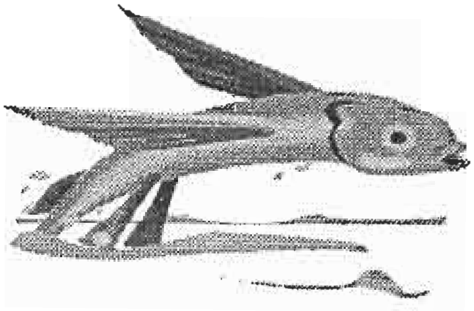
1) Documentation of the distribution of species in time and space. In many cases we only know if a species range has changed over time because of the existence of historic museum specimens with accurate data. Specimens of skins can also document changes in species over time within an area. Egg specimens validate nesting seasons and presence of nesting in an area, as well as providing documentation of eggshell thinning.
2) Understanding species diversity. The only way to document diversity of a species throughout an area is by comparison of museum specimens. Collections are used to study species-level taxonomy and such research often affects our interpretations of local biodiversity and endemism (Stiles 1995).
3) Discovery of new species and subspecies. To know that a new species or subspecies has been found, and to describe it, depends on having collections of similar species for side-by-side comparison. Watson et al. (1991) made extensive use of museum collections in order to describe a new subspecies of Double-crested Cormorant (*Phalacrocorax auritus heuretus*) from the Bahamas.
4) Teaching and training aides. Collections form a vital educational tool for training people in the sciences, environmental studies and conservation. Museums use their collections as teaching aides for training people in conservation of natural resources. This training opportunity can only be provided because these institutions have actively collected specimens and maintained them. While a country may not have the funding to support a full training program itself, it can still assist in these programs by supplying permits for the needed specimens and then benefit from the training available to all people.
5) Solving environmental problems. Collections that have been actively maintained and added to over time play a significant role in the problem solving process when determining the presence of and reasons for perturbations occurring to birds. Frozen tissue collections can be particularly important in documenting environmental perturbations (Remsen 1995) yet none exist for Caribbean seabirds.
6) Use of specimens by researchers. Most large museum collections contain specimens from around the world and they are also used by researchers from around the world. A significant part of the cost of maintaining a collection is making it available for researchers by having museum staff members who correspond with potential visiting researchers and process loans of specimens to institutions for research. Thus a country or a state, which may not have the money to maintain a large scientific collection, can have a series of bird specimens from their country in existence in an institution with the funding to care for it simply by approving collecting permit requests from Institutions.
7) Conservation. Sound conservation decisions must be based on the biology of the bird and a tremendous volume of information can be obtained from museum collections. "Species" and "subspecies" are the taxonomic categories most used in determining conservation priorities and evaluating these categories depends on having specimens in collections (Remsen 1995).
8) Writing of Field Guides. As ecotourism has increased around the Caribbean, there is a greater demand for field guides to the birds, and for more detail in these guides. Virtually all field

guides are written and illustrated by making extensive use of museum collections since authors and artists cannot generally afford to visit and do research in each site in order to write the guides.

Conclusion

The successful conservation of West Indian seabirds depends upon having an accurate knowledge of the species, and their biological diversity and needs. This research should be a priority for any conservation action plans for Caribbean seabirds. As human population size increases and development and pollution increase, it has never been more important to know how this is affecting our natural resources and to monitor them closely. Birds, particularly birds such as seabirds which are top-level predators, provide a sensitive indicator to our environmental health.

There are means to assist in ensuring that the research is done. Many conservation and government organizations offer aid and assistance for environmental studies (such as BirdLife, American Bird Conservancy, U.S. Fish and Wildlife Service, Organization of Eastern Caribbean States and World Wildlife Fund). These sources can help in multiple ways from advising, to providing literature, to arranging for a scientist to come and carry out a study with local resource managers. Full advantage should be taken of this assistance.



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Action Plan for Conservation of West Indian Seabirds

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Introduction

This chapter is designed to serve as a practical guide to preserving seabirds in the West Indies. It is the result of consultations with many people from the Caribbean nations and the United States, including dedicated researchers, natural resource units, and non-governmental organizations. By following these guidelines the beginning steps will be taken toward the preservation of seabirds in the West Indies. Seabird conservation has lagged far behind conservation of land bird species and this has allowed many seabird species to decline to very low levels. If we do not soon begin to acknowledge the value of preserving our seabirds and take some action many species will be lost.

There are four international Conventions instituted over the past 25 years, each having significant implications for conservation of natural resources. All four are applicable to seabird conservation: CITES, Bonn, Ramsar and World Heritage. These Conventions provide assistance to countries to protect natural resources and, very significantly, they provide a means of international cooperation to accomplish this (Oldfield 1987). Most West Indian nations are signatory to the Conventions and can take advantage of the resources they offer for assistance. Other Conventions which relate to protection of the environment and provide assistance to accomplish this include the Cartagena Convention and the Western Hemisphere Convention. Within the Caribbean, the Caribbean Conservation Association and the Organization of Eastern Caribbean States are both play an important role in conservation by providing various forms of assistance: training in wildlife and environmental protection, research, environmental education programs, establishing legislation, and an opportunity to share resources across nations.

It is often difficult for small countries to have the trained personnel and monetary resources available to undertake conservation programs. This makes conservation a more difficult task, where funding and expertise must both be found. The above conventions and organizations can provide valuable assistance. Information and help also are available from other groups such as BirdLife International, the World Wildlife Fund, RARE, U.S. Fish and Wildlife Service International Division, local natural history groups or birding societies. Full advantage should be taken of all these resources in our efforts to conserve seabirds in the West Indies. All of these groups can be reached through the internet (world wide web). Information on the four international conventions which help protect birds and their habitat can be found there also.

Some of the nations in the Caribbean do not have laws to protect seabirds and their habitat or do not enforce laws if they do exist. If seabirds are to continue to be an important part of the marine ecosystem or even continue to survive in the Caribbean region, the birds and their habitat must be actively protected. It is not only for seabirds that it is important to preserve habitat: this same habitat supports plants, other animals and us. When feral goats destroy an

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island for birds they are also destroying the surrounding reef as the overgrazed land washes into the sea and kills the reef. Then the fish populations that feed and live on the reef then die, also. All parts of the environment are connected and the loss of one resource can affect many other resources.

Tourism is a very important reason for preserving seabirds and their habitat because of the economic benefit (jobs) gained by maintaining an appealing natural world in the Caribbean islands. People have always come to this area to enjoy the natural beauty and with the growth of eco-tourism, this is happening even more so. A significant portion of many Caribbean nations' income is from tourists. If the natural beauty, birds and reefs of these islands are lost, many millions of dollars will be lost to local economies. Nature preserves such as the Baths on Virgin Gorda, the Booby Pond Nature Reserve on Little Cayman Island, and the Frigatebird colony on Barbuda, bring thousands of tourists to the islands, encourage young people to get training in the natural sciences to serve as tour guides, and encourage locals to support conservation of natural resources. There is a great need to establish more preserves in the West Indies and to protect those that do exist. There is also a great need for training in the wildlife sciences. The wildlife and natural resources of the West Indies can continue to provide income and a healthy environment as long as we learn to properly protect these resources.

On the following pages I provide descriptions of:

1) the primary threats to the survival of West Indian seabirds,
2) categories used to rank declining species,
3) criteria used to place species in specific categories,
4) a list of species falling under each threatened category, and
5) a plan of needed action to preserve seabirds and their habitat.

Primary Threats to Seabirds in the West Indies

In order of estimated severity:

1) Continued loss of nesting habitat owing to development. Thousands of acres of seabird habitat have been irrevocably lost to development and more are destroyed every day.

2) Human disturbance in colonies. Disturbing birds off their nests at a minimum can cause eggs and small chicks to be cooked in the hot sun. It also can cause adults to abandon nests and desert nesting islands when it occurs too frequently. Increasing uncontrolled tourist visits to islands have put increased pressure on seabird colonies. When adult birds are disturbed off nests eggs and chicks are easy prey for predators such as frigatebirds, Laughing Gulls, hawks, dogs, and others. Often people have no idea what harm they are causing when they enter a seabird colony.

3) Introduced predators, feral animals in colonies, uncontrolled livestock grazing. Predators are a tremendous problem for nesting seabirds. Animals such as goats, sheep, donkey, pigs, cats, and mongeese are present on many seabird nesting islands. They eat eggs and/or young, trample nests, and eat the vegetation that prevents erosion and provides nesting habitat. Livestock grazing has destroyed many colonies of burrow nesting seabirds such as petrels, as well as causing erosion. Grazing mammals not only kill birds by trampling on them, but also the surrounding reef can be destroyed by the erosion caused by loss of vegetation.

4) Limited data on natural resources and limited expertise on management of these. Conservation efforts are hampered by the lack of knowledge about the status of seabirds, their annual reproductive success, and the health of their environment. Added to this lack of data is the need for professional expertise in both gathering and interpreting data.

5) Human predation on eggs and birds. This was a much more severe problem 50-100 years ago, but still does occur in some areas.

6) Pollution of the waters in which seabirds feed can cause the decline or loss of their food source. Pollution can also cause insidious effects on the birds that are not easily seen. For instance ingestion of petrochemicals by seabirds can alter the immune system response of birds and increase mortality (Briggs et al. 1997). Considerable amounts of pesticides and herbicides are imported into the Caribbean but we do not have good data on the effects of their use. It is known that water pollution (including the use of pesticides and herbicides) has been responsible for fish-kills in the past (Towle 1991). There are many sources of water pollution around the Caribbean basin:
   a) Agricultural runoff, including fertilizers, pesticides, herbicides and waste.
   b) Soil runoff from denuded islands that have lost their natural vegetation from overgrazing, and farming.
   c) Ocean dumping of industrial waste which includes heavy metals. These metals get into the food chain and eventually end up in the food that seabirds eat, fish. Heavy metals are known to cause hormonal disruptions and development of deformities in embryos.
   d) Ocean dumping of untreated human waste.
   e) Ocean dumping of untreated garbage.

7) Over fishing by humans. We do not have good data in the West Indian region on the commercial fish resource but the number of people fishing and the amount of fish taken has increased greatly over the past 50 years.

8) Hurricanes which are a natural occurrence were not a problem when seabird populations were large. Today, with a few small remaining populations, a hurricane could easily destroy a major nesting site of a species. With the reduced bird populations present today the loss of a colony site is a severe problem. Since we believe many of these species are philopatric, they will not readily move to another island to nest and the loss of their nesting colony represents the end of their breeding.

Status of Species of Special Concern and Criteria for Listing

Population levels of some Caribbean seabird species are low enough to warrant special designation. There are some problems with trying to rank species status owing to the lack of information about the species in the Caribbean. We have used the basics of the International Union for the Conservation of Nature (IUCN) criteria (Collar et al. 1994) for putting species on the "Red List" as a guideline to categorize seabird populations in the West Indies. The Guidelines were designed to be applied to any taxonomic unit at or below the species level and to either the global population or a regional sub-population (Gärdenfors et al. 1999), which for our purposes is the West Indies. The IUCN criteria can be applied to regional sub-populations which are geographically distinct with little demographic or genetic exchange with other populations (IUCN/SSC Criteria Review Working Group 1999). Data are beginning to be gathered which show that individual seabirds do not readily move between regions for nesting (see Schreiber chapter on boobies in this publication) and West Indian populations may, in fact, represent separate breeding populations of these species from those in Central and South America. While definitive taxonomic studies on the status of West Indian populations are lacking, what little data exist on morphometrics of some species indicate that there is some separation of populations within the Caribbean basin.

The categories of designation for birds in trouble, beginning with the most critical are "Critically Endangered", "Endangered", "Vulnerable" and "Near Threatened". These categories reflect the extinction risk of a taxon. The data used in this assessment and assignment of species to the specific categories is the regional population size (number of nesting pairs) as described for Red List criteria, and thus indicates status within the West Indies. The IUCN uses the number of mature individuals in the population, not the number of nesting pairs. To obtain this figure for the species herein, simply multiply the number of pairs in the tables by two. The criteria for each category provide a means to quantify population status according to adult population size, trends in adult population size, and range size as reflected in the number of colonies.

The IUCN criteria work well for land birds but there are some difficulties applying them to seabirds. Some of the criteria were changed to make them more appropriate for seabird nesting habits. For instance, the IUCN categories have a criteria based on the area (100 – 20,000 sq. km.) in which the species occurs. Since seabirds are colonial, a highly concentrated portion of a species population can occur in only one or two small nesting areas (nesting areas of 0.1 – 0.2 sq. km). Much of the area in which they occur during the breeding season is open sea, not actually inhabited by the birds but used for feeding. We have changed the IUCN area criteria to specify a number of nesting locations with a viable population (30 or more pairs), rather than the size of the area used by the birds. The population size criteria we set for seabirds reflect the fact that they nest in colonies and a whole colony can easily be lost (to human destruction, hurricane, etc) representing an immediate massive loss of individuals. Because we have so few data on changes in population size over time, we were basically unable to use this criteria in categorizing species. Specifying a probability of extinction within a certain number of years also requires more data than we have for any seabird species in the West Indies, and thus this criteria is not used here.

Critically Endangered

1. a decline of greater than 80% of the population in 40 years or 2 generation (1 generation is considered 20 years for seabirds).
2. nesting either at two or fewer locations <u>or</u> experiencing continuing decline (locations with fewer than 30 pairs are not considered viable populations for this category).
3. fewer than 1,000 mature individuals or 500 nesting pairs remaining.

Endangered

1. a decline between 50% and 79% in 40 years or 2 generations.
2. nesting at four or fewer locations (with a minimum of 30 pairs each) <u>and</u> experiencing continuing decline.
3. fewer than 3,000 mature individuals or 1,500 nesting pairs remaining.

Vulnerable

1. a decline between 20% and 49% in 40 years or 2 generations.
2. nesting at eight or fewer locations (with a minimum of 30 pairs each) <u>and</u> experiencing continuing decline.
3. fewer than 6,000 mature individuals or 3,000 nesting pairs remaining.

Near Threatened

1. a decline between 10% and 19% in 40 years or 2 generations (40 years).
2. nesting at fewer than 10 locations (with a minimum of 30 pairs each) <u>and</u> experiencing continuing decline.
3. fewer than 10,000 mature individuals or 5,000 nesting pairs remaining and under continuing decline.
4. taxon is the focus of a continuing taxon-specific conservation program, the cessation of which would result in the taxon qualifying for one of the above categories.

Table 1. Species designations and estimated number of nesting pairs remaining.

Species and Designation	**Number of Pairs**	
A. Critically Endangered		
Black-capped Petrel (*P. hasitata*)*	1000-2000	
Jamaica Petrel (*P. caribbaca*)*	0-15	
Gull-billed Tern (*Sterna nilotica*)	100-500	
Cayenne Tern (*Sterna sandvicensis eurygnatha*)*	10-100	
Common Tern (*Sterna hirundo*)	50-100	
Black Noddy (*Anous minutus*)	fewer than 100	
B Endangered		
Masked Booby (*Sula dactylatra*)	550-650	
Brown Pelican (*Pelecanus occidentalis*)*	1500±	← G
Royal Tern (Sterna maxima)	450-800	
C. Vulnerable		
White-tailed Tropicbird (*Phaethon lepturus*)	2500-3500	← G
Red-billed Tropicbird (*Phaethon aetherus*)	1800-2500	←
Sandwich Tern (*Sterna sandvicensis acuflavida)*	2100-3000	
Least Tern - (*Sterna antillarum*)	1500-3000	
D. Near Threatened		
Magnificent Frigatebird (*Fregata magnificens*)	4300-5300	
Audubon's Shearwater (*Puffinus lherminieri*)*	3000-5000	

* indicates an endemic subspecies

Recommended Action for Seabird Preservation

A combination of actions is needed for the preservation of West Indian seabirds. Although number one below, surveys of existing colonies, is the most important thing to do immediately, the other actions following that are not listed in order of importance. Each country is a unique situation and the order of priorities will vary. The order will also vary by species. I do strongly recommend that natural resource managers not hesitate to ask for assistance if they are unsure about what needs to be done. As mentioned in the introduction, they are many avenues available to obtaining assistance. In most cases these recommendations will be better carried out with some outside assistance. No one of us could attempt to save a species alone. We all need expertise in addition to that we have ourselves, and we can be most effective in concert with others trying to accomplish the same goals.

In the past controlled egging (harvesting some eggs for human consumption) of some seabird colonies (particularly of sooty terns) has been attempted (Gochfeld et al 1994). While it is an added incentive to conserve a species if some harvesting can be done, this activity must be closely monitored by trained wildlife people and maximum harvest levels set. It is recommended that no more than 20% of the total eggs laid be taken and that they be taken in only one part of the colony (Feare 1976a, Feare pers. comm.). Monitoring and banding of the birds is needed to ensure continued survival of the colony under this added pressure (Feare 1976a, 1976b).

1) Survey existing seabird colonies. Since we know little about current population sizes and even current nesting areas for some species, surveys are very important and have been a major recommendation in the past (Croxall et al. 1984, King 1985). We cannot determine what areas to protect for some species because we do not know for sure where they nest. Data are also needed on population sizes and perturbations occurring to the birds in order to make decisions about conservation. Surveys should collect data on location of nesting (including location on a specific island and type of habitat used), number of nests present, and potential threats to the birds (such as the presence of predators). It may not be possible to do the survey in one visit since not all species lay at the same time of year, and some species lay over an extended period. If trained people are not locally available to conduct surveys, help should be sought from the outside. Human disturbance in seabird colonies can cause severe damage. The use of appropriate techniques when working in seabird colonies is very important.

2) Develop monitoring and management plans for seabirds. Monitor known nesting colonies to determine nest success. If birds are not successfully reproducing, determine the reasons why. Outside experts may need to be called in to help set up a monitoring program. Barbuda, with the assistance of the Organization of Eastern Caribbean States and World Wildlife Fund, has developed a monitoring plan for their frigatebird colony and carried out training programs for colony wardens and tour guides (Schreiber 1998a, 1998b). This program could serve as a model for other Nations. A monitoring network could be set up with neighboring countries to share data and methodologies. A central data base of Caribbean seabird colonies should be established. A group of birds does not necessarily nest in just one country. There is movement between countries and to truly monitor the size of Caribbean seabird populations it must be done across islands. A web-based database would make data accessible to all.

Set appropriate species goals and habitat preservation goals. Establish a timeline for action. Carryout a consistent monitoring plan to collect data that can be compared from year to year in order to determine if changes in populations are occurring.

3) Legally protect seabirds and their habitat once important sites are determined. Pass laws that protect seabirds, their eggs, their young and their habitat. These laws should state penalties for possession of birds or parts of birds, for disturbance of colonies and any harassment of birds. Specific islands should be listed as protected for the use of seabirds and human access should be monitored. The physical stress to birds of being constantly disturbed in breeding and roost sites decreases nesting success (Highsmith 1997) and tourists should not be allowed in colonies during the breeding season, unless on specific, conducted tours.

4) Post existing colonies with signs. Signage can be an effective deterrent to disturbance. Visitors to an island have no way of knowing if areas or birds are protected unless signs tell them so. In areas that are protected by law signs can tell people that, but even in legally unprotected areas, signs are effective to ask people to please respect the birds and stay away.

5) Training in wildlife management and monitoring techniques. Each West Indian country should have qualified personnel who have been professionally trained in monitoring and management techniques. Untrained people working in colonies can easily cause more damage than good. All West Indian Universities should offer courses in wildlife monitoring and management, and there should be regional coordination of training for policy-makers involved with wildlife (Walker 1998).

   A multispecies, ecosystem based approach to conservation of seabirds would well in the Caribbean, where the same habitat is used by several species.

6) Remove introduced predators and grazing animals from nesting colonies. No introduced mammal or reptile species should be present on nesting islands. They do tremendous damage to nesting populations of seabirds. Predation is the cause of extinction for 42% of lost island bird species and is a major factor in the listing of 40% of the endangered island species (King 1985).

7) Patrol colony sites and roosting sites. Enforce laws that protect wildlife. Patrols and some monitoring could be carried by local conservation groups in conjunction with the government employees as a means of extending government resources. Working with local groups also helps to educate more people about seabirds.

8) Protect existing undisturbed coastal habitat, mangroves, wetlands, and other areas that are used by birds for feeding or roosting. Nesting sites are not the only important places for seabirds. If birds are to be preserved as a valuable resource, then they must have healthy feeding areas, and safe roost sites. Roost sites are needed for birds to have a safe place to sit and preen and rest. Without these protected sites in an area, birds will leave.

9) Develop a public education program. The cultural context plays an important role in wildlife conservation programs (Blanchard 1994) and education plays an important role in changing attitudes about wildlife so that people are concerned about preservation of their natural history. No country can afford the cost of constant policing and patrolling to save species from human persecution. Once people learn about birds they begin to care about them and

want to preserve them as an important part of their culture. This is accomplished through education programs and non-government groups can be enlisted to help with these. A workshop was held at the Society of Caribbean Ornithology meeting in Guadeloupe (July 1998) at which representatives from 18 Caribbean countries determined that their top conservation priority was education (Walker 1998). These education programs will need to be developed as they do not currently exist in a relevant form for the West Indies. Needed are:

a) School instruction programs. These educational materials need to be developed at all school levels.
b) Development of adult instruction and educational pamphlets for local inhabitants and tourists. Educational programs and materials for hunters are needed, also, since seabirds are still shot in some countries. These education programs can help stop the taking of eggs and birds for food.
c) Development of appropriate material for decision makers.
d) Training of colony wardens and monitors, including training in data collection and information management.
e) Dissemination of information through posters, magazine articles, radio announcements and programs.

10) <u>Encourage research on seabirds</u>. This will help promote further understanding of the resource and provide valuable management data to better protect the resource (see chapter on "The Role of Research and Museum Collections in Conservation of Seabirds".

11) <u>Additional conservation priorities</u>.

a) Create economic incentives or alternative sources of income generation that preserve seabird habitat and the birds themselves. The people of Barbuda have begun using their Magnificent Frigatebird colony as an eco-tourist site. Before beginning a large scale program of doing this they sought help from the Organization for Eastern Caribbean States and had a training program for colony wardens and guides (Schreiber 1998). Better and more extensive marketing of nature based tourism is needed, in conjunction with development of eco-tourist sites and programs.
b) Manage tourism, recreational activities and coastal development that will affect seabirds and their habitat. Develop comprehensive coastal zone management plans that include seabirds by integrating economic and land use planning.
c) Evaluate fisheries and the consequences of over fishing to seabirds and humans.
d) Determine if seabird bycatch is a problem for fisheries.
e) Work with existing local conservation groups to draw attention to seabird needs and to enlist their help with monitoring and protection activities.
f) Introduced plants may need to be removed (such as Australian Pines [*Casurina*] so that appropriate habitat is available for the birds to use.
g) Start a natural history museum. This will provide an opportunity not only for educational experiences but to involve the whole community in the effort.

Conclusions

The above listings of Critically Endangered (6 species), Endangered (3 species), Vulnerable (4 species), and Near Vulnerable (2 species) West Indian seabirds illustrates the severity of the problems seabirds have in this area: 14 species and one subspecies of 21 total nesting species are listed as being in trouble. If even one of these species goes extinct it represents a loss of 6.6% of the seabird biodiversity of the region. Jamaican Petrels may already be extinct. More species have probably become extinct but the archaeological evidence has not yet been extracted from digs (Steadman 1997). Other areas surrounding the Caribbean have similar problems with the loss of bird biodiversity: Brazil, Colombia, Venezuela and Mexico (Steadman 1997). Immediate action is needed in the West Indies to preserve seabirds.

Obviously funding for conservation programs is badly needed. The organizations discussed at the beginning of this chapter can help with this. But funding conservation can be accomplished in innovative ways, also. There could, for instance, be a tax on tourist visits to the country that goes directly to conservation programs. Sales of some wildlife-related items could carry a special conservation tax that also goes directly to conservation programs. To help get such taxes implemented, it may be necessary to collect data on the extent of eco-tourism in the country to present to policy makers.

An integral part of preserving seabirds is the protection and management of the whole ecosystem or landscape. Birds cannot survive without nest sites and food sources so that just protecting the birds is not enough. The end results of successful management for seabirds and their habitat are beneficial to all of us in several ways:

1) jobs and income are gained from tourists who come to enjoy the wildlife,
2) healthy reefs are maintained that serve as nurseries for the fish we eat,
3) watersheds maintain the local water supply, and
4) a healthy environment is preserved that supports all of us.

It frequently takes an active involved public writing to and putting pressure on government officials to get action on issues. Public attention may have to be drawn to a problem to get any action. This is where communicating is important. People have to know there is a problem in order to do anything about it. Local conservation groups can be very helpful and can often provide extra manpower for monitoring, education programs and getting publicity. Cooperative efforts between governmental organizations and non-governmental organizations are very effective and useful.

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United States Department of the Interior

FISH AND WILDLIFE SERVICE
Washington, D.C. 20240

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September 10, 1999

Dear Society of Caribbean Ornithology Member and Caribbean Islanders,

At the 1998 Annual Meeting of the Society of Caribbean Ornithology, a workshop was conducted to set Society priorities. Highest among the priorities identified was the need for environmental education and public outreach.

Basic to raising public awareness is the availability of educational materials. One fundamental tool is a pamphlet or booklet to the common birds of each island. Such a booklet, simply written, attractively presented, inexpensively produced, and widely distributed, particularly within local schools, could contribute significantly to the promotion of public awareness and interest in bird conservation.

The U.S. Fish and Wildlife Service and the Society of Caribbean Ornithology are now jointly launching an initiative to collaborate with any interested islands in the preparation of such a booklet for their island. The goal is to produce booklets such as "The Common Birds of the Turks and Caicos," "The Common Birds of Anguilla," etc., which contain illustrations and text regarding common or well known island birds. The write-ups for each species would include basic information (habitat, distribution, etc.), interesting facts, and folklore. The number of birds in a booklet will vary island by island. Some islands may want as few as 15-20 species, larger islands may want many more, perhaps 60-80. Keep in mind that these booklets are not meant to be definitive guides to the birds of each island. They are intended to stimulate interest and serve as basic primers.

Preceding the bird write-ups would be an introduction describing the conservation problems facing local birds, a discussion of endangered species, a summary of steps underway or suggested to improve their status, and any other material the author finds relevant.

Local island authors are responsible for: (1) preparing the above material; (2) identifying possible publishers; and (3) developing a plan for distributing the booklet upon its completion.

Authors may be individuals or groups. Authorship is open to any interested party, not just to members of the Society of Caribbean Ornithology. On islands where more than one potential author may be interested in undertaking this initiative, efforts should be made at the earliest stages, on-island, to sort out roles and promote collaboration.

The U.S. Fish and Wildlife Service, the Society of Caribbean Ornithology, and the authors of "A Guide to the Birds of the West Indies" are prepared to support booklet authors with the following: (1) use of the appropriate drawings from the West Indies Guide to illustrate the island booklets; (2) editing; (3) publication expenses; and (4) possibly a workshop in July or August of next year to bring authors together to finalize the first series of booklets.

Frankly, we see this as a true opportunity for Society members and islanders to make a real difference with regard to stimulating local bird conservation. No proposals have to be written, no funds have to be raised. But, you will have to do some work. Booklets will only be prepared for those islands which take the initiative to draft sound manuscripts. If only one island chooses to do so, so be it, if twenty do--fantastic. This initiative will go only as far as local commitment drives it.

Attached for your information is a sample page from a guide along the lines of what we envision, though the sample is a bit too technical and short on local color and focus.

To start this initiative off, the U.S. Fish and Wildlife Service will be accepting manuscripts through March 31, 2000, for initial consideration. Development of a follow-up workshop for authors in July or August will depend on the response as of March 31.

Many of you may have questions. That's great. Feel free to contact me (Phone: 703-358-1767; Fax: 703-358-2849; e-mail: herb_raffaele@fws.gov) or Frank Rivera-Milan (Phone: 703-358-2103; Fax: 703-358-2849; e-mail: frank_rivera@fws.gov) and let's get this show rolling.

Looking forward to hearing from you,

H. Raffaele

Herbert A. Raffaele
Chief, Office of International Affairs

Enclosure

I would love to do such a guide if I had financial support....

LAUGHING GULL

Larus atricilla

Other Names: Gaviota, Gaviota gritona.

Classification: Order: Charadriiformes; family: Laridae.

Status: Common Resident.

Description: 16-17" (40.5-43 cm) A small gull with long, dark wings, which have a white trailing edge, and an all white tail. In winter, both adults and immatures have mottled gray heads and black bill and legs. The adult in breeding plummage, from March-Aug., has a black head and the bill turns dark red on most birds.

Voice: Its common name reflects their raucaus *hah-ha-ha-ha - hah-hah-hah*; in flight a hoarse *ka-ha*.

Habitat: Coastal and insular, rarely inland; roosts on sandbars, posts and piers within coastal lagoon system, as well as on rain drenched coastal golf courses. Nests on sandbars or sandy islands with patches of long grass.

Similar Species: Juvenile Herring Gull is much larger and heavier than juvenile Laughing Gull.

Distribution: Breeds w. Mexico and on east coast from Nova Scotia to s. Caribbean. Winters on Pacific coast from s. Mexico to n. Peru and on east coast from No. Carolina to Brazil.

Behavior: Not unusual for it to alight upon the head or back of a Brown Pelican and steal fish from its gular pouch. Though not an excessive scavenger, it does seek scraps at open garbage dumps and trash piles as well as trail fishing boats.

SOCIEDAD DE LA ORNITOLOGÍA CARIBEÑA
EL PITIRRE
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NORMAN ISLAND LEASED TO VINCI FOUNDATION

BRUCE POTTER
Island Resources Foundation

Norman Island - deemed by many as Stevenson's "Treasure Island" - has been leased, in its entirety, to the Virgin Islands Nature Conservation Institute (VINCI), a foundation established for the conservation of native flora, fauna, and marine life, the restoration of local ecology, and the promotion of education and research furthering the conservation of nature.

In 1750, a pirate by the name of Owen Lloyd allegedly buried some treasure on Norman Island. In fact a large amount of gold and silver was found by the Acting Lieutenant Governor of Tortola, Abraham Chalwill on the island after the pirate and his retinue had been killed by the Spaniards.

VINCI's immediate plans for the island include removal of livestock (primarily goats) to accommodate reforestation with native trees and revegetation of native ground cover and shrubs.

Further development plans include building a small natural history museum, with both public exhibits and a research facility, and planting a botanical garden highlighting the rich and diverse native flora of the Virgin Islands. All construction will be on the "design with nature" principle utilizing up-to-date environmentally sensitive materials and technologies.

In addition to the museum, new construction clustered near the existing beach bar restaurant (Billy Bones) will include amenities aimed at eco-tourism. There will also be some historical restoration of island ruins. Trails and signs designed to generate understanding of ecology, wildlife, and geology will be developed. A dock will be constructed far south of the current beach. Plans will be made to make the Island and museum accessible to school children and college students.

The Island Sun has learnt that in its initial stages, the VINCI project on Norman Island will be directed by Dr. James (Skip) Lazell of the Conservation Agency. Dr. Lazell has worked on conservation in the BVI continuously since 1980 and is known internationally for his direction of scientific activities at Guana Island, to which he brought hundreds of scientists over the past twenty years.

Norman Island has a rich history and an enormous potential for environmental restoration. The VINCI Foundation told this newspaper that the project ensures a secure environmental future for the island.

Asked what will happen to Billy Bones Restaurant and Beach Bar, a Vinci spokesperson said that Billy Bones Restaurant and Beach Bar is an attraction that benefits eco-tourism. It is leased to its present managers, Valerie and David Sims, who themselves have a substantial commitment to the island's environmental future. It is anticipated that the restaurant and bar will continue to prosper.

This newspaper also asked, how will the goats be removed? VINCI will ask the goats' owners to remove them in a reasonable period of time. If they are not removed, VINCI will encourage others to come and remove them.

According to the Foundation, the museum will be located on the knoll south of the beach and Billy Bones Restaurant and Beach Bar. Normal Island is owned by Audubon Holdings, Ltd., which is directed by a group of BVI residents and Belongers, including the Jarecki family of Guana Island.

Submit reply directly by emailing other-newswire@sidsnet.org.

Subj: **Sombrero (Invertebrates)**
Date: 04/26/2000 1:07:47 PM Eastern Daylight Time
From: bob@eastcaribbean.com (Bob)
To: jcinjtown@aol.com (Skip Lazell)

INITIAL REPORT, INVERTEBRATE BIODIVERSITY SURVEY OF SOMBRERO, 08-15 NOVEMBER 1999

Prof. Michael A. Ivie, Ph.D.
Montana State University

Accompanied by Justin B. Runyon, MSU Graduate Student, I left Bozeman, MT, USA, on 06 November 1999, over-nighted on St. Thomas, and arrived in Anguilla on 07 November 1999. The eighth was spent meeting the other members of the expedition (Mr Tony Murray, Dr Jennifer Daltry, and Ms Andrea Lamboo) and people from the Anguilla National Trust, familiarizing ourselves with Anguilla, and shopping for supplies. On the morning of 09 November, we traveled to Sombrero from Anguilla via the Anguilla Police boat, the services donated for the purpose by the Anguillan Government.

The next 7 days were spent surveying the invertebrate fauna of the island (excluding marine elements), investigating the relationships of those species with the other flora and fauna, and helping the other scientists in their activities. An estimated 1,000 specimens of arthropods and plants were obtained, and returned to Bozeman, under the permission of the Anguilla National Trust. In addition, interviews with the lighthouse keepers were done to obtain further information. The expertise of these men was repeatedly proven to us during our stay by independent verification of their information.

We searched the entire island, end to end, by visual methods, closely examining each species of vascular plant, fresh water pools, dead birds, dry splash pools, under rock, etc., for specimens. In addition to nets, we used beating sheets and aspirators (pooters). A flight intercept trap was placed in the Hanging Gardens. Mercury vapor and ultraviolet lights were used on the one night without high winds. Litter was too sparse to use Berlese funnels, but what there was we spread on a beating sheet to look for specimens. Near continuous high wind precluded use of Maliase traps. Caves were examined with headlamps and aspirators. Rocks, walkways and plants were searched at night for nocturnal species.

Specimens were preserved in ethyl alcohol or papered for return to MSU, where specimens will be prepared for permanent deposition and identification.

On the afternoon of 15 November we returned to Anguilla in time to help host Hurricane Lenny.

SECTION 2. Vascular Plants Observed.

Ogden et al (1985) and ICF Kaiser (1999) have recorded nine species of vascular plants from Sombrero. We observed 8 of these, and conclude that there was one previous misidentification, and one local extinction of an introduced species. The identity, origin and distribution of these plants on Sombrero was critical to surveying invertebrates, as each species of plant had to be examined for dependent species.

We made no attempt to collect or identify the freshwater algae. However, they are obviously an important part of the Sombrero system, and deserve further study.

The plants were:

Sesuvium portulacastrum. Sea purslane or camphor, this trailing succulent with white to pink flowers is native, and occurs throughout the island where original substrate provides a foothold. It is critical to the ecosystem, providing food to herbivorous, nectar and pollen feeding insects. Many of the smaller plants of this species, growing on exposed rock, seem to be very old. Some crowns were 5 cm in diameter at ground level, with only a few short branches and leaves extending above this base, in a sort of natural bonsai. NATIVE INSECT HOST.

Chamaesyce mesembrianthemifolia (=Euphorbia mesembrianthemifolia). This pretty little native species is a ferny cushion plant, with tiny white flowers. It also occurs throughout the island on original substraight. It seems to be the second mainstay of the island's natural economy. NATIVE INSECT HOST.

Heliotropium curassavicum. This busy trailing species is not as common as the previous two, although it seems to have the characteristics of a native. The frosted leaves and scorpiod spike of white flowers make it unmistakable. It is an important food plant for native insects. NATIVE INSECT HOST.

Portulaca oleracea. A bushy succulent with yellow flowers, this species seems mostly to occur near the building and in mine pits. It does not seem to be much used by native insects, and may be a recent introduction. INTRODUCED?

Chamaesyce serpens (=Euphoria serpen)s is a fragile plant with pink stems and small oval fleshy leaves. It is not common, and occurs with Portulaca. With no native insect associates, it is probably introduced. INTRODUCED?

Opuntia sp. Recorded as O. antillana by Ogden et al (1985) [now a junior synonym of O. cubensis] and O. plana [I can't find this name] by ICF Kaiser (1999), this species is now apparently limited to a single large plant in the mine spoils north of the lighthouse. There are obvious insect mines in the pads, but no culprit could be found. I suspect that the lepidopteran Cactoblastus cactorum is the species involved. This introduced moth is sweeping through the West Indies, endangering many of our native Opuntia. The Sombrero cactus was not in flower, so no specimen was taken for identification. Because of the large number of both native and introduced Opuntia, the status of this plant as a native in unknown. No native insects were found associated with it. STATUS UNCERTAIN.

Fimbristylis cymosa. This pantropical weedy sedge is limited to the area along the walkways between the docks and buildings. No insects were found associated with it. INTRODUCED.

Ipomoea pes-caprae. The Sea Morning Glory is a very common beach plant, familiar to every naturalist with expertise in the West Indian region. It was not present when Ogden et al did their inventory in 1985, but was established by the time ICF Kaiser made their visit in 1998. In their report (ICF Kaiser 1999) it is misidentified as Sea Bean, Canavalia rosea, a member of the Fabaceae. The lighthouse keepers say the plant was introduced with sand from Anguilla used in the reconstruction after Hurricane Luis. This plant is a very large vine, highly invasive, and an agressive competitor. It is currently beginning to spread out of the immediate housing area, and is a threat to the native species of plants to the north of the bunkhouse, and the large populations of natives in the southern pit we called the Hanging Gardens of Sombrero. No native invertebrates were observed utilizing this species. INTRODUCED

Not found: Odgen et al (1985) reported a single Pluchea carolinensis (as Pluchea symphytifolium), a yellow-flowered composite, near the bunkhouse. This introduction is apparently extirpated, and it's passing is not to be mourned. INTRODUCED and EXTERPAITED.

SECTION 3. Terrestrial (Including Fresh Water) Arthropods of Sombrero, Excepting Decapoda

Sombrero holds a relatively (to area) large number of terrestrial arthropods. I expected, from information previously reported, that the natural economy of Sombrero was driven by inputs from the sea via sea bird visitation, i.e. guano, dropped fish, dead birds would provide the energy to drive the ecosystem. On the contrary, we found that a large and thriving, albeit largely cryptic, vascular plant and fresh water algae community provides the energy for a tightly intertwined and novel ecosystem (see Section 2). The scavenger community driven by sea inputs does exist, but is considerably smaller than the truly terrestrial community. The lack of beach may account for this, as virtually all of the normal West Indian beach scavenger community was absent on Sombrero.

It will take some time to fully identify the species collected on Sombrero, but enough is obvious that we can give some preliminary data. In each case below, we list the approximate number of species taken, as well as how they fit into the categories of endemic, native but widespread, introduced resident, and non-resident migrant. This last category is larger than expected because of an unusual storm out of the west that occurred on 13 November 1999. On the morning of 14 November, we awoke to clear skies, and a cloud of butterflies. At least 8 species were seen, compared to only one in the days before the storm. In addition, 2 species of moth, a long-horned grasshopper, a cotton stainer and a second species of dragonfly were seen for the first time. In these cases, the plant hosts and habitat requirements are known, and do not occur on Sombrero. During that day, many of these migrants fell prey to a similar group of migratory insectivorous birds, however, other than as an interesting biogeographic observation, these species are not important to our survey.

The assignment to the other categories is VERY PRELIMINARY. It is very likely that many species will move back and forth between endemic, native and introduced resident categories. These assignments are simply first-cut best guesses. A few species, such as the non-resident migrants, are species I know on sight, so are assigned with certainty. Several of the introduced resident and native species are also know to me, and can be assigned on the basis of known characteristics and their distribution on Sombrero. However, keep in mind that most of the species are very small, and must be identified under a microscope. In several cases, specimens will have to be sent to specialists for final identification.

A few species of special surprise or import deserve mention. Solpugids are very rarely represented in the West Indies. The possibility of 2 endemic scorpions is very exciting. The wingless flea beetle (Alticinae) and spider beetle (Ptininae) are certainly new, and the wingless darkling beetle (Tenebriondae) probably is. The sweat bee (Halictidae) is perhaps the most astounding find of all. Bees are relatively uncommon in the West Indies, and to find this very tiny species so commonly visiting the flowers of the native plants was amazing. The undescribed camid fly is the first known representative of its family in the West Indies (excepting an amber fossil). Lastly, the fairy shrimp (Anostraca) was completely unexpected. This group is famous for its narrowly endemic species, with a large number of species on the endangered species list in Califomia alone. They live in temporary fresh water pools, which are abundant on Sombrero after heavy rains. Lastly, the grasshopper (Acrididae) is of interest. It is a perfect match for the gray-and-white mottled limestone surface. It is not the common coastal grasshopper found throughout the region, and may prove to be the largest endemic insect on the island.

In the table below is a summary of preliminary species numbers and identifications, and assignment of species to categories. The number of species may go up somewhat was we get through the hundreds of tiny specimens from the trap samples. "Endemic" means the species is unique to Sombrero; "Native" that it occurs there naturally, but has a wider distribution; "Introduced Resident" is used for species breeding on the island, but that arrived through the agency of humans; and "Non-Resident Migrant" is used for those highly vagile species that arrived on the west winds associated with the storm of 13 November, and for which the habitat requirements are not present. Assignment to categories in the table below is VERY tentative. Species are only assigned to Endemic with good evidence, so several from the Native column may move. Extra uncertainty is indicated by a "?" with a line of dots indicating the direction of uncertainty. An * is used for species that are secondarily flightless.

TABLE 1. Terrestrial Invertebrate Species of Sombrero, Preliminary Identifications and Resident Status

Taxon	Endemic	Native	Introd.Res.	Non-Res.Mig.	TOTAL
TOTAL	12	47	13	13	85

[FULL TABLE CAN BE SENT AS AN ATTACHMENT BY REQUEST]

SECTION 4. Species Interactions

4A Plants and Invertebrates

None of the species on Sombrero exist in a vacuum. The animal species found fell into the categories of herbivore, algophage, detritovore, predator, parasitoid and parasite. Until we have all the identifications in, we will not be able to be sure of all the connections we can document, and even then, many will remain undocumented until a full ecological study of energy flow has been conducted.

However, several things seem obvious. First, the native plants are critical to the production of herbivorous insects, especially the endemic flea beetle and spider beetle, as well as the likely endemic (certainly native) sweat bee, grasshopper and seed bug, and the native (possibly endemic) leaf beetle, moths and plant hopper. These species were observed exclusively on native plants.

Specific host associations include:

Sesuvium supports the leaf beetle (Galerucinae), spider beetle (Pitnus), sweat bee (Halictidae), ants (Formicidae) and grasshopper (Acrididae).

Chamaesyce mesembrianthemifolia supports flea beetle (Alticinae), seed bug (Lygaeidae) and grasshopper (Acrididae)

Heliotropium supports ants (Formicidae)

Opuntia supports the non-native Cactoblastus (Moth)

These plants are also critical to the detritovoures, such as the possibly endemic (certainly native) cricket, springtails, psocids, darkling beetle, sowbugs (woodlice), tineid moths and ants

Indirectly, these plants also support the large invertebrate predator element dependent on these plant-dependent species - scorpions, solpugids, centipedes, spiders, ground beetles, rove beetles, feather-wing beetle, etc. Finally, the parasitoids require one or more of these species of insect.

Second, the algal community is equally important. Inhabiting the seeps in caves and on cliff faces, as well as the numerous fresh water pools on the surface, algae support most of the fly species, the water boatmen and fairy shrimp. These in turn support the predatory shore bug, dragonfly and backswimmer, as well as many of the terrestrial predators mentioned above.

4B Sea Birds and Invertebrates

Although the majority of species on Sombrero are dependent on terrestrial or fresh water photosynthesis, sea birds dependent on Sombrero directly support a large number of species of lice, mites, and hippoboscid flies. These often-neglected elements of biodiversity are unique to each host (sometimes to a particular PART of a host), often far more geographically restricted, and not all individuals in a host population may support each species of parasite. Thus, they are often far more endangered than their hosts are. Well-meaning but benighted humans often actually consider these species pests, sometimes going so far at to dust captive-bred or captured birds to rid them of these parasites. However, not only do these species have the same long and unique evolutionary history of any other, they are part and parcel of the host species' habitat and biology. As such, they deserve the same consideration as other elements critical to the species' survival.

Dead sea birds, dropped fish, and broken eggs support detritivoure ants, earwigs, springtails, and psocids. These in turn support predators, apparently especially the centipede and spiders. A surprising new species of the fly family Camidae is associated with birds and their nests.

A study of nitrogen flow on Sombrero may show that the inputs by sea bird may be critical to the land plants and algae, further tying the system into an even more fragile web of relationships.

4C Invertebrates and Reptiles

All of the 3 terrestrial vertebrate residents of Sombrero, Ameiva corvina, Anolis sp. and Sphaerodactylus sp., are dependent on invertebrates for food. The evidence indicates that with the exception of human-provided cooked food and the possibility of some carcass and broken egg scavenging (not observed by our team) by Ameiva corvina, all food for these species is provided by invertebrate species. The evidence provided here contravenes the allegations that Ameiva feeds on plants.

Ameiva corvina was observed by Dr. Daltry to feed on the grasshopper. I observed them feeding on the leaf beetle larvae. Examination of 4 small fecal samples showed that adult and larval flies, plant hoppers, crickets, ants, spiders, bees, centipedes, plant bugs, and flea beetles all contribute to their diet. Contrary to unsupported allegations, no plant material was found in these fecal samples. The material in these small samples was highly digested, but never-the-less, distinct hard parts were available for identification. Therefore, healthy invertebrate populations are critical to the survival to this endemic and endangered species.

Fecal samples from 4 Anolis provided even larger numbers of invertebrates. Perhaps because of the size of the samples, differences in eating and digestion systems and other factors, many of these specimens were nearly intact. Bees, ants, spiders, crickets, flea beetles, seed bugs, plant hoppers, leaf beetles (adults and larvae) and tineid larvae were common in these samples. More rare but represented were isopods, midges and other flies, caterpillars and spider beetles.

No fecal samples from Sphaerodactylus were obtained.

It is very interesting that the species utilized by these lizards for food seems virtually (if not totally) limited to native species. Abundant introduced anthropophilous species are avoided or not encountered as food.

SECTION 5. CONCLUSIONS

Sombrero's terrestrial ecosystem is a small, tightly interwoven and very fragile unique system - a Galapagos in miniature. The presence of all the major trophic levels in the animal component of this ecosystem – herbivore, pollinator, detritivore, predator, parasitoid and parasite - indicates that it is a true functional ecosystem. The extremely harsh physical environment and isolation have provided the context for the evolution of a high proportion of endemic taxa. Periodic natural events, such as hurricanes and droughts, coupled with the very limited size of the island, push populations through genetic bottlenecks on a regular basis. For species that cannot readily recolonize, this bottleneck contributes to rapid evolution through extreme selection and founder effects, and unique new species evolve that are specifically adapted to the site. The high number of secondarily flightless species on Sombrero, in keeping with Darlington's "Mountains and Islands" hypothesis, testify to this fact. The expectation is that an ecosystem of this sort will be composed of K-selected species, and as such, be highly susceptible to disruption by invasive species and habitat destruction.

The only major animal community not documented by our work is the fungivores - with the possible exception of some of the mites, springtails and unidentified flies. Although fungi are undoubtedly present on Sombrero, no large, obvious fruiting bodies were noted. It should be specifically noted that no member of the team was qualified to address the presence or uniqueness of the fungal flora, which may play critical roles in decomposition and as mycorrhizae.

The conclusions of the ICF Kaiser report that are based on the idea that only the Ameiva is endemic, that virtually no invertebrates are resident on the island, that the Ameiva feeds naturally on Seuvium, and that habitat disturbance relative to all endemic species can be easily offset by planting more of this plant are shown to be invalid by these findings. Further, it must be noted that the assertion that the Anolis and Sphaerodactylus were introduced to Sombrero via human activity is without evidence.

SECTION 6. RECOMMENDATIONS

Protection of invertebrates on an individual species basis is not normally possible or advisable. They exist in communities with their plant hosts and vertebrate associates. In general, understanding the tropic interactions and nutrient flows in a system, and protecting the habitat integrity of the whole will provide for the invertebrate conservation needs. Therefore, specific recommendations include actions involving species beyond the invertebrate community.

A team should be sent to study the algae.

A team should be to search for and study fungi.

Conduct an energetics review of the terrestrial system, and organic nitrogen flow through the system before risking modification of the environment.

Remove introduced Ipomoea by pulling.

Remove Mus musculus through trapping [use live traps to avoid killing Ameiva].

Vigorously protect island from introduction of rats, cats, and other invasives.

Conduct a genetic study of all native or possible native plants to determine if they are unique at any level.

Consider a return visit of entomologists in a different season, to look for species missed on this expedition. This would be most important at peak bird nesting season, to detect species that have highest population levels as a result of bird inputs.

Prevent potential for damage to natural vascular vegetation through loss of habitat area, increased trampling or pollution from fuels, lubricants and coolants.

Avoid damage to algal populations through spills of fuels, lubricants and coolants which will pollute or change percolation of water to cave and cliff drip surfaces.

Protect all freshwater pools from spills of fuels, lubricants and coolants.

Consider full protection for Sombrero and its unique ecosystem.

Although I have no real expertise to suggest this, the fact that the Anolis seems to feed only on native arthropods, coupled with the behavioral differences between the Sombrero and Anguilla Anolis (he Sombrero population does not hunt on buildings or vertical surfaces, and goes down, not up, to avoid threats), the rarity of precedent in the introduction of Sphareodactylus species between islands, and the general distribution on the island (most introduced species seem clustered around the buildings and dock) indicate to me that it is likely all 3 lizard species are native to Sombrero,. If this is true, the Anolis and Sphaerodactylus should be closely reexamined by qualified herpetologists in light of modem species concepts.

Subj: **Re: Sombrero Gecko**
Date: 04/27/2000 3:41:43 AM Eastern Daylight Time
From: JDaltry
To: JCINJTOWN
CC: a.malhotra@bangor.ac.uk

note date ...

Dear Skip,

Good to hear from you. Sorry there has been a delay - I was working in Cambodia from January through March, and have since been laid up with malaria and dengue.

The gecko specimens have been forwarded to the herpetological research group in Bangor for genetic analysis (the group has sequenced many other Sphaerodactylus spp in the Lesser Antilles) to help determine status. Yes, we should compare the MCZ specimens. As an NGO, I assume it would not be possible for Fauna & Flora International to accept a formal museum loan from the MCZ. Would it be possible for you to help obtain them for me?

Best wishes,

Jenny

In a message dated 4/26/00 3:53:39 GMT Daylight Time, JCINJTOWN writes:

> Dear Jenny, What progress on the sphaero? I note the MCZ specimens have not
> been borrowed. Have your specimens been accessioned into a museum? Best, Skip

Subj: **Sombrero Report, Lizards**
Date: 04/26/2000 1:08:04 PM Eastern Daylight Time
From: bob@eastcaribbean.com (Bob)
To: jcinjtown@aol.com (Skip Lazell)

{The author of this report is Jenny Daltry, see address at bottom}

EXECUTIVE SUMMARY AND RECOMMENDATIONS

Sombrero was visited from 9 to 15 November 1999 to assess the conservation status of the Sombrero ground lizard (Ameiva corvina) and to conduct preliminary investigations into its population biology and ecology. The ground lizard was found to be a critically endangered species (CR B1+C2), and one of the rarest animals in the Caribbean.

To determine population size, 115 individuals were caught and temporarily marked with nail varnish. A mark-resight study estimated that there were between 396 and 461 ground lizards on Sombrero, of which approximately 200 were mature adults. The population has increased in recent years, but is apparently still lower than it was before September 1995, when Hurricane Luis struck the island.

The visit increased the known maximum size for this species: the largest male measured 134.5mm in snout-vent length, while the largest female measured 108.3mm. There was a strong tendency for body size (an approximate indicator of age) to decrease with distance from the lighthouse. The majority of the lizard population was in the western half of the 38.5-ha island. Few were seen on the northern and southern peninsulas or in the barren expanse of quarry waste in the centre of the island. The distribution range of A. corvina is therefore in effect much smaller than the total area of Sombrero.

32 point counts were conducted in randomly chosen locations on the island. These entailed recording all ground lizards seen within a radius of 5 metres during a period of five minutes. A partial Mantel test was used to compare the number of lizards seen with various abiotic and biotic environmental variables recorded within the point count circle. Density of ground lizards was found to be significantly correlated with vegetation cover alone ($P = 0.0001$).

Faecal analyses revealed that Sombrero ground lizards principally feed on insects, which are in turn dependent on the island's sparse cover of terrestrial plants. Towards the lighthouse, they also opportunistically feed on food scraps discarded by the lighthouse staff, both near the kitchen and at the garbage dump. Ground lizards also scavenge carrion and one case of cannibalism was observed. None of the lizards captured appeared to be ill or underweight.

The Sombrero ground lizard inhabits a harsh, severely restricted and unpredictable environment. Any further human activity or infrastructure anywhere on the island could endanger this vulnerable population still further, especially in view of the increased frequency of hurricanes in recent years.

The following conservation measures are recommended:

Legislation:

Propose the 'Red Listing' of the Sombrero ground lizard by the World Conservation Monitoring Centre.

Develop and enforce protective national and international legislation for the Sombrero ground lizard.

Develop and enforce protective national legislation for Sombrero.

Education:

Enhance awareness of the Sombrero ground lizard and Sombrero among the general public, tourists and national decision-makers (including the appropriate British authorities).

Research:

Develop and implement a standardised protocol for monitoring the number, distribution, health and demographic structure of lizards throughout Sombrero.

Survey Sombrero regularly for the presence of invasive animals and plants and develop a contingency plan for the eradication of potentially harmful species.

Conduct more detailed studies of the autecology of the Sombrero ground lizard, in particular its reproductive biology and diet.

Devise and implement a project to survey and monitor invertebrate and plant populations on Sombrero.

Investigate the feasibility of maintaining a breeding colony of Sombrero ground lizards in captivity ex situ.

98 ground lizards of both sexes and various sizes were permanently marked with passive transponder tags to assist long-term studies of their individual survival and growth rates.

In addition to A. corvina, Sombrero supports populations of two other lizards: an anole (Anolis sp.) and dwarf gecko (Sphaerodactylus sp.). Both species were found during this visit. They are almost certainly indigenous to Sombrero, and one or both may prove to be new (and potentially threatened) species. Morphometric and genetic analyses should be conducted to verify this. A conservation assessment and further studies of both species on Sombrero are strongly recommended.

It is important to note that the present study was conducted immediately prior to Hurricane Lenny (17 - 19 November). This may have caused significant mortalities among all three species of lizards and their prey base.

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Human Impact on Ancient Environments

Charles L. Redman

This is a generally interesting and excellent book. I have culled out a few passages about the Middle East that seem especially relevant to the B.V.I. Skip

The University of Arizona Press
Tucson

1999

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Lessons from a Prehistoric "Eden"

Perhaps the greatest challenge facing humans today is for us to live in concert with our environment. For people to seek creature comforts, economic prosperity, and maximum enjoyment sometimes seems to be in direct conflict with preserving the richness of the natural environment, maintaining human health, and even insuring the continuity of life on Earth. Is humankind on a fast track to self-destruction? Is there a realistic balance that can be reached? Or, in fact, are the problems not as grave as some would have us believe? Scholars, philosophers, and lay people of all persuasions are asking these questions, and their resolution will affect people in every part of the globe.

Recognition of the gravity of the *environmental crisis* has become widespread over the past thirty years, galvanizing scientists from diverse disciplines into a pursuit of urgently needed answers. *Science,* the prestigious journal of the American Association for the Advancement of Science, recently devoted an entire section to the latest findings on how humans are impacting virtually all of Earth's ecosystems. Among their startling revelations are that more than half of the accessible fresh water on Earth is used by humans, nearly half the land surface of the globe has been transformed by human action, more atmospheric nitrogen is fixed by human activities than by all natural terrestrial sources combined, and about one-quarter of the bird species on Earth have been driven to extinction (Vitousek et al. 1997:494). Nevertheless, almost all research by ecologists and other natural scientists has attempted to understand the operation of the biological and physical systems in isolation from human impacts and have focused their investigation only on current situations. The articles in *Science* are a clear admission that "most aspects of the structure and functioning of Earth's ecosystems cannot be understood without accounting for the strong, often dominant influence of humanity" (ibid.:494).

[redacted] Heavy grazing, however, is clearly detrimental in more ways than the direct removal of the plant parts through eating. Among them is compaction from trampling that makes soil more vulnerable to wind erosion and reduces the soil's capacity for moisture infiltration. Grazing may also reduce the plant's photosynthesis ability by removing leaves, or it may kill it directly. As desirable plants are eaten or killed, the reduced competition allows for the spread of unpalatable plants. This usually favors the spread of xeric species, low-to-the-ground plants and "tough" plants in general.

In the Levant it is estimated that about 17% of the land is natural pasture, often in the steppe and predesert zones. This contemporary distribution does not put grazing activity in competition with farmers for land, but we can expect that in the early era of farming, the same lands would be utilized and grazing would be a major factor in the deterioration of potential farmland. The nature of the Levantine climate would exacerbate the effects of grazing. Mild winters with no snow cover would mean that grazing could continue year-round and that there would be no season when the plants and soil were protected from animals. This year-round grazing also meant that the concept of storing forage for the bad season (as is the practice in more temperate climates) was not prevalent; instead, the general attitude was that animals would look out for their nutrition on their own. This lack of concern for the impact of grazing on the plant resources of a region was not a serious problem as long as the population density (and density of animals) was relatively low versus the regenerative ability of the natural vegetation.

This ability to expand the number of animals kept to fill the environment may have been a key factor in animals becoming the major form of wealth in many societies. Moreover, investing available capital in animals often paid a very handsome return. The people of the Levant saw the keeping of goats, in particular, as a great investment. Requiring a very small expenditure, goats multiply quickly, providing a possible return of 15% to 30%. One pair of goats can produce 100 animals in as little as five years. In this same period, sheep would produce 32 and cattle, 10. In addition, the goat is the best domesticate for poor vegetation zones where they are satisfied with a woody forage, agile enough to reach difficult places, resistant to thirst, and intelligent in seeking their own food. The well-known omnivorous habits of goats meant that widespread removal of vegetation would result, and the taste preferences of goats would lead to young shoots and seedlings disappearing first, reducing the chance of new plants regenerating. The productivity of domestic goats was a tremendous resource for the early villagers of the Levant, but their potential impact on the environment was even more awesome.

[redacted]

Sheep and goats were the primary domestic animals kept by the early villagers of the Levant. In the north, sheep were the predominant animals, but due to the rougher topography and more arid climate of the south, goats were the animals of choice among the villagers there. Sheep are grazers that focus on eating grasses, while goats are browsers that are happy with coarser vegetation. The goats kept by the villagers would have a serious effect on seedlings and young saplings that were trying to grow in areas that had been logged for house construction or fuel for plaster burning. This would retard the regeneration of forest cover and lead to a degradation of the plants that did return to include more scrub and thistles. These plants were less desirable to many foragers, but this did not prevent the goats from continuing their consumption. It is likely that the farmers kept the goats and other animals off their agricultural fields during the winter growing season, but logically they would let them feed on the stubble in the fields during the arid summers and early fall. This would make the field most vulnerable to erosion just as the rains would begin in late autumn. The overall impact of herding goats as part of the agricultural strategy was to expose more of the landscape to erosional forces at a bad time of year, putting the already fragile soil at greater risk.

The topography of the southern Levant is deeply dissected, with water available only near springs or in *wadi* bottoms (wadi is the Arabic word for a seasonally dry streambed). Hence, human settlements would need to be near water, and farming would most likely be on adjacent terrain. Some farming could be done in the wadi bottoms themselves, but the area was very limited. So from the beginning, the slopes of the wadis were essential to farming success. Areas with sloping surfaces like these would be particularly vulnerable to erosion, and if there was little or no vegetation to hold the soils in place, the fall and winter rains would surely wash away some of the valuable soil.

These factors combined to make a reliance on agriculture the logical short-term choice, but they were troubling in the long term. On an immediate time frame, cutting trees for home construction, plaster burning, and the domestic hearth all helped clear nearby fields that then could be planted with the newly domesticated cereal grains. At first the goats must have also seemed like the perfect complement to agricultural fields, manuring them in the off-season and consuming the seemingly useless stubble of the fields. However, the cumulative effects were quite harmful. During the growing season, the goats would be kept off the agricultural fields. [redacted]

[redacted] It is said that the denuded lands are largely the result of overgrazing of goats during the period of Ottoman Rule and that in ancient times these were the lands of "milk and honey." This assertion is probably true to some extent in that the Ottoman political system discouraged local infrastructure development and encouraged small-scale social groups that would rely on herded animals. However, this interpretation is an oversimplification that takes our attention away from the needs of the domestic hearth and industrial kiln from as far back as the earliest civilizations 5000 years ago. The goat is the most destructive of the grazers, but its effects are largely secondary; that is, it usually is not the one to destroy the trees themselves, but only the shoots, leaves, and young sprouts. This does diminish the primary production of the trees as well as keep young trees from reestablishing themselves. Thus, goats are strong contributors to keeping an area from regenerating trees and ground cover and consequently exposing it to the elements and leading to degradation of the fertility of the topsoil and, ultimately, to complete loss from erosion. Complementing these pressures is the hearth and kiln that need not just twigs and thin branches, but timber as well. The heavy weight of wood also dictates that when possible, people will completely denude local sources, rather than draw on larger, more distant sources in an effort to conserve forest growth. The importance of securing fuel for the domestic hearth continues to this day to force the gathering of forage from great distances (fig. 6.8).

Mexico and Central America

Mexico and Central America were home to a wide variety of impressive prehistoric societies. The Maya to the south and a variety of central Mexican societies to the north each built strong agrarian systems that supported very high populations and elaborate urban centers (Coe 1982). The main New World crop in North, Central, and South America was corn. First domesticated about 5000 B.C., or somewhat earlier, corn started out as a very small cob, not economically viable as the dominant food source. This differs from Old World species like wheat that were nearly as productive in the wild as under early cultivation. Early forms of corn were pioneering weeds basically used by Central Americans as a back up or famine food. However, over a long period of low-level use, the nature of corn changed, with larger cobs and kernels being selected for by the early users. It took three or four millennia of slowly increasing the size of the cob, the number of kernel rows, and the size of individual kernels before corn as a crop become so productive that people