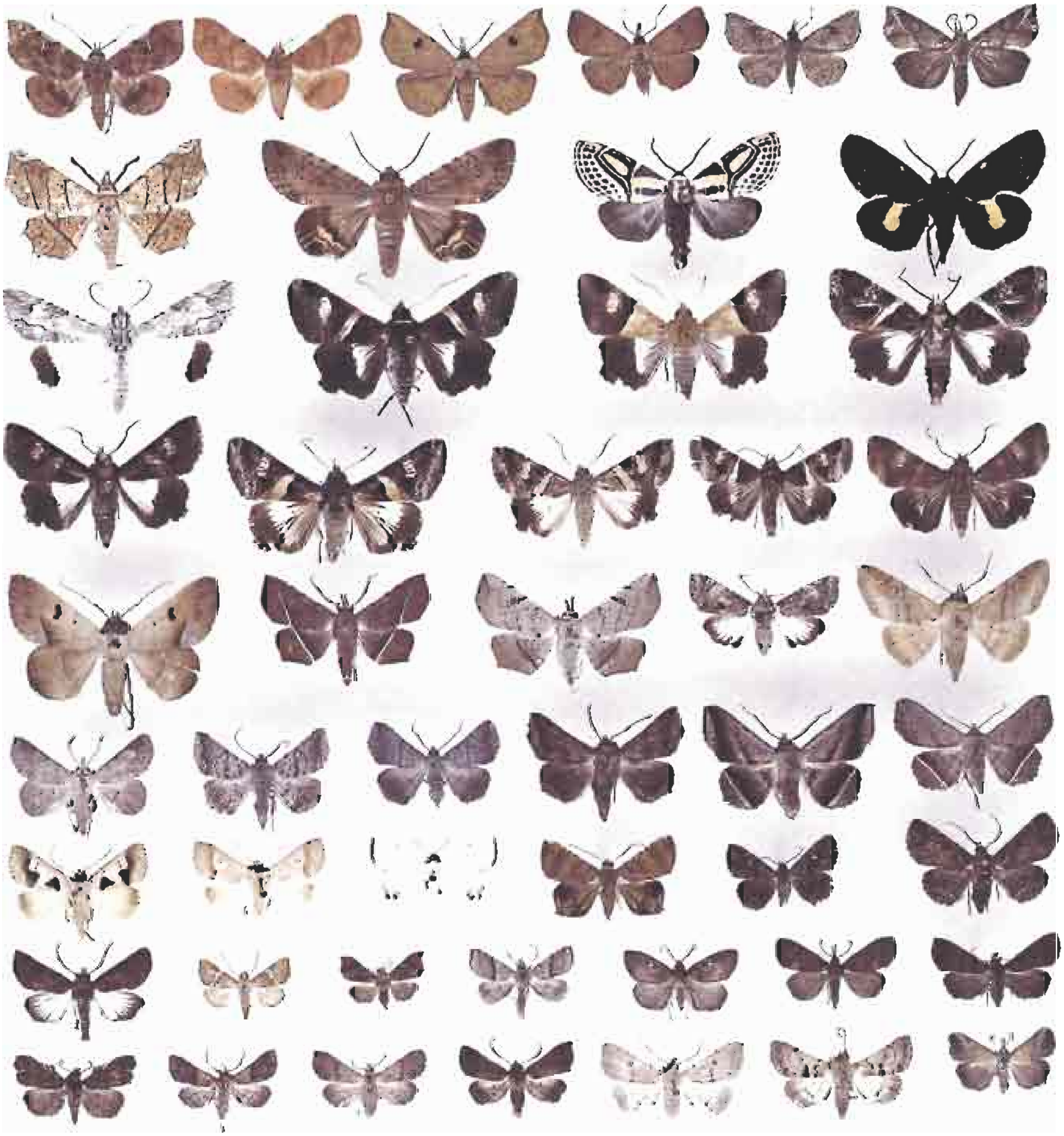
Guana Report for 2002



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15 May 2003

Dr. Henry Jarecki
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Dear Henry:

Here is my works and progress report for 2002. After our conversations of 3-4 May, 2003, I realize I have failed to make clear just how important the long-term, ongoing aspects of our program are and where we fit in the broad scope of research on ecology, evolution, biogeography, and biodiversity conservation. Two important papers have recently been published that help demonstrate the significance of our research. I have not included them in my report below -- but I can send you copies if you want them. These are:

Sanford, G., W. Lutterschmidt, and V. Hutchinson. 2002. The comparative method revisited. Bioscience 52(9): 830-836.

Emerson, B.C. 2002. Evolution on oceanic islands: molecular phylogenetic approaches to understanding pattern and process. Molecular Ecology 11: 951-966.

In the first paper, Sanford *et al.* describe the history of the "August Krogh principle." Krogh was a comparative physiologist who won the Nobel Prize in 1920 and stated: "For a large number of problems, there will be some animal of choice on which it can be most conveniently studied." Not very good grammar, but we can see his point. Guana examples include evaporative water loss resistance; intraisland physiological, morphological, and genetic variation; energetics, behavior, and adaptive success; population biology; migration; and species packing or hyperdiversity.

In the second paper, Emerson describes five exemplary groups which are being actively investigated to great advantage: Canary Island beetles, Hawaiian silversword plants, Hawaiian fruit flies, Galapagos finches, and -- you guessed it -- Greater Antillean anole lizards. You may recall several years ago the U. MD team of Denno, Thorne, and Hawthorne undertook an intra- and interisland study of morphological and genetic variation in three species of insects with very different dispersal potentials. They only got results so far for the saltgrass planthopper: it comes in winged and wingless morphs and Guana's North Beach population (winged) has different DNA sequences than Guana's Salt Pond population (wingless): indeed, the two are as distinctive as many geographically remote populations (Anegada vs. Tortola). September 11 stopped them in 2001 and Thorne's son had a terrible accident last year (recovering nicely; see letter at end of Termites in this report). This year they plan to get back to work. This is a terrific project that will help make us famous (we are already getting very well known). Last year, Greg Mayer's student Kristi Mico initiated molecular analysis of our crested anoles, sampling many BVI populations. She is finishing up and will have results by October. We have demonstrated inter- and (just last year) intraisland differences in water loss resistance in our lizards (see Abstracts of Presentations in Reptiles, below). Jason Cryan and Lou Dietz, 2002 (see below) used our treehopper (bug) in a molecular phylogenetic study.

You may recall, Mike Haverty and Barbara Thorne did pioneering work on cuticular hydrocarbon biochemistry of termites a decade ago. This is not "molecular" in the usual sense of DNA or RNA, but it proved to be of considerable phylogenetic -- systematic -- value. For example their techniques often allow specific identification of termites from their *frass* (excrement), which in turn usually allows for specific treatment: see Thorne's letter (again) at the end of Termites.

So, many of Guana's animals are becoming "model organisms" in Krogh's sense (and that of Sanford *et al.*). This is excellent, but only works as long as we are able to do long-term studies so that we can respond to our own discoveries and go through doors that we open. I would love to see more molecular work done on Guana's species, and have been looking for people to do it. (We *almost* had a molecular frog study going, but the investigators got side-tracked; I have been trying to get that moving again.)

Our ornithology is critically important. Fred Sibley has switched over entirely to dragonflies, so I have recruited a new "bird man," see below. There will be complete continuity: Fred and Clint know each other and Clint has Fred's years of data. In the big McNair paper below, Guana is one of only two banding stations in the entire Caribbean east of Puerto Rico. The other one, on out-of-the-way Barbados, has now closed. We are it. We have gotten really good stuff. Diseases like West Nile virus and avian malaria give major importance to our project. I hope we can expand it.

Of course we are still doing major work in systematics (see Moths, below), but to call this "splitting and lumping" is really derogatory and unfair. Harvard's famous E. O. Wilson, among many prominent biologists, loudly calls for greatly increased effort in "alpha taxonomy" -- just finding out what lives on this planet. Many groups remain unstudied (there will be two more even bigger papers on moths coming along). We even have an unnamed *Sphaerodactylus* lizard from Carval Rock that Padre Sanchez keeps promising to get formally described (he needs help; I am working on Bob Powell to assist him). This is not splitting: no one has ever claimed that lizard belongs to a known species. This is pure discovery. We have only just begun. Nobody has even looked at thrips yet!

All the best

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ECOLOGY AND CONSERVATION OF *SIDA EGGERSII* (MALVACEAE), A RARE TREE OF THE VIRGIN ISLANDS

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ABSTRACT.—The ecology of the tree *Sida eggersii* Baker (Malvaceae) was studied from 1991 to 2001 on Guana Island in the British Virgin Islands (BVI). Known from less than 30 individuals since its discovery, the Guana Island population of *S. eggersii* increased from over 200 in 1991 to over 1100 in 2001, and I report smaller populations from other islands in the BVI. The species is most common in low-elevation, dry scrub habitat with a NE- to SE-facing aspect. Flowering and fruiting begin in and continue slightly past the winter wet season. The species appears to be relatively *r*-adapted, showing rapid maturation, high growth rates, and high population turnover. Maturation can require less than two years but appears to generally ensue at 4-5 years age. Growth rate (increase in stem diameter) is approximately 5.0 mm/yr in young plants but decreases to an average of 2.6 mm/yr in large specimens. Mortality was high, averaging 5 %/yr, but was not evenly distributed among years. Germination and mortality seemed to be highly influenced by hurricanes.

INTRODUCTION

Sida eggersii Baker is a small tree of the Malvaceae (mallow) family described by Baker (1892) from a specimen collected on Tortola in the British Virgin Islands (BVI). The species was considered very rare and remained poorly known since its description, having been otherwise collected on Culebra, off the eastern coast of Puerto Rico, in 1906 and 1913, and on Jost Van Dyke in the British Virgin Islands in 1967 (Little et al., 1974). The tree on Jost Van Dyke was thought to be the only living specimen of the species (Little et al., 1974) until 23 trees were discovered in 1986, in a remote ghut (ravine) on nearby Guana Island, BVI (G. Proctor, P.R. Dept. Nat. Environ. Res., pers. comm.).

Guana Island is privately owned, with most of the island covered by intact native forest and scrub largely undisturbed by humans at present, although sheep have roamed it for decades. Guana occupies 340 ha, is hilly, and rises to an elevation of 245 m. In 1991, the opportunity arose to conduct a series of conservation initiatives on Guana, one of which was to ascertain the status of *S. eggersii* at its largest known population and obtain information on the species' numbers, distribution, and reproduction. I continued these studies to determine growth rates, mortality, and population trends to better understand the conservation status of a plant known from fewer than 30 individuals over a century of botanical surveys.

MATERIALS AND METHODS

Location of populations

From March through October, 1991, I censused the population of *S. eggersii* in Grand Ghut (Population 6, Table 1), Guana Island, and marked all trees with numbered aluminum tags tied to the stems with Monel wire. I searched by foot or boat appropriate habitat throughout the island to identify additional individuals. Discovery of new populations with binoculars was facilitated by the species' distinctive light grayish-green leaf color. I verified all presumptive discoveries by reaching trees on foot and tagging as above. An assistant helped map two of the three largest populations of *S. eggersii* on Guana (Populations 4 and 6, Fig. 1, Table 1) to facilitate relocation of trees. The third population (Population 10) did not require mapping because of

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TABLE 1. Size of *Sida eggersii* populations depicted in Figure 1. Dashes denote populations that could not be accessed after 1991.

Population	1991	Mortality	Ingrowth	2001
1	4	3	4	5
2*	5	1	0	4
3*	74	12	2	64
4	13	4	78	87
5	3	2	0	1
6	130	58	727	799
7	5	–	–	–
8	1	–	–	–
9	6	–	–	–
10	47	24	164	187

*Outplanted populations

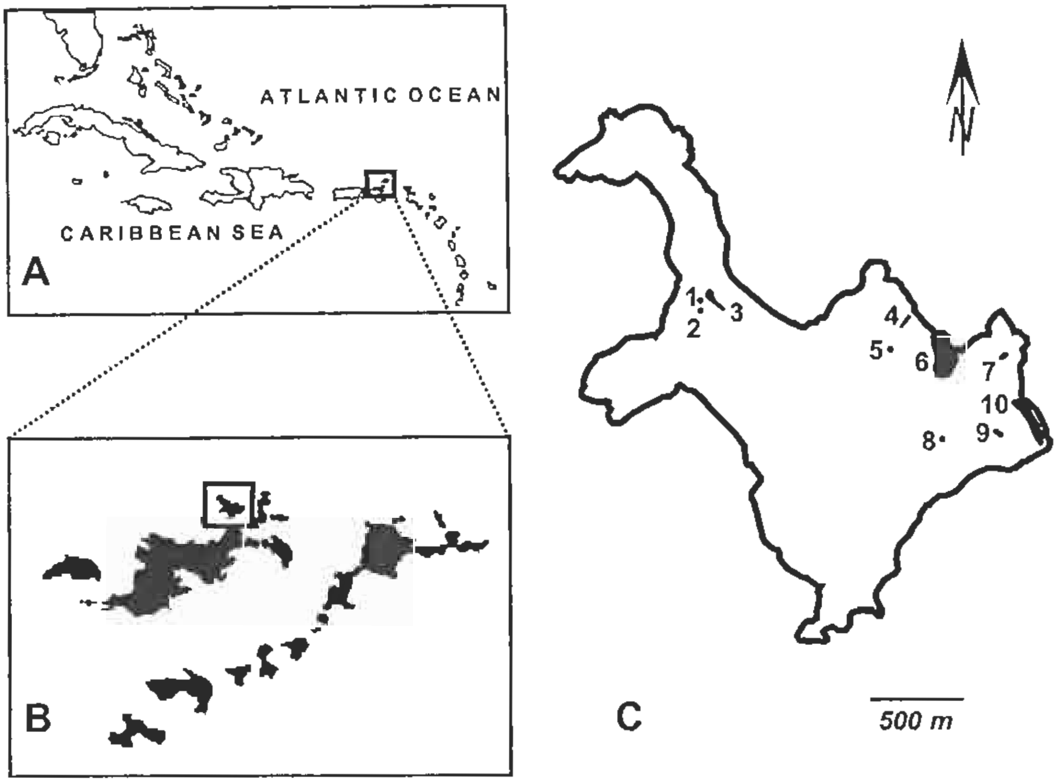

FIG. 1. Maps of A) Caribbean region, showing location of the Virgin Islands; B) the British Virgin Islands, showing location of Guana Island; and C) Guana Island showing locations of *Sida eggersii* populations. Population numbers correspond to those in Table 1.

its linear distribution along a coastline. I also searched appropriate habitat on other islands in the BVI as opportunity allowed.

I measured the size of most trees by recording stem diameter at approximately 15 cm above the soil surface, due to the tree's relatively short stature and invariant branching below breast height. For plants in which lateral branches sprouted below 15 cm, I measured diameter just below stem bifurcation. Sapling stem diameter was measured 2-3 cm above the soil surface because this region is morphologically equivalent to that measured in adult plants.

Germination

I collected seeds from 21 fruiting trees in March, 1991, and attempted to germinate them in one-gallon pots of native soil or Pro-mix. I transferred seedlings to individual one-gallon pots when they reached approximately 10 cm and reared them in open sunlight until October, 1991, when I outplanted them at new locations on Guana Island (Populations 2 and 3, Fig. 1, Table 1). I recorded stem diameter and height and attached numbered aluminum tags to all plants. Outplanting was done to better determine growth rates of young plants (wild plants were all of a larger size), light requirements for growth, and relative survivorship, as well as to increase population size.

The locations of saplings discovered in 1996 and 2001 were recorded and mapped relative to the trees numbered and mapped in 1991. Exact distances from saplings to adjacent numbered trees were not measured directly. In 2001, sapling density at two of several dense stands was measured by counting sapling numbers of specific stands and measuring the occupied area.

Growth rate and survivorship

I remeasured outplanted individuals in July 1992, July 1993, October 1996, and July 2001. In July 2001, I also searched for all but 17 trees originally marked in 1991 to estimate survivorship rates (a similar effort in 1996 covered approximately half of the wild plants and indicated high levels of mortality), measured all individuals not present in 1991 (also counted but not measured in 1996), and measured the height of 639 plants to determine its relationship to stem diameter.

Other

Habitat was characterized in 2001 by noting common plant associates and recording aspect for Populations 1-6 and Population 10 (Fig. 1). A soil sample from the area occupied by Population 6 was analyzed in 1991 with a commercial LaMotte test kit to evaluate macronutrient levels. Herbivory was assigned to insect feeding guilds based on characteristic patterns of damage to leaves and stems. Two termites and one psyllid were collected for identification. All statistical tests employed SigmaStat®, version 2.0.

RESULTS

Habitat

Sida eggersii occupies the Subtropical Dry Forest life zone (Ewel and Whitmore, 1973) and is most common in low-elevation (0-60 m), dry scrub habitat with a fairly open and low (4-5 m) canopy. It may also occur in higher-elevation (up to 150 m on Guana, up to 240 m on Jost Van Dyke [Little et al., 1974]) dry forests with taller (7-10 m) and denser canopies.

Common woody associates in the scrub habitat include *Adelia ricinella, Bourreria succulenta, Bursera simaruba, Capparis cynophallophora, C. flexuosa, C. indica, Cestrum laurifolium, Citharexylum fruticosum, Croton astroites, C. flava* ssp. *rigida, Eugenia biflora, Guapira fragrans, Jacquinia berteri, Krugiodendron ferreum, Maytenus laevigata, Oplonia microphylla, Pictetia aculeata, Pilosocereus royenii, Piscidia carthagenensis, Psychotria microdon, Randia aculeata, Rauvolfia viridis, Reynosia guama, Schaefferia frutescens, Solanum polygamum*, and *Tabebuia heterophylla*. Common understory plants in this habitat include *Agave missionum, Cissus trifoliata, Melocactus intortus, Opuntia repens, Stigmaphyllon emarginatum*, and *Tragia volubilis*.

Most *S. eggersii* on Guana occur on slopes facing NE to SE (45°-130°), but some specimens face NW (325°-340°) and others NNE (15°-20°). Soils are shallow, dry, rocky, and poorly consolidated. Frequent slippage causes rocks and soil to accumulate on the upslope side of most trees. The soil sample, taken from the largest grove of mature trees in Grand Ghut, had a pH of 6.8 and nutrient concentrations of 16.8 kg/ha for nitrogen, 36.1 kg/ha for phosphorus, and 359.3 kg/ha for potassium.

Numbers and distribution

In 1991, 210 individuals were discovered in eight disjunct populations on Guana. Most individuals were confined to the lower slopes of Grand Ghut (Population 6, Fig. 1, Table 1), but two other populations of modest size also occurred (Populations 4 and 10, Fig. 1, Table 1). All trees identified on Guana in 1991 were mature, with the exception of a few saplings (not measured) found in Population 6. In 2001, 1145 individuals (mostly saplings) were discovered and measured (Table 1).

During a 2 h visit to Ginger Island in October 1991, I discovered approximately 30 adult *S. eggersii* and 300-400 saplings approximately 1-2 m tall. Time did not allow measurement of these plants, which represent the second-largest population. *Sida eggersii* has been reported in small numbers from unspecified localities on Culebra (n=?, Little et al., 1974), Tortola (n=?, Baker, 1892; n=?, Acevedo-Rodriguez, 1996), Jost Van Dyke (n=1, Little et al., 1974), Great Thatch (n=1, E. Gibney, St. John, pers. comm.), and Dead Chest (n=?, L. Jarecki, H. Lavity Stoutt Comm. College, pers. comm.). The species has not been reported from the U. S. Virgin Islands, but it may have occurred on St. Thomas (Britton and Wilson, 1924).

Reproduction

I observed many flowering plants during March of 1991 (13 of 14 plants on 5 March, 1991; 36 of 83 on 24 March, 1991). Flowering ended by late March/early April and resumed sparsely in late October/early November. The species has been observed flowering on Guana Island during February (J. Lazell, The Conservation Agency, pers. comm.; L. Jarecki, H. Lavity Stoutt Comm. College, pers. comm.). Seed set occurs soon after flower production, but seeds were largely unavailable by late April (6 of 40 plants had seed on 24 April, 1991). Seed production resumed sparingly in one plant in early November 1991.

One plant flowered 22 months after germination; its diameter at 27 months was 1.8 cm. The smallest trees observed flowering in 1991 had diameters of 2.8, 3.4, 3.7, and 3.9 cm. Assuming 2.8 cm diameter as the average size of first reproduction, 37 of 62 (60 %) outplanted individuals attained this size by their fifth year and 3 of 77 (4 %) attained it by their third year. Based on these growth rates, most plants probably reach reproductive age within 4-5 years of germination. The largest trees observed flowering were 15.5, 17.5, and 23.2 cm in diameter, which are at the upper size distribution for the species, indicating that reproduction occurs throughout life.

Seed dispersal and germination

Seeds are dispersed primarily by gravity and wind. Fruits are dry capsules, unlike the fleshy and colorful fruits normally dispersed by birds, which showed no interest in *S. eggersii* fruits. In March 1991, many seeds were found scattered under fruiting trees, declining markedly in abundance a few meters away. Virtually all new saplings observed in 2001 were within 4-5 m of established or recently dead trees.

Seeds planted in Pro-mix failed to germinate; those planted in native soil germinated 5-14 days after planting. Seedlings resulted from seed of eight parent trees. Seed longevity was not investigated, but seeds seem capable of remaining viable for at least a year or two in the soil; this inference is based on 12 saplings present in 2001 in the area occupied by an isolated tree that died in 1996. These saplings must have germinated at least 1-2 years after the parent's demise.

In 1991 virtually no saplings existed on Guana, but in 1996 there were hundreds and in 2001 almost 1000 were counted. Most saplings were in areas where adult trees had been toppled and killed by hurricanes in 1995 or 1996. For example, 59 of 83 saplings (71 %) occurring in Population 4 in 2001 were within 4 m of two trees killed in this manner, even though they comprised only 15 % of the adult trees of the 1991 population and formed a miniscule percentage of available habitat within that area. Similarly, in the section of Population 6 with the lowest density of trees in 1991 (thereby avoiding the confounding effects of live trees occurring next to dead trees in 2001), 140 of 206 saplings (68 %) in 2001 occurred within 4 m of trees killed in 1995/1996. In many instances, these saplings occurred in high densities; for example, 20 saplings were found in one 8.7 m^2 area around one adult tree (2.3 plants/m^2), and 136 saplings in a 24.5 m^2 area around another (5.6 plants/m^2).

Growth

The mean growth rate of 159 plants measured in 1991 and still surviving in 2001 was 3.31 ± 1.89 mm/yr. For the 66 surviving outplanted specimens, growth rate averaged 3.77 ± 1.96 mm/yr. For the 93 surviving wild plants, growth rate averaged 2.99 ± 1.78 mm/yr. Differences in growth rate between wild and outplanted individuals were significant (Mann-Whitney rank sum test, T = 5983.5, $p = 0.014$). Given the larger sizes of the wild specimens, this difference would be expected if growth rates decline with age. Using original plant size as a surrogate measure of age, this appears to be the case (linear regression, df = 158, F = 12.26, $p < 0.001$); however, variance in growth rate is great (Fig. 2) and relatively little of this variance is explained by original size ($R^2 = 0.072$). A clearer relationship does not appear by recourse to polynomial regression.

Declining growth rates and increasing variance in plant size with increasing age are also indicated by following the outplanted population through time (Fig. 3). The same relationship is evident by comparing growth rates among plants of different size classes. Growth rates for the outplanted individuals for their first five years of life post-outplanting were 5.22 ± 2.27 mm/yr, allowing them to attain an average of 3.26 ± 1.12 cm diameter by the end of that time. Wild plants between 3-10 cm diameter had an average 10-year growth rate of 2.98 ± 1.90 mm/yr, and wild plants greater than 10 cm diameter had an average growth rate of 2.67 ± 1.42 cm.

Plants grew faster when watered: the 79 outplanted individuals reached an average of 0.65 cm (range = 0.42-0.85) diameter within six months of germination while maintained in pots. The relationship between plant height and stem diameter is non-linear (Fig. 4), indicating that upon reaching a height of approximately 3-4.5 m plants direct most of their

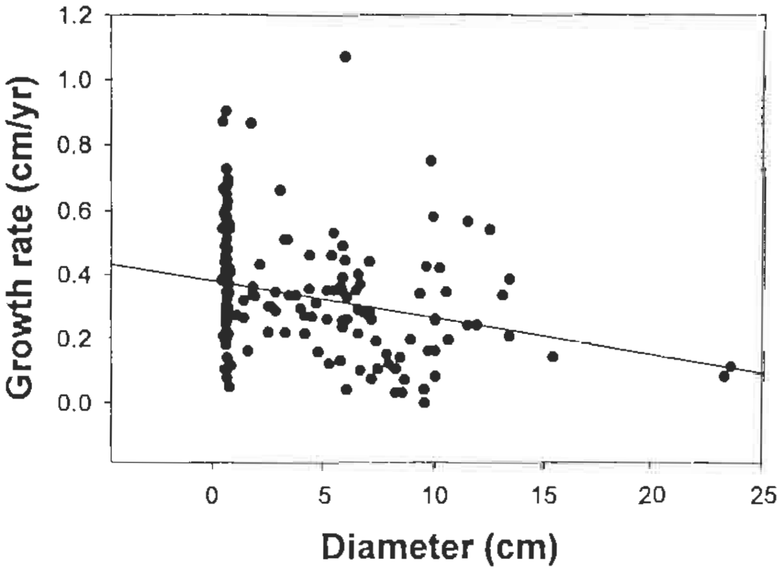

FIG. 2. Relationship of growth rate to original plant diameter, indicating a slight average decline in growth rate with increasing size. Slope = −0.117, intercept = 3.814, df = 158, F = 12.26, $p < 0.001$.

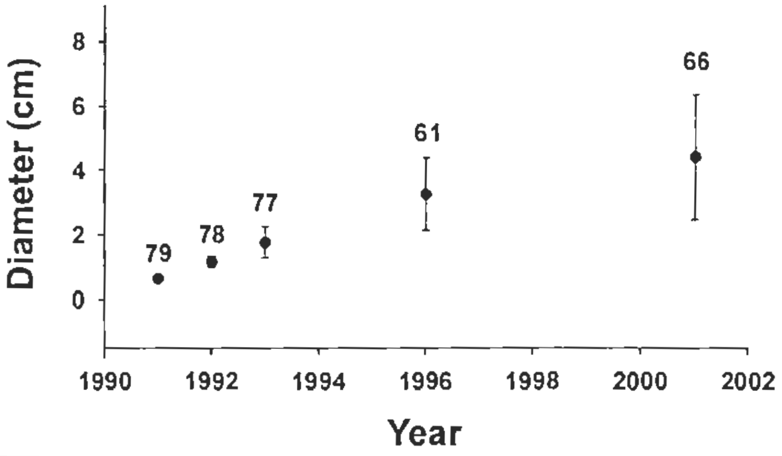

FIG. 3. Growth rate of outplanted trees during their first ten years. Note decline in average growth rate and increase in variance of growth rate over time. Points are means; bars are one standard error. Numbers above bars are sample sizes for each year.

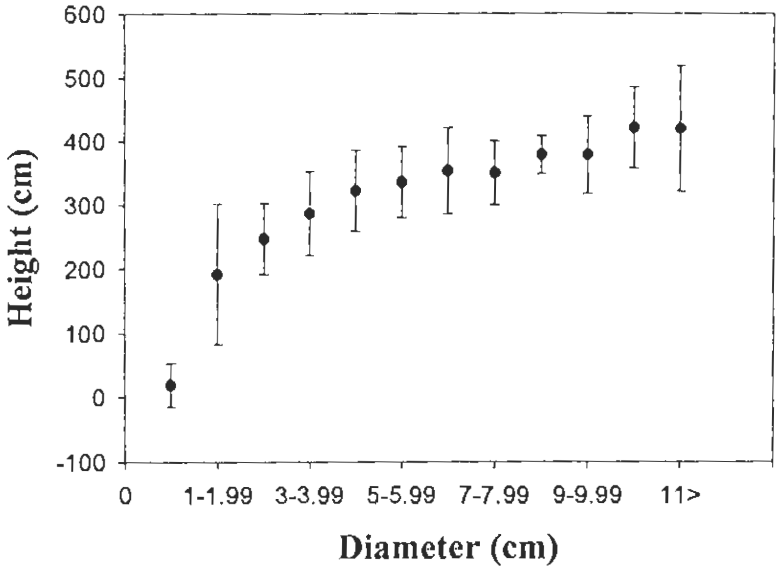

FIG. 4. Relationship of plant height to stem diameter, indicating declining height gain with advancing size. Points are means; bars are one standard error. N = 639.

remaining growth into increasing mass but not height. Maximum observed height was 5.4 m.

Survivorship and Mortality

Ten-year mortality was high; only 100 of 192 specimens (52 %) marked in 1991 remained alive in 2001. Survivorship of outplanted individuals was higher (66 of 79 trees, or 84 %). Contrasting the size distributions of surviving and dying trees in wild populations (Fig. 5) indicates that trees dying between 1991-2001 were significantly larger, and presumably older, than those surviving that period ($t = 6.901$, $df = 161$, $p < 0.001$). This skewed mortality, coupled with strong recruitment from 1995-2001, significantly changed demographic structure during the course of this

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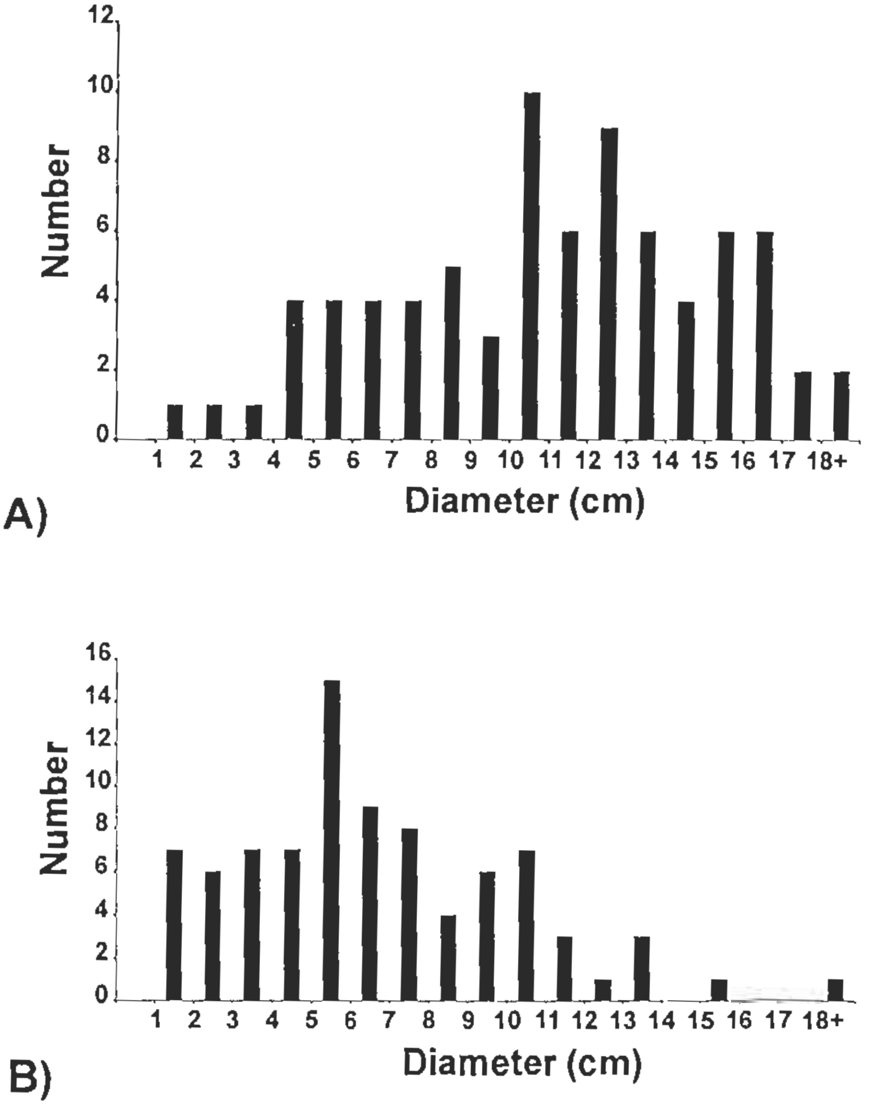

FIG. 5. Size distributions of wild *Sida eggersii* (A) dying, and (B) surviving, during the period 1991-2001, indicating differential susceptibility to mortality among plants of different sizes.

study (Fig. 6) and slightly reduced the population of mature trees from 155 old trees in 1991 to 149 much younger trees in 2001 (assuming all trees >3.0 cm diameter to be mature).

Average yearly survivorship in the wild population was 0.95, but this average is deceptive because mortality is strongly clustered around hurricane events. This was clear in October 1996, when the effects of Hurricanes Luis and Marilyn, which hit the BVI during September 1995, and Hurricane Bertha, which hit during July 1996, were still obvious. Fallen trees with numbered metal tags were readily found in many places and wholesale loss of small stands due to slumping of hillsides was apparent in two locations. Consequently, 73 % of the ten-year mortality observed in Population 4 occurred as the result of those hurricanes. Seventy-eight percent of the ten-year mortality of 87 plants from Population 6 assessed in 1996 occurred during those same weather events.

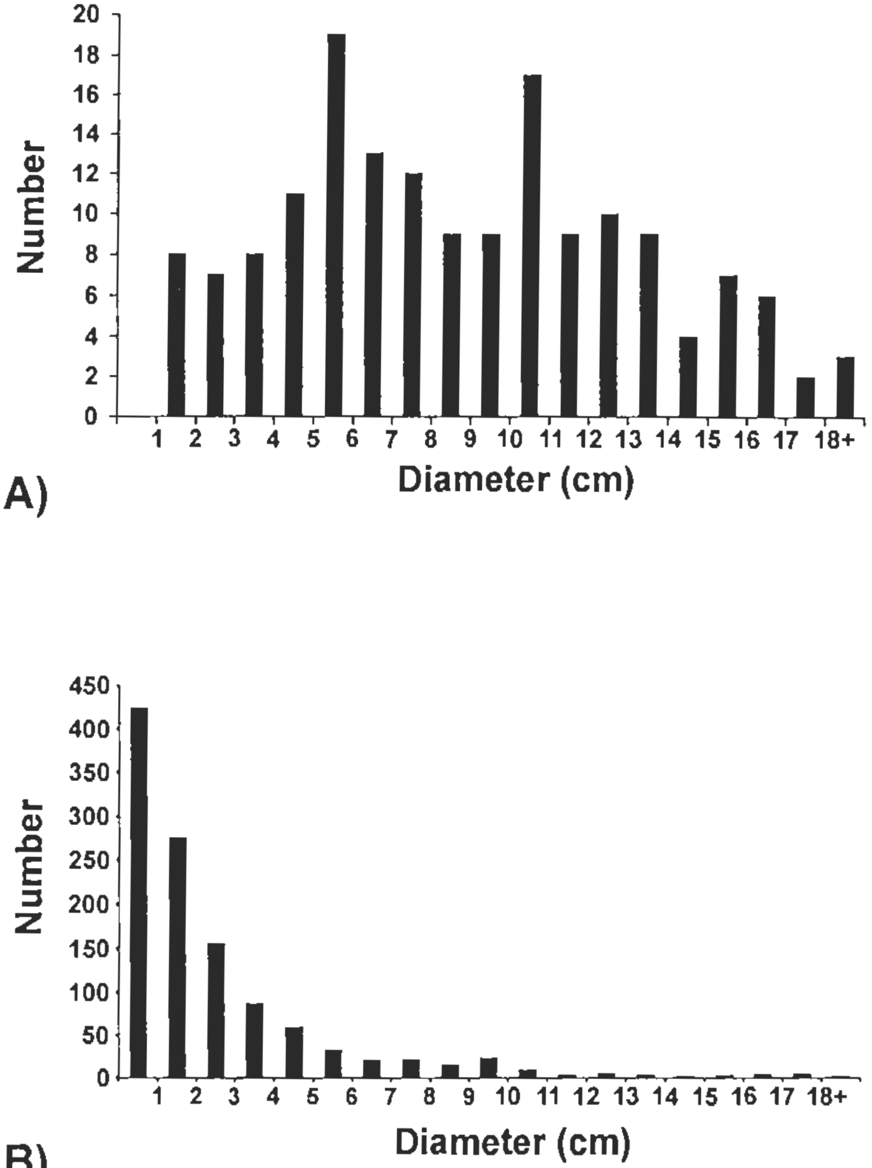

FIG. 6. Size distributions of wild *Sida eggersii* in (A) 1991, and (B) 2001, showing marked change in demographic structure following three mid-decade hurricane events.

Sapling mortality could not be measured because of their virtual absence during 1991-1993. Some of the few saplings recorded in May 1991 had died by July 1991 apparently due to water stress (plants shriveled but entire). An unidentified borer caused some stem morbidity and mortality in 2001.

Biotic relationships

Flowers were very actively visited by bees, skippers, and butterflies. Trees were attacked by a variety of insects, with varying effect. Leaf miners created noticeable damage on the leaves, but were not abundant enough to threaten survival. Greater damage was caused by orthopterans, which can remove large amounts of leaf tissue, giving even large adults a ragged appearance. Of greater importance is a stem borer that causes frequent loss of lateral stems and central shoots, especially in saplings. These borers frequently kill the top half or more of plants, causing growth setbacks and occasional death. Termites frequently colonized dead stems; *Neotermes mona* and *Incisotermes schneideri* (M. Collins, U.S. Nat. Mus., pers. comm.) are reputed to live only in dead wood, but I also observed termite entry into living wood on one occasion, suggesting that perhaps more termite species live in association with *S. eggersii*.

A single *S. eggersii* planted for horticultural purposes on St. John, USVI, has been almost completely defoliated by the psyllid *Paracarsidara dugesii*. The host plants of this insect, which has a wide distribution in the Neotropics and is apparently native to the Virgin Islands (Hodkinson and White, 1981), includes the Malvales genera *Malva* and *Bombyx* (Hodkinson and White, 1981) in addition to *Sida*. The psyllid has not been observed on Guana Island.

Sheep were introduced onto Guana in the 1930's and, despite intermitent severe hunting pressure, persist there. They currently seem to have little effect on *S. eggersii*, but in one instance several saplings and young adults had their bark stripped by them.

DISCUSSION

Sida eggersii appears to have an *r*-adapted life-history strategy. It grows more quickly than other dry-forest Virgin Island trees (Weaver, 1990), matures at an early age, produces large amounts of small seed, and seems to have a relatively short life span, with a maximum age of approximately 80 yr (estimated by assuming an average growth rate of 5 mm/yr for plants smaller than 3 cm diameter, a decline to an average of 3 mm/yr until reaching 10 cm diameter, and a further decline to 2.7 mm/yr thereafter). Most plants probably die before reaching such an advanced age (most probably do not reach 50 years), but this indicates that even under extremely favorable circumstances, *S. eggersii* is not a long-lived species.

These *r*-adapted characteristics suggest that *S. eggersii* should be relatively resilient to natural disturbances, an expectation borne out by the high recruitment observed in response to hurricanes in 1995 and 1996. Hurricane-dependent recruitment is further bolstered by the population structure seen in 1991. Using the above growth formulae, the numerically large 1991 size cohorts at 5-5.99 cm and 10-10.99 cm (Fig. 6a) are estimated to have germinated in approximately 1975-1978 and 1959-1962, respectively. These years experienced three of the eight hurricane/named storm events to occur in the BVI from 1950-1985 (Jones, 1996; http://www.caribwx.com/climate.html). Furthermore, three of the other five hurricane/named storm events during that period occurred in 1955 and are also likely to have contributed to the 10-10.99 cm size cohort, given the considerable variance seen in growth rates (Figs. 2, 3). These data suggest that recruitment in *S. eggersii* is dependent on canopy opening by hurricanes/severe storms and, hence, is highly sporadic. Hurricane-induced mortality, coupled with the following flush of new saplings, allows the demographic structure of *S. eggersii* populations to change quickly (Fig. 6). Consequently, interpretations of population viability or conservation status in this species based on short-term surveys must be undertaken with caution.

The conservation status of *S. eggersii* in the BVI has been listed as indeterminate by the IUCN (World Conservation Union) (Walter and Gillett, 1998), citing information in Kraus (1991). The species is not included in the IUCN's list of threatened taxa (Hilton-Taylor, 2000). The fieldwork reported herein establishes that the species occurs in more populations and at higher numbers than previously believed (e.g., Little et al., 1974; Kraus, 1991; G. Proctor, P.R. Dept. Nat. Environ. Res., pers. comm., 1991) and verifies that the Guana Island population has remained vigorous even while undergoing significant demographic

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turnover. Based on current information, the species fits the category "endangered" using IUCN criteria B1 or D (http://www.redlist.org/info/categories_criteria.html) due to the small number of mature individuals and populations. Categorization as endangered using criterion B3 might have been possible immediately following the hurricane-induced mortality events of 1995/1996, but that criterion failed to be met in 2001 as saplings recruited after the hurricanes reached maturity. The ability of *S. eggersii* to undergo rapid, though apparently non-threatening, population turnover suggests that reliable use of IUCN criteria, such as B3, that are based on population decline requires some caution: the time interval and circumstances for which the decline is observed must be specified.

Except for the Ginger Island population, additional large populations are unknown, perhaps due to inadequate survey effort, especially in the low-elevation exposed habitat that *S. eggersii* prefers. It is surprising that this tree is unrecorded in the USVI because it had a range extending from the BVI to Culebra. The most promising locations to search for the species are the northern shoreline of St. John and its satellite cays because of the appropriate nature of the habitat and the close proximity to Great Thatch Island, which recently supported at least one adult tree. The possibility that the species' range is restricted by feral ungulates, which roam most of the Virgin Islands, needs to be better assessed. The only large populations of *S. eggersii* currently known occur on islands from which ungulates have been recently eradicated (Ginger Is.) or severely reduced in numbers (Guana Is.).

The conservation status of *S. eggersii* seems fairly secure despite its relatively small numbers and potential threat from insect and sheep predation. However, a better understanding of its distribution in the region would be desirable for determining to what extent the future of the species depends upon the status of the Guana Island population. The most likely threats to its near-term persistence appear to be either a radical change in management practices on Guana Island or the unintentional introduction of herbivorous insects on imported horticultural material. The former does not seem immediately likely, but could result should ownership of the island change; the latter concern has been discussed by Miller (1994), who documented the introduction of a variety of invertebrates to Guana Island on imported horticultural material from Florida. A concern for alien introductions pertains generally throughout the Virgin Islands, where meaningful and general pest-prevention programs are nonexistent although clearly needed (Miller, 1994).

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The BVI Beacon Vol. 19, No. 22, pp. 1 + 24. November 7, 2002

Century plant devastation

• *Importation of foreign species suspected*

BY JAMES OSBORNE

When scientists arrived on Guana Island last month for their annual field study, the news was not good for the century plant.

Almost all of the plants, also called agaves, found on Tortola, Beef Island, Guana, and the Camanoes are dead or dying.

To blame is a 3/4-inch weevil, which burrows into the plant and lays larvae, which eat the host. Dr. James Lazell, director of the Guana Island Wildlife Agency and president of the U.S.-based Conservation Agency, thinks the weevil was first introduced to the BVI through the importation of another species of agave native to the southwestern United States commonly used ornamentally in gardens.

Those plants possess natural defences that keep the weevil at bay until they've already flowered — agave only flower once and then die.

But native agave lack those defences and are being killed off before they have a chance to flower and reproduce. Their numbers have dropped off rapidly since the Guana scientists first noticed the problem last October.

Now the weevils have been found on Jost Van Dyke, a puzzle for scientists. The creatures can fly, but usually only for short distances. In the case of the outer islands such as Guana, Dr. Lazell said, evidence suggests the weevil flew across from Tortola — a

continued on p. 24

Century *— from p. 1*

much shorter distance.

"Maybe if the wind was right they could have made it (to Jost Van Dyke)," said Dr. Lazell.

The weevil epidemic hit the USVI in the mid-1980s. While century plants there were obliterated almost to the point of extinction, Dr. Lazell said they are now making a comeback.

There is hope here, too. One in 20 of the BVI agave is immune to the weevil, and while scientists are not sure why, Dr. Lazell theorised those plants might be producing a chemical repellent. There is also the tendency in any ecosystem to move towards equilibrium, namely that another species, in this case the parasitic wasp, will eventually move in and bring the weevil population under control.

"If you don't have total extinction there's a good chance you'll have recovery," said Dr. Lazell.

But there are a number of birds and insects, most notably butterflies, which rely on the century plant as a food source. While scientists haven't observed any decline in their populations yet, Dr. Lazell said it is expected to come soon.

"There are alternate food sources for these animals in the drier months. The crutch will probably be next winter," he said.

Cucurbits

By

Angela Davis, Ph.D.

USDA-ARS, Lane, Oklahoma

Cucurbits are plants of the cucumber, squash, and melon family, Cucurbitaceae. Many are of major economic importance virtually worldwide. Apart from the cultivated species, there are many little-known wild species that we believe are a potential genetic treasure trove for pest resistance, climatic hardiness, increased fruit production, and other useful characteristics. We are engaged in two kinds of projects to elucidate the features and genetics of wild cucurbits: a germplasm bank and publication of a series called "Profiles in Cucurbits."

Climbing *Cayaponia americana.*

Results

Numi found *Cucumis sp.* and collected seed and Wenhua collected foliage on Necker Island. Mike Ivie found *Cayaponia americana* (species still to be verified) on the ridge above the laundry facility. I collected seed from this plant. Rudy and I found a *Cayaponia americana* (yet to be verified) and 2 *Doyerea emetocathartica*. No fruit was found. All three plants were on the West side branch of the trail that leads to Muskmelon Bay.

The *C. americana* had one tendril per node that branched into 3 tendrils about half way. The stem had longitudinal ridges, many branches, and new stems from old nodes. The plant was found at the top of a ridge at meter marker 425 in a dry, rocky, open area. The plant climbed to about 7 feet high and was about 15 feet wide.

The *D. emetocathartica* was prickly on top of the leaf with smooth pubescence on the underside of the leaf. The stems were pubescent. The plants had a fleshy stem near the ground with multiple branches coming off it. Both plants were found in the under-story leaf litter and were small (one plant had one branch about 1.5 feet long, the other had several branches to about 4 feet long.) The plants were found at meter markers 675 and 15 feet before 775.

Leaves from *C. americana* and *D. emetocathartica*.

C. americana seed.

Correspondence

Hi Deena,

Last October I went to Guana Island in the British Virgin Islands. I was helping out a colleague with some fieldwork but while I was there I looked for cucurbits. I found two interesting species, *Cayaponia americana*, and *Doyerea emetocathartica*. The *C. americana* had set fruit and a botanist in the VI is saving the seed for me. I'm trying to find out who to ask about permission to have them shipped into the U.S. so I can propagate and submit seed to the USDA Germplasm Bank. These plants are both the first reported sightings of these species on this island. Would you be interested in having one or both of them written up for a Profiles in Cucurbits?

Take care,
Angie
Angela Davis adavis-usda@lane-ag.org

From: CucurbitNetwork@netscape.net
Sent: Friday, December 27, 2002
Subject: More Cucurbits.

Dear Angie,

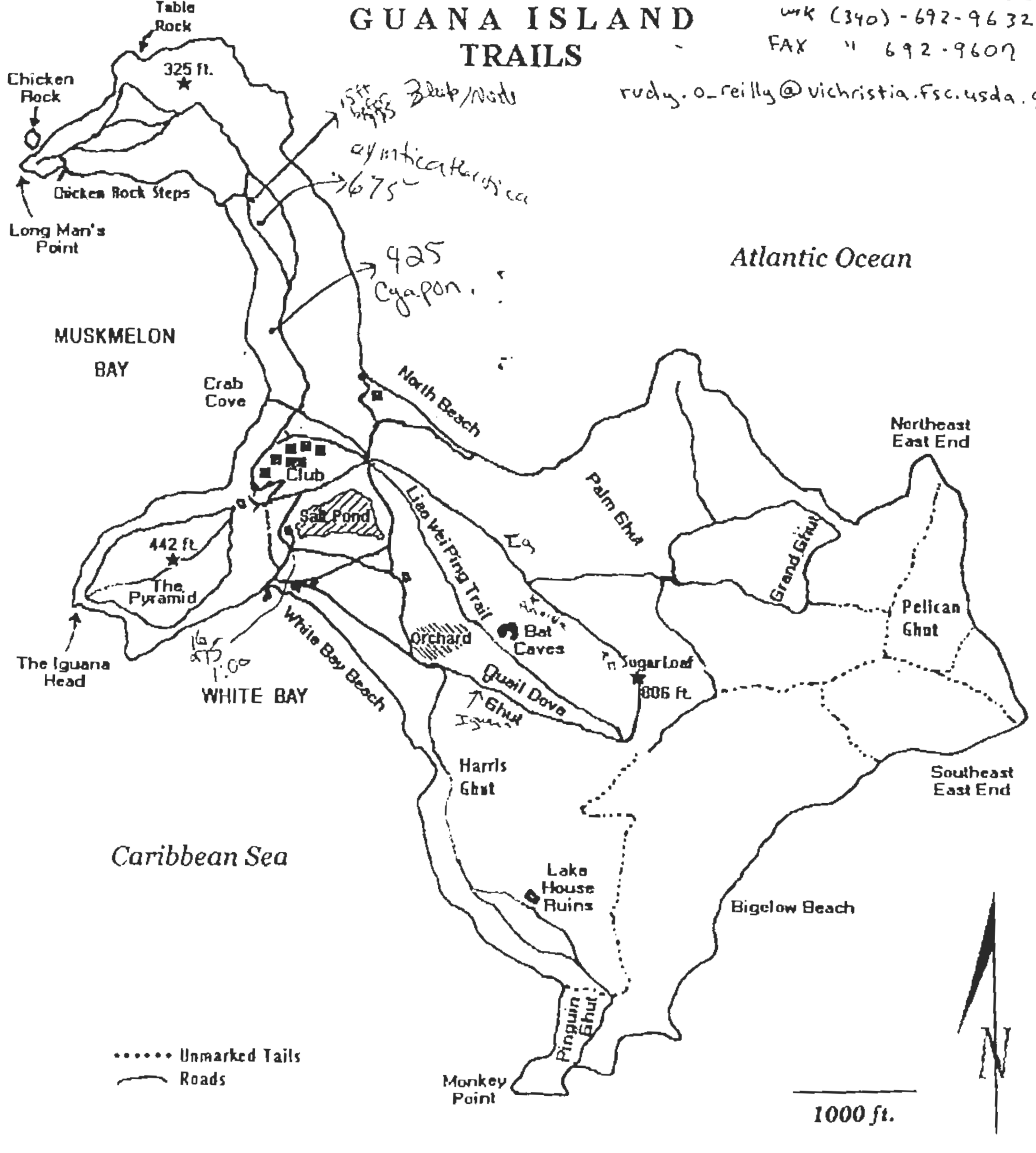
Your BVI findings sound exciting, especially the Doyerea emetocathartica, about which I know little. This species is listed as Corallocarpus emetocatharticus in the 1925 Scientific Survey of Porto Rico and the Virgin Islands (Vol VI, Part 1, in Britton and Wilson's Descriptive Flora - Spermatophyta). Cayaponia americana is listed as occurring in various islands, including Tortola and Virgen Gorda, but Guana Island is not mentioned.

In any case, either of these species would make good topics for a future Profiles articles. Also, any seeds you can spare would be appreciated. Even if I don't plant them, I can make them part of my seed identification inventory.

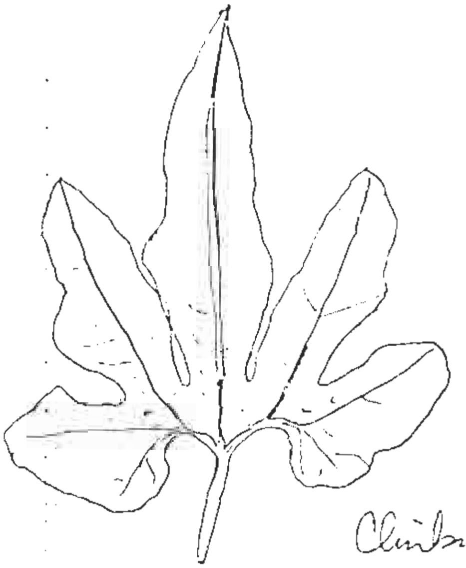
Take Care, Deena
The Cucurbit Network
P.O. Box 560483
Miami, FL 33256
U.S.A.

Rudy G. O'Reilly, Jr.
P.O. Box 875
C'sted, VI 00821-0875
Tel. hm (340)-773-2138
wk (340)-692-9632 (106)
FAX " 692-9607
rudy.o_reilly@vichristia.fsc.usda.gov

GUANA ISLAND
TRAILS



all 3 plants were on west side branch of trail ~~that~~ leads to muskmelon trail.

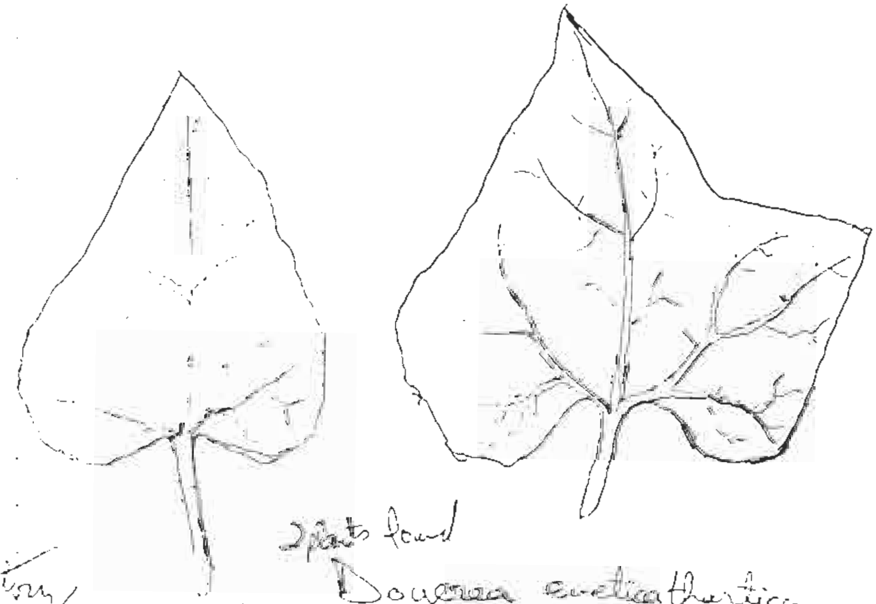


Cayaponia americana:

One tendril per Node branching into 3

Stem longitudinal ridges, many branches New stems from old Nodes @ top of Mt. dry rocky

Climbing up to ~7 ft.



Understory

1 was prostrate the other Climbing to about 4 feet.

2 plants found

Doyerea emetocathartica

prickly on top Smooth pubescent on underleaf

Stem pubescent - fleshy Stem? Root? from ground, multiple branches

From: "Rudy O'Reilly" <Rudy.O_Reilly@vichristia.fsc.usda.gov>
To: "Wenhua Lu" <wenhua@etal.uri.edu>
Sent: Wednesday, February 19, 2003 2:19 PM
Subject: Re: royal palm

Hi Wenhua:

Tell Skip that I spoke to Gary Briggs of Cruzan Gardens here in St. Croix. He has three Royal Palms with eight to ten foot trunks. Please contact him to see if they can be shipped to Guana. His number is (340)-773-7654. Let me know how the search is going.

Rudy

> Wenhua Lu wrote:
>
> Ruddy: Happy New Year! Skip asks again about the royal palm. We are
> off to New Caledonia this coming Monday, until late February.... WH
> Wenhua Lu, Ph.D.
> Oklahoma State University
> Wes Watkins Agriculture Research & Extension Center
> P. O. Box 128
> Lane, OK 74555
> 580-889-7343 (phone) 580-889-7347 (fax)
> 580-364-0543 (home)

Cheers! Jason

27 September 2002
PROC. ENTOMOL. SOC. WASH.
104(4), 2002, pp. 868–883

ENIGMATIC TREEHOPPER GENERA (HEMIPTERA: MEMBRACIDAE): *DEIRODERES* RAMOS, *HOLDGATIELLA* EVANS, AND *TOGOTOLANIA*, NEW GENUS

JASON R. CRYAN AND LEWIS L. DEITZ

(JRC) Laboratory for Conservation and Evolutionary Genetics, New York State Museum, Albany, NY, 12230 U.S.A. (e-mail: jcryan@mail.nysed.gov); (LLD) Department of Entomology, Box 7613, North Carolina State University, Raleigh, NC 27695-7613, U.S.A. (e-mail: lewis_deitz@ncsu.edu)

Abstract—Two poorly known Neotropical treehopper genera, *Deiroderes* Ramos and *Holdgatiella* Evans, are revised and redescribed based on adult morphology. The Caribbean genus *Deiroderes* (unplaced within the subfamily Stegaspidinae) has three valid species including ***D. inornatus*, new species** (Jamaica). The Neotropical genus *Holdgatiella* (currently unplaced within Membracidae) has two valid species including ***H. stria*, new species** (Venezuela). In addition, a previously unknown Caribbean genus is here described, ***Togotolania*, new genus,** with two species: ***T. longicorna*, new species** (Dominican Republic) and ***T. brachycorna*, new species** (Guadeloupe). All species included in these three genera are illustrated, and keys are given for the identification of adults.

Key Words: Membracidae, *Deiroderes*, *Holdgatiella*, *Togotolania*, Caribbean, taxonomy

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Treehoppers (Hemiptera: Membracidae) are traditionally recognized by the enlarged pronotum, which in many species is conspicuously ornamented with stalks, spikes, or bulbs. In most genera, there is at least a posterior pronotal process extending over (or even concealing) the scutellum. However, the pronota of the Neotropical treehopper genera *Deiroderes* Ramos and *Holdgatiella* Evans are remarkably unremarkable. A third genus, *Togotolania*, described here as new, also has a simple pronotum, adorned only with a median horn. These three genera are probably not closely related, indicating that enlarged pronotal ornamentation was likely gained or lost multiple times in Membracidae. Other treehopper genera lacking a posterior pronotal process occur in the subfamilies Nicomiinae, Endoiastinae, Centrotinae, and Stegaspidinae (fossils), though these may be cases of secondary loss.

Following the most recent reclassifications of Membracidae (Deitz and Dietrich 1993a, Dietrich et al. 2001a), *Deiroderes* and *Holdgatiella* were among several genera that remained unplaced within the taxonomic framework. Although these two genera were originally described in the subfamily Centrotinae (Ramos 1957a, Evans 1962a), emerging morphological (Dietrich et al. 2001a, Cryan et al. in press) and molecular (Cryan et al. 2000a, Cryan, unpublished data) evidence is revealing support for new phylogenetic placements within Membracidae, as discussed below.

MATERIALS AND METHODS

Protocols used during this work follow the materials and methods described by Cryan and Deitz (1999a). The following codens are used to refer to the collections in which relevant specimens are located or have been deposited. Arnett et al. (1993a) listed the full postal addresses for most of the institutions; those not found in that publication are indicated by a dagger (†) following the coden.

CIRAD†: Labo Entotrop (Faunistique-Taxonomie), Montpellier, France.
CNCI: Canadian National Collection of Insects, Agriculture and Agri-Food Canada, Ottawa, Canada.
JARC†: J.A. Ramos Collection, University of Puerto Rico, Mayagüez, Puerto Rico.
JWEC†: J.W. Evans Collection, c/o Australian Museum, Sydney, Australia.
MNHN: National Collection of Insects, Muséum National D'Histoire Naturelle, Paris, France.
NCSU: North Carolina State University Insect Collection, Department of Entomology, North Carolina State University, Raleigh, North Carolina, USA.
SHMC†: S.H. McKamey Collection; current address: Systematic Entomology Laboratory, USDA, ℅ National Museum of Natural History, Smithsonian Institution, Washington, D.C., 20560-0168, USA.
USNM: National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA.

Genus *Deiroderes* Ramos 1957

Deiroderes Ramos 1957a: 96. Type species: *Deiroderes inermis* Ramos 1957a: 96, by original designation.

Diagnosis.—The genus *Deiroderes* includes small stegaspidine treehoppers with simple pronota (lacking well-developed suprahumeral horns and posterior pronotal process) and dark tubercles along the veins of the forewings.

Adult.—*Dimensions* (mm): total length (from head to apex of forewings at rest) 3.2–3.9. *Structure: Head* (Figs. 1–2, 8–9, 14–15): broad, wider than long, with fine pubescence; ocelli not raised, above centro-ocular line; foliate lobes small, rounded or quadrate; postclypeus weakly or strongly trilobed. *Thorax: Pronotum* (Figs. 2, 9, 15): simple, convex; either low or elevated; suprahumeral horns represented by low carinae, or absent; posterior pronotal process absent. *Pronotal surface sculpturing*: finely punctate, each pit associated with one short seta; setae clubbed, normal, or flattened. *Scutellum* (Figs. 2, 9, 15): short, acuminate; anterior half slightly raised; posterior half flattened, with slight median depression. *Legs* (Figs. 3, 10): metathoracic femur with or without dorsal row of cucullate setae; metathoracic tibia with enlarged setal rows I, II, and III, all with cucullate setae; metathoracic tarsomere I with 1 apical cucullate seta. *Forewing* (Figs. 4, 11, 16): punctate, coriaceous basally; venation simple; 1 [rarely, 2] r-m and 1 m-cu crossvein present; dark tubercles, each bearing one stout seta, spaced irregularly along veins and crossveins. *Hindwing*: venation essentially identical to *Microcentrus* hindwing venation as illustrated by Deitz (1975a, fig. 37c) and Dietrich et al. (2001a, fig. 2B). *Genitalia:* ♀ 2nd valvulae (Figs. 5, 17) narrow throughout, with distinct dorsal serrations; ♂ lateral plates (Figs. 6, 12) free, without hook; aedeagus and styles (Figs. 7, 13) variable; aedeagus with anterior face of posterior arm not denticulate.

Range.—Caribbean, from Virgin Islands to Cuba.

Remarks.—Ramos (1957a) originally described *Deiroderes* as a member of the subfamily Centrotinae, indicating the genus was closely related to *Lophyraspis* Stål (now in Aetalionidae: Biturritiinae: Biturritiini) and *Tolania* Stål (now in Membracidae: Nicomiinae: Tolaniini). *Deiroderes* was later removed from Centrotinae and considered unplaced within Membracidae (Deitz and Dietrich 1993a). Dietrich et al. (2001a) found that *Deiroderes* was included within a monophyletic Stegaspidinae in some of the most-parsimonious cladograms resulting from a more detailed morphology-based phylogenetic analysis of the family Membracidae. Nevertheless, evidence for placement of *Deiroderes* remained equivocal, and therefore the genus remained unplaced in Membracidae.

In a phylogenetic analysis of basal treehopper groups, Cryan et al. (in press) found that *Deiroderes* groups with the genus *Antillotolania* Ramos at the base of Stegaspidinae. Morphological features that placed the genus within Stegaspidinae included the forewing's distal m-cu crossvein (fused basad of the fork of vein M) and hooklike apex of the male styles.

Within Stegaspidinae, some features—forewing with one r-m and one m-cu crossvein; vein R_{2+3} fused basally with R_1; and male lateral plates free, lacking posteroapical hooks—suggest that *Deiroderes* is more closely related to the tribe Stegaspidini (reviewed in Cryan and Deitz 1999a, b, 2000a). Nevertheless, phylogenetic analyses based on morphological (Dietrich et al. 2001a, Cryan et al. in press) and molecular (Cryan et al. 2000a, Cryan, unpublished data) evidence suggest either that *Deiroderes* might be more closely related to Microcentrini or that placement is equivocal. Therefore, pending more definitive resolution, we refer *Deiroderes* to Stegaspidinae but propose that the genus remains unplaced to tribe.

When creating a generic name that refers to a feature of the prothorax, it is customary to modify the Greek noun "*dere*" to "*deres*," thereby making the name masculine (G. Kuschel, personal communication). The first part of the compound name, "*deiro*-," means to behead something, or to cut the neck; thus, "*Deiroderes*" best translates as the "beheaded" treehopper, probably referring to either the lack of pronotal horns or the relatively flat head.

KEY TO THE SPECIES OF ADULT *DEIRODERES*

1. Forewing vein M branching at, or immediately distad of, crossvein r-m, M_{3+4} extending posteriorly at right angle to M (Fig. 4); metathoracic femur with dorsal and ventral rows of cucullate setae (Fig. 3) .... *D. inermis* Ramos
– Forewing vein M branching distinctly distad of crossvein r-m, M_{3+4} extending obliquely to wing margin (Figs. 11, 16); metathoracic femur without rows of cucullate setae (Fig. 10) ... 2
2. Pronotal metopidium produced dorsally, with well-developed median carina; pronotum with suprahumeral carinae (Fig. 15) .... *D. punctatus* (Metcalf and Bruner)
– Pronotal metopidium low, dorsal median carina not well developed; pronotum without suprahumeral carinae or horns (Fig. 9) .... *D. inornatus*, new species

Deiroderes inermis Ramos
(Figs. 1–7)

Deiroderes inermis Ramos 1957a: 96.

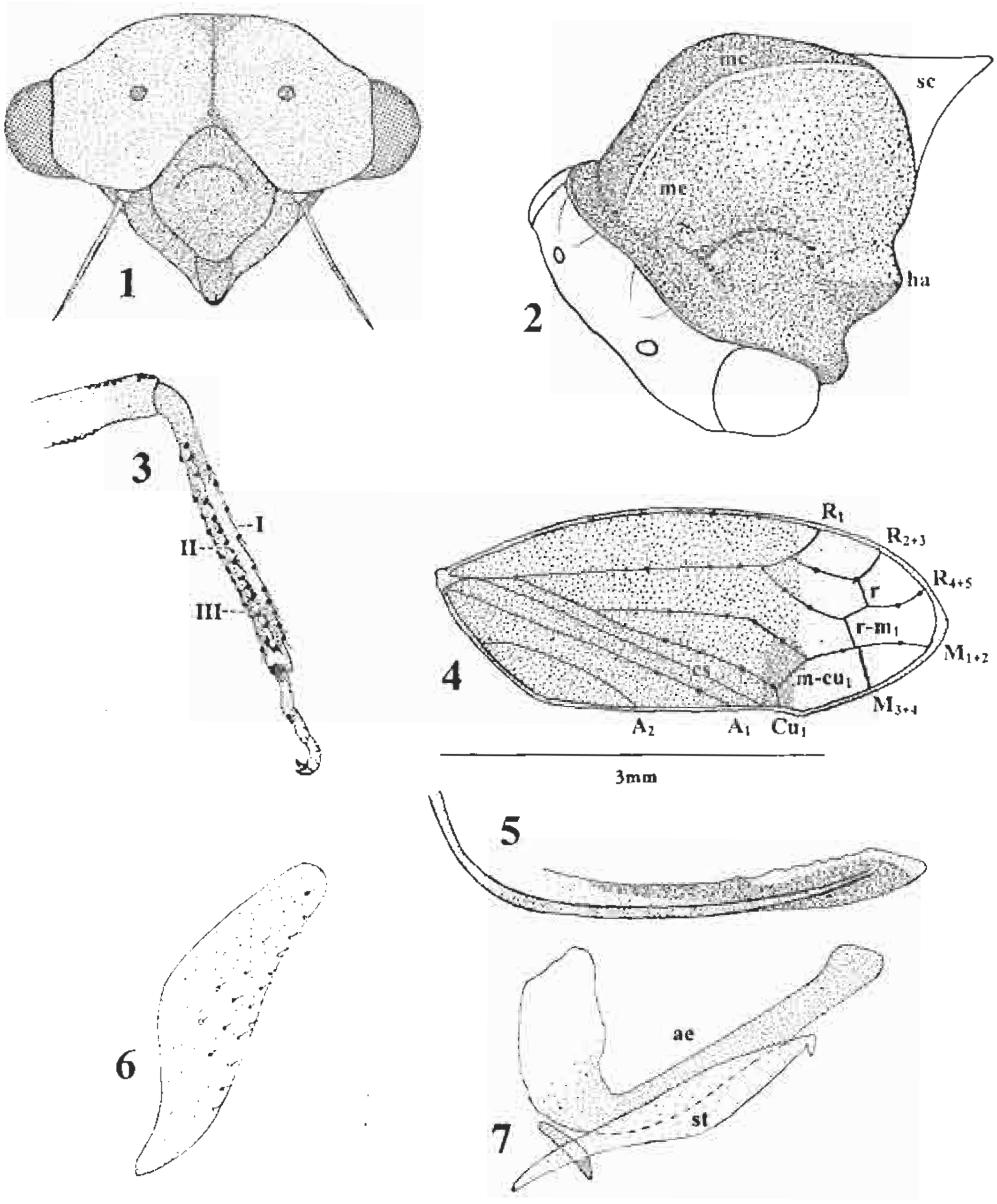
Type locality.—Guánica, Puerto Rico.

Diagnosis.—*Deiroderes inermis* has the forewing with vein M branching immediately distad of the r-m crossvein, M_{3+4} extending directly to the posterior margin of wing (nearly forming a right angle with M).

Adult.—*Dimensions* (mm): total length ♀ 3.2–3.5, ♂ 3.5; width between humeral angles ♀ 1.2–1.4; ♂ 1.3; pronotal length ♀ 0.8–1.0, ♂ 0.9; wing length ♀ 2.6–2.8, ♂ 2.4; width of head including eyes ♀ 1.1–1.3, ♂ 1.2. *Coloration:* body tan to dark brown; forewing dark basally, dark coloration sometimes extending ⅔ of wing length, with dark spot at distal end of vein Cu. *Structure: Head:* dorsal projections (Fig. 1) indistinct. *Thorax: Pronotum* (Fig. 2): metopidium low; humeral angles short, blunt; middorsal crest weakly produced; suprahumeral horns and carinae absent. *Legs* (Fig. 3): metathoracic femur with dorsal and ventral rows of cucullate setae; metathoracic tibiae with cucullate setae row I less robust than setae in II or III. *Forewing* (Fig. 4): M branching immediately distal to r-m crossvein, M_{3+4} extending to posterior edge of wing, at right angle to M. *Genitalia:* ♀: 2nd valvulae (Fig. 5) narrow throughout, apical ⅓ with distinct dorsal serrations. ♂: lateral plates (Fig. 6) free, lacking hooks, sparsely setose; styles (Fig. 7) with small hook apically; aedeagus (Fig. 7) with posterior arm straight.

Nymph.—Unknown.

Distribution.—British Virgin Islands: Guana Island [NCSU], Virgin Gorda



Figs. 1–7. *Deiroderes inermis.* Structures of the holotype (male genitalia illustrated from a non-type specimen). 1, Head, anterior aspect (face). 2, Head, pronotum, and scutellum, anterolateral aspect. 3, Left metathoracic femur, tibia, and tarsus, ablateral aspect. 4, Right forewing. 5, Female second valvulae, lateral aspect. 6, Male left lateral plate, lateral aspect. 7, Male aedeagus and left style, lateral aspect (illustrated with connective tissue). Abbreviations: A_n, anal vein(s); ae, aedeagus; Cu_n, cubital vein(s); cs, claval suture; ha, humeral angles; $m\text{-}cu_n$, medial-cubital crossvein(s); M_n, medial vein(s); mc, median carina; me, metopidium; sc, scutellum; st, style; r, radial crossvein; $r\text{-}m_n$, radial-medial crossvein(s); R_n, radial vein(s); I, II, III, enlarged setal rows.

[NCSU], Tortola [NCSU]; U.S. Virgin Islands: St. John [JARC]; Puerto Rico [NCSU].

Material examined.—Holotype [♀] [NCSU, deposited on indefinite loan to USNM] with labels: "Insular Forest/Guanica P.R./3-Aug. 1945./On Capparis nitida.," "J.A. Ramos/Collector," "Holotype," "Deiroderes/inermis Ramos/145." Paratype [♀; forewings missing] [NCSU] with labels: "Cambalache/P.R. 11-7-47," "Caldwell &/Martorell/Collectors," "Paratype," "Deitz Research/83-227e ♀," "JARC," and "PARATYPE/Deiroderes/inermis/Ramos." Other specimens: 1 ♀ (Deitz Research #83-227f ♀) from JARC; 2 ♂ (Cryan Research #94-286a ♂ and Cryan Research #94-273b ♂) from NCSU; 1 ♀ from USNM.

Remarks.—The holotype of *D. inermis* was collected on *Capparis* sp. (Capparaceae), though there is a discrepancy concerning the host species. In the original description of *D. inermis* (Ramos 1957a), the holotype is listed as "on *Capparis indica* (L.) Fawc and Rendle"; however, the holotype label information indicates the host as *C. nitida* (*C. indica* and *C. nitida* are not synonyms). This insect's Latin specific epithet translates directly to "unarmed" or "weaponless," presumably referring to the complete absence of pronotal projections (suprahumeral horns and posterior process).

A specimen of *D. inermis* from the British Virgin Islands was included in a molecular systematic investigation of membracid relationships (Cryan et al. 2000a). Results based on parsimony and maximum likelihood analyses of DNA nucleotide sequence data from two nuclear genes (EF-1α and 28S rDNA) indicated that *Deiroderes* was a member of a clade that also included *Antillotolania* Ramos and *Microcentrus* Stål.

Deiroderes inornatus Cryan and Deitz, new species
(Figs. 8–13)

Type locality.—Jamaica.

Diagnosis.—*Deiroderes inornatus* has a simple, unadorned pronotum, strongly deflected postclypeus and beak, and sinuate aedeagus.

Adult ♂.—*Dimensions* (mm): total length 5.1–6.0; width between humeral angles 1.9–2.1; pronotal length 1.4–1.5; wing length 4.0–4.9; width of head including eyes 2.1–2.3. *Coloration:* body tan to dark brown; forewing tan or dark brown basally, light brown apically. *Structure: Head:* dorsal projections (Fig. 8) small or indistinct; postclypeus and anteclypeus strongly deflected under thorax. *Thorax: Pronotum* (Fig. 9): metopidium low; humeral angles weakly produced; mid-dorsal crest weakly produced; suprahumeral carinae and horns absent. *Legs* (Fig. 10): metathoracic femur without rows of cucullate setae. *Forewing* (Fig. 11): vein M branching well after r-m crossvein; M_{3+4} extending obliquely to posterior margin of wing; some specimens with 2 r-m crossveins on one or both forewings. *Genitalia:* lateral plates (Fig. 12) free, without hooks; styles (Fig. 13) sinuate, hooked apically; aedeagus (Fig. 13) with posterior arm sinuate, narrowing apically. ♀: unknown.

Nymph.—Unknown.

Distribution.—Jamaica [USNM, CNCI].

Material examined.—Holotype [♂] [USNM] with labels: "Jamaica/19-VII-35," "Sta 16/Chapin and/Blackwelder," "Voucher Specimen/Cuticular Hydrocarbon/Analysis Study/Jason R. Cryan, 1995," and "HOLOTYPE ♂/*Deiroderes/inornatus*/Cryan & Deitz." Paratype [♂] [CNCI] with labels: "JAMAICA, 4000′/Hardwar Gap/VII-23-1966/Howden & Becker," "Specimen data/captured—NMNH/Biota (Colwell) file," and "PARATYPE ♂/*Deiroderes/inornatus*/Cryan & Deitz." Paratype [♂, dissected; head and pronotum missing] [USNM] with labels: "Jamaica/19-VII-35," "Sta 16/Chapin and/Blackwelder," "CRYAN RESEARCH/#94-273a ♂," and "PARATYPE ♂/*Deiroderes/inornatus*/Cryan & Deitz." Other specimens: 1 ♂ from CNCI; 1 ♂ from USNM.

Remarks.—*Deiroderes inornatus* is de-

TERMITES

The following major paper illustrates the increasing problem -- after nearly a quarter century of fieldwork -- of the disappearing source in derivative, synthetic works. People simply forget where they got their information. Data generated on Guana long ago are now entering the scientific literature as "common knowledge." In a sense, that is good: our material is not only entering the mainstream, it is becoming it. This paper, for example, relies considerably on information about the termite family Kalotermitidae: I have put arrows in the margin indicating where. Four of Guana's eight termite species are kalotermitids and two of these -- *Incisitermes incisus* and *Neotermes mona* -- have been intensely studied by Jan Krecek, Barbara Thorne, Margaret Collins, Mike Haverty, and other termite experts on Guana. Much, if not most, of the world's knowledge of kalotermitid societies, life histories, and behavior was generated on Guana. But check that paltry acknowledgement at the end of Barbara's paper: not a word about us.

When Wenhua found this paper she asked me about Guana's role, and I called Barbara. "Oh, yes," Barbara said, "You should definitely regard that as a Guana publication." So I do.

Barbara wants to come back this October specifically to try new, highly specific poison baits on the drywood termites that invade Guana's buildings. There has been little defense against them before, but she thinks she has got a method now. I said I thought you would be delighted: a *useful* scientist, at last.

REVIEWS IN ADVANCE

Annu. Rev. Entomol. 2003. 48:283–306
doi: 10.1146/annurev.ento.48.091801.112611

COMPARATIVE SOCIAL BIOLOGY OF BASAL TAXA OF ANTS AND TERMITES

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■ **Abstract** Lacking a comprehensive fossil record, solitary representatives of the taxa, and/or a definitive phylogeny of closely related insects, comparison of the life history and social biology of basal, living groups is one of the few available options for developing inferences regarding the early eusocial evolution of ants and termites. Comparisons of a select group of basal formicid and isopteran taxa suggest that the reproductive organization of colonies and their patterns of division of labor were particularly influenced, in both groups, by nesting and feeding ecology. Opportunities for serial inheritance of the nest structure and colony population by kin may have been significant in the evolution of multiple reproductive forms and options. Disease has been a significant factor in the evolution of social organization in ants and termites, but the adaptive mechanisms of infection control differ. Evaluations of the convergent and divergent social biology of the two taxa can generate novel domains of research and testable hypotheses.

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INTRODUCTION

The study of the evolution of complex traits is greatly facilitated by the existence of phylogenetic intermediates that express gradual transitions in character states, and the comparative analysis of these transitions often provides the most compelling data for revealing patterns and developing robust hypotheses regarding selective factors that influence evolutionary change. Such stepping stone intermediates, however, are rarely present as a relatively complete fossil or living series, reflecting incomplete preservation and discovery of fossils, species extinction, the evanescence of annectant forms, and the fact that evolution is not always a gradual process. Eusociality is a highly complex trait of profound evolutionary interest because of the existence of subfertile or sterile colony members. Comparative studies of sister groups and basal taxa have been insightful in examining the evolution of eusociality in clades of bees and wasps because modern species show a cline of life histories that range from solitary to eusocial. Similar cladistic analyses are absent in ants and termites because all the roughly 10,200 species of living ants and over 2600 species of extant termites are eusocial, and solitary ancestors are sufficiently distant to obscure the linkages among selective regimes.

The structural elements of social organization in the Hymenoptera and Isoptera are highly convergent. Unlike the haplodiploid Hymenoptera, however, both sexes of termites are diploid, rendering explanations for eusocial evolution based on asymmetries in genetic relatedness generated by meiosis and fertilization inapplicable to termites. Nevertheless, the similarities and differences in the preadaptive characteristics of each group and ecological forces that impelled the evolution of social organization may offer significant sociobiological insight. Lacking the opportunity for comparative study within taxa, here we explore commonalities and contrasts in the life history, colony structure, reproductive dynamics, and socioecology of the most primitive living lineages of ants and termites. Although these phylogenetically divergent insects differ in fundamental ways (such as holometaboly in Hymenoptera and hemimetaboly in Isoptera), eusociality is based on the elaboration of family units in both groups, and eusocial evolution may be constructively discerned through focused comparative assessments. Observations on the biology of extant taxa cannot be used to definitively reconstruct ancestral states prior to the evolution of worker subfertility or sterility and thus cannot appropriately be used to test hypotheses or predictions regarding the evolution of eusociality. Once protoants or prototermites crossed the threshold of eusociality, life history constraints, especially those related to reproductive division of labor, may have

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been essentially irreversible. Data that allow specific comparisons are not always available, so a collateral goal of this paper is to identify domains of research that would further advance such an approach. We begin with an overview of the phylogenetic origin of ants and termites, identify the basal taxa considered in the review, and justify the inclusions of those groups central to our comparative analysis.

ORIGIN OF ANTS AND BASAL ANT SYSTEMATICS

The origins of the formicid theme of social organization have been sought in the vespoid wasps. There is a void in social behavior between basal ants and their closest vespoid relatives, although the fossil record offers some evidence of how and when ants attained their morphological distinctiveness and suggests a basic timeline for the emergence of the socially advanced groups. The hypothetical ancestral vespoid wasps are thought to be linked to ants through the subfamily Sphecomyrminae, the pleisiomorphic sister group to all ants, with its extinct Cretaceous fossil genera *Sphecomyrma* and *Cretomyrma* (124). *Sphecomyrma freyi*, dating from New Jersey amber of the late middle Cretaceous, exhibits a constellation of nonsocial wasp and ant traits: short bidentate mandibles, a reduced and wingless thorax, a petiolar constriction, and significantly, what appears to be a metapleural gland (33). It is considered the "nearly perfect link between some of the modern ants and the nonsocial aculeate wasps" (33, p. 23). *Kyromyrma neffi*, the first specimen of an extant ant subfamily (the Formicinae), also collected from the New Jersey amber (c. 92 million years ago, has an acidopore and is 50 mya older than *Sphecomyrma* (23). This suggests a divergence of the basal lineages of ants from the Sphecomyrminae approximately 105–110 mya. Further details of the fossil record and adaptive radiation of ants are given in Hölldobler & Wilson (33) and Crozier et al. (14), which provide molecular data dating the origin of ants to the Jurassic.

The basal division of the 17 ant subfamilies (5) separates the Myrmicinae, Pseudomyrmecinae, Nothomyrmeciinae, Myrmeciinae, Formicinae, and the Dolichoderinae from the remaining subfamilies. The Nothomyrmeciinae, Myrmeciinae, and Ponerinae include genera considered pivotal in ant social evolution because of their comparatively primitive morphology and social organization (33). The final basal group of ants is the Aneuretinae, a formicoid complex subfamily once global in distribution but today represented by a single species, *Aneuretus simoni*, found in limited areas of Sri Lanka (41).

The subfamily Nothomyrmeciinae is monotypic, known only from the single extant and elusive *Nothomyrmecia macrops* Clark from Australia. Its rediscovery in 1978 (104) was somewhat akin to finding the "Holy Grail" of myrmecology, and the collection and observation of queenright colonies made possible detailed accounts of the social organization of this relict species (31, 104). The basal characteristics of this ant include a wasp-like morphology (104), an exceptionally high level of inactivity, and low levels of social exchanges among workers in their small colonies (40). Queens do not receive food or other preferential treatment; indeed, queens and workers rarely interact. Remarkably, queens living in intact laboratory colonies collect and feed on insect prey on their own. The subfamily Myrmiciinae is represented by the Australian bulldog ants of the genus *Myrmecia*, which forms colonies of 600–900 workers (25). Colonies can be founded independently by single queens or polygynously by groups of females (12).

The Ponerinae is a large and diverse subfamily whose representatives display a mixture of basal and derived morphologies and social characters. Primitive ponerines include *Amblyopone*, an ant that exhibits morphologically and behaviorally primitive traits, although other genera in the tribe Amblyoponini show highly derivative characteristics. Because of the great diversity of ponerine ants, including numerous species with clearly derived traits (81, 82), we concentrate on the more primitive forms, using *A. pallipes* as a model, while noting that other species of *Amblyopone* may vary widely in their biology and even include queenless forms (37). In *A. pallipes*, alate queens discard their wings to establish new colonies and forage during the colony foundation stage (33). Nests, which house small colonies averaging roughly a dozen workers, are composed of simple chambers and galleries in soil and decayed wood. Populations of *A. pallipes* are patchy but can be locally abundant (112).

ORIGIN OF ISOPTERA AND INTERFAMILIAL RELATIONSHIPS

The higher-level phylogeny of termites has received considerable interest in the past decade. Although monophyly of the Dictyoptera is accepted (28, 50), relationships among the dictyopteran orders Blattaria, Mantodea, and Isoptera are not fully resolved (6, 17, 42, 44–47, 51, 57, 59, 108). Despite the topological uncertainty regarding whether cockroaches or some lineage(s) of a paraphyletic cockroach clade are the sister group to termites, there is consensus that study of the life history and social organization of the relict wood roach genus *Cryptocercus* provides constructive comparison and potential insights into the biology of prototermites and potential selective forces favoring the evolution of eusociality (10, 67, 68, 107). To date, the fossil record exposes no missing links that indicate intermediate stages between the orders, so identifying the most immediate ancestors of Isoptera, and gleaning the hints that they might reveal regarding the transition from solitary to eusocial life histories, has been impossible.

The early evolution and intrafamilial relationships of Isoptera also are not fully understood, but several lines of evidence identify the most basal lineages and provide increasing definition of their phylogeny. The earliest known fossil termites are from the Cretaceous and are representatives of the Hodotermitidae, Termopsidae, and possibly Mastotermitidae. These Mesozoic termites are distinctly primitive but reasonably diversified, suggesting an origin of the order in the Upper Jurassic (109). Hodotermitidae, represented in modern fauna by three genera (19 species) of highly specialized "harvester" termites, has the oldest described fossil (~130 mya) (52) and a total of six genera (seven species) in the Cretaceous. Although the foraging behaviors and colony organization of extant hodotermitids are derived, they retain plesiomorphic morphological characters (18).

Termopsidae, the sister group of Hodotermitidae [(16, 18, 73); but see (105)], is represented by at least four known genera (five species) in the Cretaceous and five modern genera (20 species, the "dampwood" termites). Termopsids, especially the relict Himalayan *Archotermopsis wroughtoni* Desneux, are considered by many to be the most primitive living termites with respect to colony size, social organization, nesting biology, and caste polyphenism (35, 71, 101, 105, 107, 108).

Mastotermitidae, apparently represented in the Cretaceous by two genera and radiating broadly by the Tertiary (4 genera with more than 20 species known from Australia, Europe, North and South America, and the Caribbean) (109), now exists as only a single species, *Mastotermes darwiniensis* Froggatt, with a natural distribution in moist, tropical regions of Northern Australia. Mastotermitidae is viewed uncontroversially as the most basal living lineage within Isoptera and as the sister taxon to all other living termites (16, 17, 43, 47, 48). *M. darwiniensis* has distinct plesiomorphic characters, but it also features a number of highly derived characteristics. For example, *M. darwiniensis* has an early and apparently irreversible split in development of nondispersive forms, soldiers secrete a defensive chemical, male reproductives have a unique type of multiflagellate sperm, colony population sizes can be large (several million individuals), gallery construction occurs within nests, and extensive foraging tunnels connect food sources located away from the nest (21, 53, 105, 108). *M. darwiniensis* thus exemplifies a common evolutionary pattern: It retains some primitive features but also has apomorphic anatomical and life history elements.

Along with these three confirmed ancient families, some classic (48, 75) and one recent family-level phylogeny (43) place Kalotermitidae, including the "drywood" termites along with some dampwood species (53), as among the most basal clades. Kalotermitids do not appear in the fossil record until the Paleocene; there are 446 modern species in 21 genera (11). Current hypotheses of relationship among the four basal termite families Mastotermitidae, Hodotermitidae, Termopsidae, and Kalotermitidae differ only in the position of Kalotermitidae. Taxonomic sampling issues and lack of integration between morphological and molecular studies have impeded resolution of family-level phylogenies, but for the purposes of this paper we assume that Mastotermitidae, Hodotermitidae, and Termopsidae comprise the most basal living termite clades. This is in accordance with recent phylogenetic analyses that differ in topology, but include the same three families as most basal [((((((T, R), S), K), (Tp, H)), M), B)[1] (105); (((((((T, R), S), K), Tp), H), M), B)] [Donovan et al. (16) and Eggleton's (17) "majority consensus rule" phylogeny].

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[1] B, Blattaria; M, Mastotermitidae; H, Hodotermitidae; Tp, Termopsidae; K, Kalotermitidae; S, Serritermitidae; R, Rhinotermitidae; T, Termitidae.

ANCESTRAL ECOLOGY OF TERMITES: FOCUS ON TERMOPSIDAE

Because social organization of living members of the Mastotermitidae and Hodotermitidae appears to be derived, we typically draw inferences regarding ancestral socioecology from life history patterns of modern Termopsidae. This interpretation has been broadly held among termitologists (18, 72, 76, 101, 107), although there is some controversy regarding whether the developmental flexibility typical of Termopsidae is an ancestral or derived characteristic of termites. The traditional view is that "true workers," i.e., individuals that diverge early and irreversibly from the imaginal line, are a derived feature in termites (1, 70, 72, 76). According to this view, the worker caste developed at least three times independently because true workers occur in Mastotermitidae, Hodotermitidae, Serritermitidae, Rhinotermitidae, and Termitidae (3, 29, 66, 76, 77, 85, 86, 107). In Termopsidae, Kalotermitidae, and the most primitive Rhinotermitidae, helpers have marked developmental flexibility throughout their lives; all individuals except soldiers may differentiate into reproductives (70, 76, 87, 101, 107) or undergo regressive molts to revert from the nymphal line into "pseudergates" (76).

Based on hypotheses of interfamilial phylogenetic relationships, however, Thompson et al. (105) follow Watson & Sewell (118, 119) in supporting irreversible worker differentiation as an ancestral element of termite social evolution rather than a derived, phylogenetic state. It is difficult to evaluate this postulate, however, because there are so few living representatives of taxa key to this interpretation, i.e., the families Mastotermitidae and Hodotermitidae, and those species that exist are highly derived in other social attributes (18, 48, 101, 107). Nesting and feeding habits may drive the evolution of social behaviors, obscuring phylogenetic analyses based on presumed homologous traits. For example, true workers are invariably found in species that forage away from the nest exploiting multiple resources, and helpers with lifelong flexible developmental options occur in "one-piece nesting" groups that consume only the wood in which they live and therefore face eventual resource limitation and instability (1, 3, 29, 53). This correlation suggests biological significance between termite nesting biology and presence or absence of true workers in modern species. The ancestral worker hypothesis (105, 118, 119) thus carries linked implications, suggesting for example that organized foraging away from the nest is an ancestral trait and that the one-piece life type with minimal nest architecture and foraging restricted to the nest wood is secondarily derived. Eggleton (17) rationally advocates resolution of phylogenies before attempting to map social, behavioral, developmental, or biogeographic characters.

INFERENCES REGARDING ANCESTRAL LIFE HISTORIES

Considering extant basal ants and termites as "windows" into ancestral life histories, it is apparent that individual species in either taxon rarely provide an entirely credible model reflecting the biology of the group early after the evolution of eusociality. Modern species belonging to even the most basal lineages have blended assemblages of primitive and derived traits, thus confounding interpretations. DNA sequences help resolve this issue for phylogenetic analyses, but no methodological safety net exists for evaluating social evolution because homology of behavioral traits can be difficult to verify and may be influenced by ecology or other derived life history attributes. We are thus left to draw inferences based on suites of characters considered to be primitive, compiled from a number of living taxa to yield a composite of likely traits and ancestral ecology of extinct lineages relatively close to the cusp of eusocial evolution. Our comparisons of likely ancestral character complexes from ants and termites ideally will yield productive insights regarding both commonalities and differences, and therefore potentially significant influences, favoring the evolution of eusociality in these insects. We focus on four broad and interrelated areas: reproductive plasticity, division of labor, foraging biology, and evolutionary pathobiology. We then conclude with a discussion of potential commonalities influencing the evolution of eusociality in these groups.

REPRODUCTIVE PLASTICITY IN ANTS AND TERMITES

Colony Structure, Gynes, and Replacement Reproductives

Developing a conceptual framework for the comparative analysis of reproductive variability in ants and termites has historically been impeded by the number and complexity of fertile and sterile forms, the existence of anatomical and physiological intermediates, nomenclature differences, and semantic controversy. To facilitate comparison and clarify our discussion we catalog the types of reproductives found in each group using currently recognized terminology (33, 88, 106).

In ants, reproductive division of labor presents itself in the typical dimorphic queen and worker castes: The queen is derived from the dispersing alate form, establishes a new colony, and is distinguished from her daughters by size, the extent of ovarian development and behavior. Among basal ant species, the wings may be reduced [as in the case of *Nothomyrmecia* (31)] and size differences may be limited to a somewhat broader thorax bearing the scars of the wings that are discarded following the dispersal flight. Some basal ants have fertile forms (ergatogynes) that are morphologically intermediate between independent, dealate colony-founding queens and workers and inseminated workers (gamergates). Ergatoid queens, which are found in some species of *Myrmecia* (13, 26), have a greater number of ovarioles than workers do, a filled spermatheca, and may replace a typical queen. Some ponerine ants, including *Amblyopone* (37, 83), are queenless. Reproduction by gamergates, which possess a functional spermatheca and are inseminated, occurs in these species. Colonies having gamergates occupy stressful environments, have reduced dispersal, mate within or nearby the nest, and reproduce by fission, as may colonies with ergatoid queens (83).

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Recent research (96, 97) has begun to uncover unexpected and exciting details of the reproductive and genetic organization of colonies of *Nothomyrmecia macrops*. This basal ant is facultatively polyandrous; sampled queens were singly or multiply mated to unrelated males, with an overall average of 1.37 matings per queen (96). Worker nestmates are related by $b = 0.61 +/- 0.03$. Workers appear to be incapable of laying eggs. The mechanism of queen replacement in colonies of *N. macrops* is rare among ants and bears some resemblance to the pattern of colony inheritance exhibited by some basal termites. Although newly inseminated queens found *N. macrops* colonies monogynously, comparisons of worker and queen genotypes in some sampled colonies contained resident queens that were the sisters rather than the mothers of workers. Furthermore, larvae were genetically identified as the queen's progeny and not the offspring of reproductive workers. The likely explanation for this genetic structure is that the original colony-founding queen had died and been replaced by one of her daughters.

The colony life cycle of *N. macrops* has been reconstructed as follows (96, 97): New queens, one of which may inherit the parental colony, are produced from overwintering larvae that can develop from eggs laid in the autumn into gynes during the following year, even in the event of death of the queen mother. A replacement queen can produce sexual offspring in her first year. Overall, *N. macrops* illustrates a low level of serial polygyny; primarily daughters, but at least occasionally unrelated queens, are adopted by orphaned colonies. Under the condition of colony inheritance by daughters, inclusive fitness benefits extend to the original colony-founding queen (through the rearing of grand-offspring following her death) as well as to workers (through the production of nieces and nephews). The brachyptery of new queens may reflect limited dispersal and a reproductive strategy designed to favor replacement of the mother queen by her daughters. Ecological constraints such as habitat patchiness, nest site limitation, and the risk-prone foraging behavior of the partially claustral founding queens may have favored colony inheritance in *N. macrops*.

Does the presence of such reproductive flexibility in one of the most primitive extant ants accurately reflect an ancestral condition? Although it has been argued that the brachypterous queens of *N. macrops* favored the evolution of daughter replacement (97), it is also possible that brachyptery evolved concomitantly with daughter adoption under the selective pressure of dispersal-related mortality. Again, we note the difficulties inherent in analyzing the evolution of social traits in basal species whose biology may be a constellation of primitive and derived characters.

Several types of reproductives exist in termites. The terms *king* and *queen* typically refer to the colony-founding male and female. These *primary* reproductives are imagoes (alates) that drop their wings after pairing. Founding pairs in basal groups are nearly always monogamous, although there are some records of associated groups of primary reproductives (27). *Neotenics* are termite reproductives that are not derived from alates, but differentiate within their natal colony, breeding with a parent, sibling, or other inbred relative. Neotenic differentiation typically occurs upon death or senescence of the founding reproductive of the same sex (55). Multiple neotenics of each sex develop, persisting as typically consanguineous reproductive groups in most basal termites (21) but surviving as only one pair in Kalotermitidae (72). Neoteny, literally meaning reproduction as an immature, is related to hemimetaboly, requiring one or two molts that modify morphology and produce functional sex organs (72, 106). In *Mastotermes*, neotenics may develop from workers (119); in termopsids neotenics may form from any individual in instar four or above (except soldiers or imagoes) (71), although no true neotenics are known in *Archotermopsis* (35, 89). Soldier neotenics occur in six species of termopsids (64, 107). In *Archotermopsis*, the gonads of all soldiers are as well developed as in alates (35).

All offspring helpers in termopsid families (except soldiers) retain the capacity to differentiate into fertile reproductives (in the case of termites, either alates or neotenics). They are thus poised to potentially inherit their parents' resources of a nest, food, and established family (65, 107). In such a system of serial reproductive inheritance by kin, as in the cases of ergatogyne and gamergate ants reproducing in their natal nest, all colony members gain inclusive fitness benefits and some individuals attain direct fitness advantages. These cumulative fitness components may well exceed average individual fitness prospects of dispersing, fertile offspring in a similar, solitary species, thus favoring helpers that remain in their natal colony. In *Zootermopsis*, numerous colonies may be initiated in the same log, eventually resulting in intercolony interactions, which can lead to death of reproductives and opportunities for replacement by neotenics (107).

In ancestral groups, the reproductive skew between reproductives and helpers may have been less discrete. Imms (35) reported that worker-like individuals of *Archotermopsis wroughtoni* have extensive gonad development and a fat body equivalent to alates. He observed a captive worker-like *A. wroughtoni* lay seven eggs. The eggs did not develop normally, but whether due to sterility, lack of fertilization, or laboratory conditions is unknown. Eusociality itself is viewed as a continuously varying categorization depending on the portion of progeny that reduces or foregoes reproduction (101, 103).

The possibility of merged or indistinct colonies functioning within single pieces of wood has been raised several times. Concerning *Archotermopsis*, Imms (35, p. 126) observed, "I have, on several occasions, come across three or four queens with a single large colony of ova and larvae, which probably represent several colonies which have become confluent." Fused colonies or colony complexes have also been suggested in *Stolotermes* (20, 63, 110) and *Zootermopsis* (B.L. Thorne, personal observation). These observations and their generality, context, and implications are difficult to evaluate; identification of discrete but adjacent colonies within a log is often impossible. Sufficient descriptive evidence exists, however, to encourage genetic examination of these circumstances, especially relationships among the reproductives found with the possibly merged groups. Recent work on *M. darwiniensis* (21) suggests that although neotenics within a colony are often inbred, they sometimes originate from more than two genetic

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lineages, as has been indicated in some more derived termites (8). Extensive study on colony genetic structure and the possibility of merging or introduction of foreign reproductives is required for both basal ants and termites.

Reproductive Conflict

Conflict among nestmates whose fitness interests are incongruent is common in social insects. The apparent rarity of nuptial flights in some basal ant genera (13), the presence of fertile helpers in both ants and termites, and multiple replacement reproductives raise the possibility of intracolony reproductive conflict. Reproductive conflict is manifest in oophagy, the existence of inhibitory pheromones, dominance structures, mutilation, and policing behaviors (37, 62). In basal ants, larval hemolymph feeding by queens has been described in *Prionopelta* and *Amblyopone silvestrii* (38, 60) and has been interpreted as a form of queen nutrition, although the behavior could also represent a mechanism to regulate reproductive capability.

Because of the monogynous and monoandrous organization of basal termite societies, conflicts similar to those observed in ants would not be expected until colony members approach a state of reproductive competence; then policing or other related mechanisms of reproductive competition might be evident in species with flexible development because nearly all individuals have the potential to differentiate into reproductive forms. Roisin (85) cites reports of intracolony mutilation in termopsids, kalotermitids, and some rhinotermitids and proposes that competition among late instar helpers, including nymphs attempting to become alates might explain such behaviors. He suggests that siblings bite wing pads, which causes some individuals to deflect from alate development, creating "lower status" helpers with reduced chances of future dispersal. Subsequent wing bud regeneration and formation of a normal alate is possible, but with delay and additional molts (107, 118). Roisin (85) proposes that the mutilated "losers" in intracolony conflicts formed the original helpers in termites. The contexts under which primitive termites lose wing buds need to be better understood before this hypothesis, or the implications of mutilation behaviors in termites, can be rigorously evaluated (107). For example, wing bud scars in termopsids are often due to self-induced abscission rather than mutilation by colony members (35, 107). Research on complete colonies of *Zootermopsis* in the laboratory suggests that self-abscission occurs when there are opportunities to become a replacement reproductive, perhaps inducing pre-alates to shed wing pads and differentiate into a neotenic in the natal colony (107).

DIVISION OF LABOR

The primary axis of division of labor in basal ant and termite species is reproductive, but colonies theoretically may partition tasks according to the size and age of subfertile or sterile individuals. Pheromones, temperature, and nutrition direct caste expression in both ants and termites (33, 71, 72). Historical factors, including development, cause ant and termite castes to form in fundamentally different ways and therefore potentially preadapt these two groups toward disparate mechanisms of task partitioning. In ants, morphological variation is generated through allometry within a single adult instar; size variation and polymorphism in termites is found across instars, from immature through imago. Although the caste systems of termites with true workers show a strong convergence with ants, similarities among basal species may be obscure because of the prevalence of monomorphism in ant workers. Due to hemimetabolous development, immature termites contribute to colony needs as juveniles, whereas ant larvae are seemingly unable to meet labor demands unless they are involved in food processing and nutrient distribution.

Basal ant species such as *Amblyopone pallipes* have small colonies, and activity is restricted to a limited number of nest chambers and associated tunnels where prey capture occurs (112). Workers, which hunt vermiform arthropod prey, initiate foraging soon after eclosion. Foraging and brood-care are codependent tasks because larvae are carried to freshly paralyzed prey where they feed directly. Brood-care is thus reminiscent of the direct provisioning habits of solitary wasps, and the same individual often performs both foraging and brood-care tasks. *A. pallipes* lacks age-based division of labor (111), but interspecific comparisons of polyethism in *Amblyopone* suggest that age-related division of labor might take on elements similar to that of higher ants (61), although the reasons for such differences are unclear. Colony demography, feeding specialization, and the retention of ancestral behavioral traits seem to be important determinants in division of labor in ants (40, 111, 113). The degree of sociality, which varies in ants, may also influence patterns of division of labor in *A. pallipes* and *N. macrops*, in which queen-worker and worker-worker interactions are rare and polyethism is lacking (40). In addition, some *Amblyopone* species are queenless but contain multiple inseminated gamergates that form dominance hierarchies (37), which could influence division of labor (84). Among basal ants, *Aneuretus simoni* exhibits an age-related polyethism that foreshadows the form of temporal task partitioning typical of ants of the higher subfamilies.

Like primitive ants, basal termopsid species have small colonies (35, 53), activity is limited to nest galleries, and there has been no indication of age-based division of labor (94). It has been hypothesized that termite caste systems should be fully discretized due to hemimetabolous development (79). Noirot (72, p. 9) notes that the combination of helpers of both sexes and hemimetaboly gives termites, in comparison to Hymenoptera, "many more possibilities for the diversification of polymorphism and consequently, for its adaptations." Termites may also advance, regress, or retard their metabolic development (71, 76, 87) to respond to colony needs or individual fitness initiatives. During its postembryonic development, an individual termite, especially in Termopsidae and Kalotermitidae, may "belong to different physical castes in succession" (72, p. 8), possibly terminating by becoming a soldier or reproductive. Noirot & Bordereau (74) termed this pattern *temporal polymorphism*, juxtaposed with *temporal polyethism*, or change in task functions of a worker during its lifetime, as is characteristic in Hymenoptera and derived termites (80, 123). Flexibility in metamorphosis in basal termite species might provide a mechanism of task switching similar to, but less rapid than, the patterns of behavioral acceleration and regression seen in more advanced species of the social Hymenoptera. The multiple age (instar) cohorts generated by hemimetaboly would divide tasks along a finely graded scale, resulting in the evolution of one caste per task (79). Yet if first and second instar larvae are inactive (94), gradual metamorphosis may in essence yield a caste distribution that resembles only moderate polymorphism, although the duration between molts would seemingly provide ample time for temporal specialization. In any case, the ergonomically adaptive nature of polyethism in basal termites is virtually unknown. There is some suggestion that demography serves a function in infection control (95).

Termite soldiers are without equivalent in Hymenoptera (72); basal ants have few allometric size variants such as majors and minors, with the exception of *Aneuretus simoni* (33, 113), although large workers, possessing a disproportionately large number of ovarioles, have been described in *Myrmecia* (39). Soldier termites appear to be monophyletic (71, 76). In Mastotermitidae and Hodotermitidae, soldiers have "continuous" polymorphism because they originate from successive and numerous worker instars (72). In Termopsidae and Kalotermitidae, all except the youngest larvae [termite terminology uses "larvae" to describe apteran immatures differentiating along a nonreproductive pathway (87, 109)], all nymphs (termites with wing pads), and all pseudergates can produce soldiers with a tendency toward a later origin, and therefore larger soldiers, in older colonies (71, 72). The first termite soldiers may have had functional gonads, as in extant *Archotermopsis* (35), but it is unknown whether soldiers appeared and were selected for as a defensive caste or as replacement or supplementary reproductives as in modern neotenic soldiers (64, 86, 107).

Single-piece nest species, such as the dampwood genus *Zootermopsis*, provide an opportunity to examine the significance of the spatial organization of tasks to the evolution of division of labor. Brood-care and foraging both occur within the same piece of wood; in ants and multiple-piece nesting termites the nursery and foraging are separated inside and outside of the nest. Maturing termite larvae are likely to eclose in the proximity of the primary reproductives and egg pile and could care for reproductives early in life and transition to nonbrood-care tasks such as nest maintenance and feeding at more distal sites before they develop into reproductive forms and leave the labor force. However, *Zootermopsis* seems to show no temporal polyethism (94); third through seventh instar larvae attend to tasks with no apparent bias.

Reproductive plasticity may also influence polyethism in Termopsidae (76). The ability of larvae to achieve reproductive status in the natal nest and potential conflicts with siblings could reduce selection for behavioral schedules that enhance colony-level fitness at the expense of individual reproductive success. The reproductive plasticity of lower termites could cause individuals to remain near the egg pile where they might deposit their own eggs or engage in oophagy, performing brood-care as they age, rather than providing labor at other work sites. West-Eberhard (121, 122) offered a similar argument concerning temporal polyethism in the social Hymenoptera, suggesting that worker reproduction should result in a brood-care bias toward newly eclosed adults that have functional ovaries. If reproductive competency in termites increases with age, older larvae could be predisposed to brood-care behavior or at least be spatially associated with brood in basal isopteran species. In any case, comparisons of polyethism among termite species indicate that worker sterility and temporal division of labor are correlated (94, 114). The loss of reproductive options among workers and foraging ecology of termites have been prerequisites for the evolution of termite polyethism. A comprehensive theory for the evolution of age-related division of labor in termites requires an understanding of how and when individuals can become reproductively competent and a species' foraging ecology.

FORAGING BIOLOGY

Striking variation is seen in the foraging biology of the basal ants; a spectrum of ancestral and derived habits has been documented (33). In some species, solitary huntresses search for arthropod prey in subterranean soil galleries and tunnels in decayed wood. In a manner reminiscent of their wasp ancestors, the sting injects paralytic venom into prey, which are subsequently transported to the nest. Feeding specialization and recruitment communication are diverse within and between genera in the tribe Amblyoponini. *Amblyopone pallipes*, for example, solitarily hunts prey such as geophilid centipedes, whereas other species may cooperate in prey capture and transport (36). Amblyoponine species, as well as species in more advanced ponerine tribes, may specialize on certain prey. *Prionopelta amabilis* workers, for example, feed exclusively on campodeid diplurans (33). Other basal ants such as *N. macrops* and *N. myrmecia* forage epigaeically as solitary individuals and use the sting to paralyze prey (31, 33). *A. simoni* workers also use the sting to subdue prey, but supplement their diet with carbohydrate foods such as decaying fruit, and have well-developed chemical trail communication (113).

The foraging ecology of basal termites, like basal ants, reflects the feeding habits of their solitary and subsocial ancestors. Termopsids are one-piece nesters (2, 53, 69), living in and consuming their host log. They do not forage away from the nest wood, and colonies do not leave one stump or log to occupy another. The galleries resulting from the consumption of their host wood become nest chambers, partitioned only by fecal pellet walls. The entire life cycle of most colony members transpires within a single piece of wood. Mature colonies produce fertile offspring (alates) seasonally, and many individuals within the colony differentiate into alates and disperse when resources in the nest wood are depleted (78).

Although termites prefer nutritionally valuable food sources that are low in secondary plant compounds (114), Termopsidae appear to have a limited array of mechanisms that could be implemented to harvest energetically rich cellulose sources. A choice mechanism exhibited by *Zootermopsis nevadensis* involves the foraging discrimination of colony-founding alates that settle on and defend nitrogen-rich wood cambium (53, 100). Whether workers in established colonies direct feeding at nutritionally rich sites in their nest log is unknown. If food selection occurs, it is likely regulated by secretions of the sternal gland, the source of trail pheromones in termites (114).

EVOLUTIONARY PATHOBIOLOGY

Many social insects nest and feed in soil and decayed-wood environments where diverse, abundant, and potentially pathenogenic microbial communities flourish. Group living may compound mortality risks through the interindividual transmission of infection (92). Adapting to disease has long been considered a major event in the evolution of sociality and the diversification of the ants (123), but only recently has the evolutionary significance of social insect pathobiology been the focus of empirical and theoretical investigation, primarily in Hymenoptera (24, 98, 99).

Ants have adapted to the constraints of living in infectious environments through the powerful antibiotic secretions of the metapleural gland (30, 33, 123). The metapleural gland is phylogenetically ancient, appearing in the extinct *Sphecomyrma* and found today in all ant subfamilies. Its evolution is considered to have been critically important to the ecological dominance of the ants (33, 123). Research on disease defenses in *Myrmecia* (58) suggests that the metapleural gland is highly significant but perhaps not the sole mechanism of infection control in basal species. Metapleural gland secretions alone, nevertheless, provide extraordinarily efficacious control of microbes.

Termites, like ants, nest and feed in areas where microbes thrive, and it is likely that pathogens have influenced their social biology. Termite life history traits (monogamy and long life span) as well as several characteristics of their host/pathogen relationships (likelihood of vertical and horizontal transmission among genetically related individuals, probability of prolonged contact with infection agents, and disease transfer through trophallactic exchanges) suggest that key aspects of termite biology could reflect adaptations to reduce pathogen virulence (19, 91). In basal isopteran species, disease resistance represents a confluence of the behavioral, physiological, and biochemical adaptations that characterized the solitary and/or presocial dictyopteran ancestors of termites and the newly adaptive mechanisms of infection control that accompanied their transition to eusociality. Although susceptibility to disease transmission was likely a cost of termite sociality, *Zootermopsis angusticollis* shows a number of infection-control adaptations such as allogrooming (92), colony demography (95), inducible humoral defenses (90), and the "social transfer" of immunocompetence (115). *Z. angusticollis* also communicates information about the presence of pathogens (90) and has antimicrobial exudates (92). In contrast to ants, termites appear to lack a metapleural gland equivalent (22), perhaps because the evolution of potent antimicrobial defenses was compromised by the need to protect their antibiotic-sensitive cellulose-digesting symbionts (92).

The life histories of primitive termites, which feature outbreeding by alates and inbreeding by offspring, may have in part allowed these insects to escape from or adapt to pathogens and lower disease risk (91). In contrast to the hypothesis that genetic similarity fosters the spread of disease in a colony (24), Lewis (54) proposed that pathogen and parasite avoidance, operating through the preferential association of relatives, could be a driving force for sociality. In this model, the spatial association of relatives and kin-directed altruism lowers the probability of infection by an unfamiliar pathogen, favoring reproduction of group members and the maintenance of its kin structure. In basal termites, the cycle of inbreeding by offspring is punctuated by the introduction of new genes through outbreeding, which may enhance disease resistance. Genetic studies on *Z. nevadensis* support alate outbreeding (102). In light of Lewis' model, inbreeding could also be considered as having a function in the avoidance of new and unfamiliar pathogens because it would favor the continued association of relatives. Based on the observation that primary reproductives of *Z. angusticollis* have significantly lower mortality when paired with sibling rather than distantly collected, nonsibling mates, outbreeding depression could occur if infections are transferred through social contact between males and females (93). Infections can be transferred socially between mates (91).

An alternative disease-related explanation for both outbreeding and inbreeding basal termites concerns selection for genetic variation and the maintenance of adaptive genotypes. Cycles of outbreeding by founding reproductives could infuse colonies with genotypes that vary in disease resistance. As colonies mature, coevolutionary interactions could result in selection of the most resistant host genotypes and/or the least virulent pathogens. Some individuals bearing these adapted genotypes may differentiate into inbreeding reproductives, thus maintaining the resistant trait in their offspring.

DISCUSSION

Insect social systems are shaped from the inertial, phylogenetic properties of species and their interaction with environmental forces. Despite the fundamental differences between Formicidae and Isoptera, such as ploidy and holo- versus hemimetaboly, formulating comparisons between basal taxa of these two diverse and entirely eusocial clades reveal commonalities and potentially constructive insights into their early eusocial evolution. This process is not as satisfying as examining evolutionary grades in a group containing a spectrum of solitary through eusocial species such as wasps or bees (123) or in a clade with recent and repeated evolution of eusociality such as halictid bees (15), but no alternative approach exists in extant ants and termites.

Here we attempt to understand the relative contribution and significance of phylogenetic history and ecology in the evolution of colony structure in ants and termites by examining their commonalties and divergences, restricting our analysis to those species that appear to most closely approximate nascent eusocial forms. In doing so we acknowledge the inference restrictions inherent in using extant taxa to reconstruct the social past and the limitations imposed upon comparisons of analogous systems, as well as confounding issues surrounding the existence of both primitive and derived traits in modern basal species. After careful consideration of these caveats, however, we remain confident that students of both isopteran and hymenopteran societies can mutually benefit from an understanding of the predispositions and ecologies that have guided social evolution in each group, and that our preliminary attempt at a synthesis of the two literatures will encourage productive discussion and collaboration.

Reproductive Structure and Division of Labor

For basal ant and termite species, we suggest that the reproductive organization of colonies and patterns of division of labor were affected by suites of ecological factors that operated at various stages of colony life histories. We identify nesting and feeding ecology as the environmental influences that impelled the adaptive modification of reproductive organization and division of labor in both groups. In basal ants and termites, the nest (including the colony it houses) represents a resource that provides nutrition, a structured environment to rear offspring, and a labor force. In termites with the most primitive social structure, the nest and the food source are the same piece of wood. In some basal ants the nest is a collection of gallery systems and chambers from which foraging excursions are conducted over short distances within restricted areas. The nutritional aspect of the ant nest lies in the quality of its foraging territory. Nest structure is the result of prior colony labor. The nest, in the broad sense including ant foraging territory, is thus a valuable resource. Opportunities to inherit the nest and colony may have been significant in the evolution of multiple reproductive forms and options in both taxa.

Ancestral ants likely foraged relatively close to the nest and had little if any polyethism because of the sequential unity of prey paralysis, transport, and direct provisioning of larvae (33, 111). Because of small colony size, relatively synchrous brood development cycles, and large prey size, foraging excursions may have been few in number, close to the nest, and within the confines of subterranean galleries or tunnels and crevices in decayed wood. Predation rates in species such as *Amblyopone* may be low in comparison to the higher ants, which have large colony size and forage epigaeically at greater distances from the nest. Our model assumes that *Amblyopone*, rather than *Nothomyrmecia*, represents a closer approximation to the biology of incipient eusocial ants. In basal termites the nest is the food source; in basal ants the distinction between nest and foraging territory is minor. The expansion of the diet, foraging away from the nest chamber, and increased colony size in termites is correlated with the evolution of a true worker caste and division of labor (3, 53). It is a reasonable hypothesis that spatial separation of nest and feeding territory and their unambiguous discrimination was also of significance in the evolution of social organization of ants. Together with nest structure, age-related changes in the reproductive physiology of helpers, predation, and decreased reproductive competition were likely interrelated and important determinants of polyethic task schedules and division of labor, although understanding the influence of these factors requires further detailed investigation. It is a challenge, for example, to explain why *Nothomyrmecia*, which forages away from the nest, shows no division of labor (40). Perhaps ancestral social states, including limited interaction and cooperation, were retained in this relict ant.

Serial Reproductive Inheritance by Kin

Similarities in reproductive structure found in some basal ants and termites are striking and potentially revealing. Recent genetic work on the primitive ant *N. macrops* suggests colony inheritance by daughters (97). Other basal ants such as *Myrmecia* and perhaps some *Amblyopone* have life histories in which family members, even helper family members in some cases, may become reproductives within the parental nest. These dynamics and the associated resource and inclusive fitness advantages of nest inheritance in ants have similarities with the developmental plasticity and colony inheritance characteristic of replacement (neotenic) reproductives in basal termites. The common feature of serial reproductive inheritance by kin means that all colony members gain enhanced inclusive fitness benefits, and some individuals acquire direct fitness advantages. These cumulative fitness components may well exceed average individual fitness prospects of dispersing, fertile offspring in a similar, solitary species, thus favoring helpers that remain in the natal colony.

The influence of potential reproductive opportunities on the evolution of helping behavior have long been recognized and are compounded by inheritance of resources and the fitness advantages of reproducing in the natal nest. West-Eberhard (120, p. 853) observed, "... Michener has long insisted that helping behavior without altruism can occur if male production by 'workers' ... is important enough (56). The significance of this argument has not generally been appreciated. Whether among relatives or not, as long as a female has "hope" of laying eggs—at least some small probability of future reproduction—her participation in the worker tasks can be viewed as possibly or partially an investment in her own reproductive future.... As long as a certain percentage of functional workers ultimately lays some eggs, then every worker—even those which never do lay eggs—can be considered 'hopeful' in the sense of having a certain probability of reproduction." The "hopeful reproductive" dynamic is influenced by colony size. As colony size increases, individual workers have a lower chance of becoming replacement reproductives (7). The most primitive ants and termites have small family sizes (33, 35), thus favoring opportunities for individual offspring to become reproductives.

Disease Risk, the Evolution of Resistance, and Social Organization

In ancestral ants, the problems that disease risk posed for coloniality may have been fully solved by one key innovation: the evolution of the metapleural gland in ancestral species. This gland is well developed in all basal ants studied to date (30, 33). In basal termites, the ability to control infection with powerful antibiotic secretions biochemically similar to those secreted by the ant metapleural gland was likely compromised by the need to maintain gut symbionts (92). In contrast to the chemical mode of infection control in ants, cycles of inbreeding and outbreeding in basal termites may have resulted in the selection and maintenance of disease-adapted genotypes. We note, however, that we do not identify disease as the sole factor influencing termite life cycles and acknowledge that other factors were also significant (101, 107). Nevertheless, the dispersal of reproductive forms from the parental nest and the colonization of new food source nest sites may have involved local adaptations to pathogens that were generated and preserved by outbreeding and inbreeding, respectively.

Conclusion and Prospects

In both ants and termites, eusociality was probably fostered by a suite of contributing factors and the interacting selective pressures that they generated. Haplodiploidy, maternal care, and female-biased sex ratios have favored the evolution of eusociality in Hymenoptera [reviewed in (33, 116)]. Kin-based explanations anchored by inclusive fitness pay-offs are also the premise of the nonmutually exclusive theories explaining the evolution of eusociality in the diploid-diploid Isoptera. These include cyclic inbreeding (66), shift in dependent care (67), intragroup conflict (85), disease resistance (92, 95, 115), and predispositions related to ecological and life history attributes that favored helping behavior and reproductive skew (101, 107).

In addition to expanded study of key primitive taxa, priority domains of future research on basal ants and termites center on further understanding their mating and reproductive biology. Specifically, topics should include: (*a*) determination of relatedness among mates and number of mates of individuals that inherit colonies (e.g., daughter queens of *Nothomyrmecia*, ergatogynes, gamergates, and termite neotenics); (*b*) study of fertility or subfertility of workers and soldiers in *Archotermopsis*; (*c*) investigation of the possibility of foreign reproductives joining an existing colony, either through immigration or fusion; (*d*) further research on the circumstances surrounding policing and mutilation, and their implications for reproductive conflict; and (*e*) detailed studies of the mechanisms and organization of division of labor. Expanded knowledge of these subjects/areas will provide a stronger foundation for resolving reproductive patterns and their fitness implications for reproductives and helpers, thus facilitating broader synthesis of patterns of evolution in ants, termites, and other eusocial animals.

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From: "Barbara Thorne" <bt24@umail.umd.edu>
To: <wenhua@etal.uri.edu>
Sent: Tuesday, January 28, 2003 1:43 PM
Subject: Hi Skip

Hi Skip,

Hope that you and Wenhua have had a pleasant fall and winter, and that wherever you are as I write this, it's a hell of a lot warmer than it is around here. When the weather gets dull and icy, I think of Guana Island, hence the motivation for this email.

My son continues to recover amazingly from the massive head injury he suffered in mid-September; the doctors can't believe it, but he's doing very well and if we can keep his head reasonably protected for another 8 months they think he'll be in the clear. Keeping a teenage boy away from sports and risk-taking is not easy, but we're trying to find a reasonable middle ground, and so far so good. We were super lucky.

I have every reason to expect that all of this will be behind me by next fall, and no matter what Hawthorne and Denno do or don't do, I would really like to come to Guana again, this time for a bit of applied termiting, with the focus on Heterotermes (those rascally creatures who mimic dry wood termites by diving into the structural beams in the ceiling beams and other critical timbers in the buildings on Guana and elsewhere in the BVI). They have been tough to treat because of their diffuse, subterranean nests, often hidden gallery system, and dislike of commercially available baits. Based on a brief trial that I did when I was there a couple of years ago, I've got a new bait that I think they won't be able to resist, and by October I think I can have a test version that will come impregnated with a not very nasty but highly effective insecticide (which would reach only termites because they would be the only beasts interested in consuming a cellulose-based bait).

So let me know what you think. I'd like to come for 10 days or so, and may well call on some of my contacts on other islands to see if we could also set up some trials on either Tortola or Virgin Gorda, or anywhere else willing to let us run an experimental treatment.

Back to braving the elements here -- sleet and ice expected for tonight - would like to catch the first flight south to the tropics!

Best wishes,
Barbara

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THE LARGE MOTHS OF GUANA ISLAND, BRITISH VIRGIN ISLANDS: A SURVEY OF EFFICIENT COLONIZERS (SPHINGIDAE, NOTODONTIDAE, NOCTUIDAE, ARCTIIDAE, GEOMETRIDAE, HYBLAEIDAE, COSSIDAE)

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> *"Good boys go to heaven, but the bad boys go everywhere"**
> Meatloaf 1993

ABSTRACT. An illustrated and annotated list of large moths of Guana, a 297 ha island located on the north side of the Caribbean island of Tortola, British Virgin Islands, is presented. Of the 148 species listed, 98 are distributed 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*, new species,** and ***Perigea gloria*, new species.** The following new synonyms and new combinations are recognized: *Leucania solita* Walker, **new synonym** [=*L. humidicola* Guenée]. *Kakopoda cincta* Smith, **new synonym** [=*K. progenies* (Guenée)]. *Drepanopalpia polycyma* Hampson, **new synonym** [=*D. lunifera* (Butler), **new combination**]. *Sphacelodes fusilineatus* Walker, **revised status,** *Idaea fernaria* (Schaus), **new combination,** *Ptychopoda curtaria* Warren, **new synonym** [=*Idaea minuta* (Schaus)]. *Pterocypha defensata* Walker, **revised status,** is recognized as the senior synonym of *P. floridata* (Walker), **new synonym,** reversing a recently published synonymy. A new genus, *Catabenoides* Poole, **new genus,** type-species: *Laphygma citrina* Walker, is described in an appendix, including *C. dubia* (Herrich-Schäffer), **new combination,** *C. seorsa* (Todd), **new combination,** and *C. terens* (Walker), **new combination,** all by Robert W. Poole. The palatability to birds of two species, *Diphthera festiva* and *Calidota strigosa*, was observed and the species were shown to be distasteful.

Additional key words: Caribbean, West Indies, biogeography, taxonomy, palatability.

Guana is a small island on the north side of Tortola in the British Virgin Islands (18°28'N, 64°35'W) (Fig. 1). While it is small, only 297 ha, and the maximum elevation is 266 m, it supports a relatively rich vegetation and has sustained less damage by feral animals and humans than have many adjacent islands (Lazell 1996). It has most of the floristic associations of the larger Virgin Islands, with the notable exception of the "aridulate rain forest" of Tortola (D'Arcy 1967). Despite its small size, Guana has a diverse insect fauna (Davies & Smith 1997). For example, Guana has 31 species of butterflies (Becker & Miller 1992), compared to the larger islands of Anegada (3872 ha) (Smith et al. 1991) with 24 species and Tortola (5444 ha) with 31 species, and St. Thomas (7660 ha) with 32 species (Miller 1994). Alminas et al. (1994) review the geographical setting of the Virgin Islands.

This is the first survey of the moth fauna of this island. John F. G. Clarke was on Guana briefly in 1956 and 1958 (see Schmitt 1959), but was unable to collect at lights there. Most of the species reported herein are known from Puerto Rico (e.g., Forbes 1930, 1931, Schaus 1940, Wolcott 1951), but most have not been recorded from the British Virgin Islands due to lack of previous sampling. The faunal similarity to Puerto Rico is expected, given that the principal islands of the Virgin Islands (except Saint Croix) lost their connection with each other and with Puerto Rico only about 8000 to 10,000 years ago, due to eustatic rise in sea level (Heatwole et al. 1981). Only scattered records exist in the literature for moths of the Virgin Islands, with two of the longest lists being Beatty (1948) for St. Croix and Greenwood and Greenwood (1971) for Peter Island.

We are treating the Lepidoptera of Guana Island in parts. Becker and Miller (1992) reported 31 species of butterflies. The present paper reports 148 species of large moths (Macrolepidoptera, including the unrelated Cossidae and Hyblaeidae for convenience), represented by 1390 specimens. The manuscript was prepared using the classification of Noctuidae by Poole (1989), before extensive recent changes in higher classification of Lepidoptera (Kristensen 1998, Holloway et al. 2001). Future papers will treat Pyraloidea and Microlepidoptera.

The moth fauna of Guana is composed primarily of species with wide distributions in the New World tropics (Table 1). Of the 148 species listed, 50 are endemic to the Caribbean Islands, many of them reaching the

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*We often pejoratively regard widespread species as "weed species" or "pests". Parodying the citation above, "Bad" species go everywhere, "good" species [may] go to Heaven [extinct]. But is it fair to consider them bad simply because they are able to get everywhere? Perhaps "efficient colonizers" is a better term?

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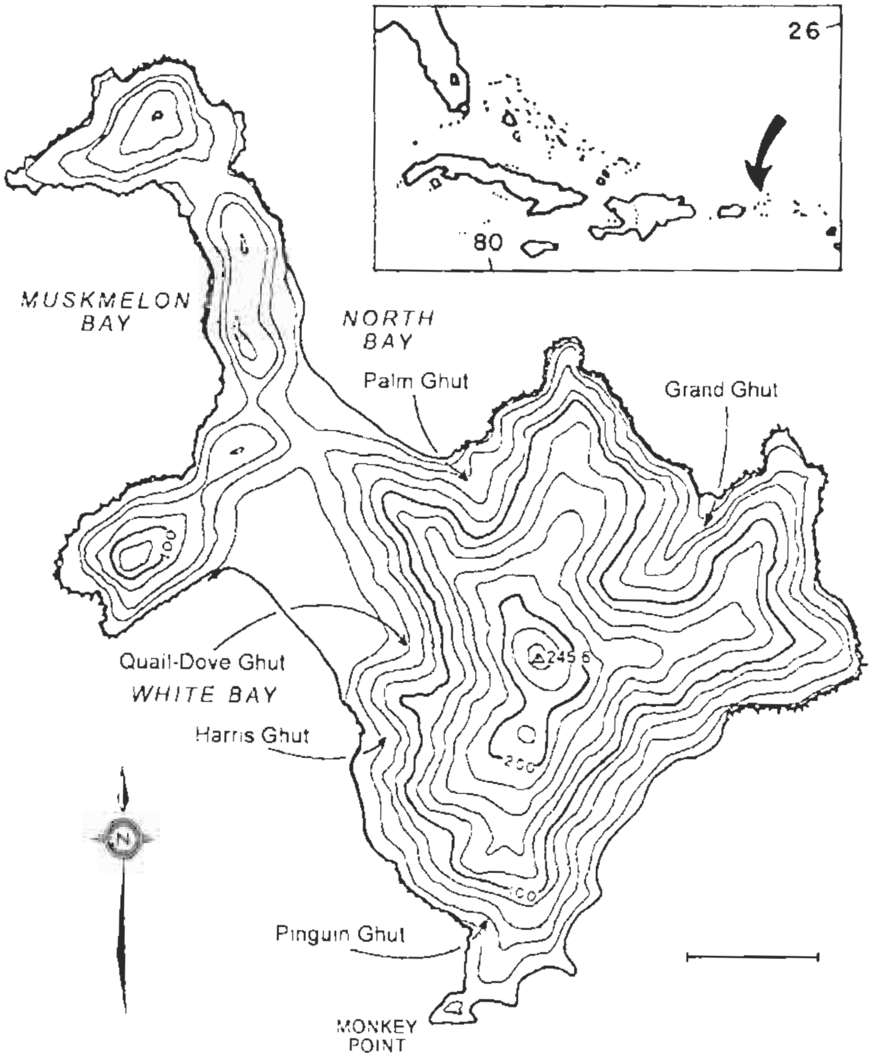


FIG. 1. Map of Guana Island. Contours are 20 m. Bar, bottom right, is 400 m. Inset shows the position of the Virgin Islands in the Antilles.

Florida Peninsula, and only nine apparently are restricted to the Puerto Rican Bank. These proportions, however, are not the same for the different families. The highest degree of endemism occurs in the Geometridae and Arctiidae, whereas the lowest occurs in the Sphingidae. This is presumably because of the powerful flying capacity of sphingids, while geometrids and arctiids are clumsy flyers.

Holloway and Nielsen (1998, following Ferguson et al. 1991) presented a chart of 12 moth genera that are widely recorded from remote islands worldwide. Of these, nine genera (including 20 species) are present on Guana (counting *Leucania* as *Mythimna*). It is likely that the remaining three genera, especially *Agrotis*, may be found on Guana in the future. Many of the species whose ranges include the southern United States (especially Sphingidae) also occur as vagrants in the Northeast United States and into Canada (e.g., Forbes 1954, 1960). Species recorded from the Galapagos Islands by Hayes (1975) are noted as indication of their dispersal ability (note that none of the Geometridae recorded from Galapagos are also known from Guana).

MATERIALS AND METHODS

The material upon which this list is based was collected in July 1984 and 1985 (by S. E. Miller & P. M. Miller), July 1986 (S. E. Miller & M. G. Pogue), July 1987 (S. E. Miller & V. O. Becker), July 1988 (S. E. Miller & C. O'Connell), October 1989 (V. O. Becker), and October–November 1990 (S. E. Miller & T. M. Kuklenski). Collections from 1984–1986 are deposited

TABLE 1. Geographic range of the species of moths collected at Guana Island.

Family	Number of species			
	Neotropical*	Antilles	Puerto Rican Bank	Total
Sphingidae	20	2	0	22
Notodontidae	1	0	0	1
Noctuidae	63	16	3	82
Arctiidae	6	5	4	15
Geometridae	6	18	2	26
Hyblaeidae	1	0	0	1
Cossidae	1	0	0	1
Total	98	41	9	148

* Includes Cosmopolitan and Pantropical species.

at the National Museum of Natural History (USNM), Washington, those of 1987–1990 are split between first author (VOB), Bishop Museum, Hawaii (BPBM), and USNM. The largest collections were made by both authors 9–23 July 1987, with over 2200 specimens representing about 300 morphospecies, and by the first author in October 1989, with over 2000 specimens representing over 350 morphospecies.

The list of species by family collected during the 1989 trip (Table 2) gives an impression of the overall fauna, especially the diversity of Microlepidoptera, still under study. Of the 359 species recorded, 243 species (two thirds) are Microlepidoptera and pyraloids, and 163 (nearly one half) are pyraloids and gelechioids.

The number of specimens listed in this work under each species does not reflect relative abundance, as our objective was only to list the species occurring on the island. Therefore, in the case of species that are common in other parts of the neotropics only one or a few specimens were collected to voucher the record, independent of their abundance. In contrast, in the case of endemic or rare species, usually all specimens were caught.

The results obtained by the first author during the 1989 trip were a surprise, as it was made 20–40 days after Hurricane Hugo had devastated the island on 18 September. The damage was still evident: all buildings without roofs and without most of their doors and windows, and fallen trees and torn branches scattered all over the island. According to people who were on the island the day Hugo hit, not a single leaf remained on the trees. At the time of arrival (9 October) the island was completely green again. That same night the collecting was fantastic, as were most nights during the next 20 days. Not only the quantity, but also the quality of the material was impressive. It seemed that all specimens had emerged that day. Certainly all caterpillars that had reached development had to pupate immediately after the hurricane, and they were all emerging together. Leaf mines were also abundant. As these tiny species usually have shorter life cycles, they had time to emerge and lay eggs in the 20 days that preceded the field work. Torres (1992) documented the impact of Hurricane Hugo on Lepidoptera populations on Puerto Rico.

TABLE 2. Moth species collected on Guana Island between 10 and 20 October 1989.

Family	Number of species
Sphingidae	10
Notodontidae	1
Noctuidae	69
Arctiidae	12
Geometridae	24
Hyblaeidae	1
Crambidae	51
Pyralidae	36
Pterophoridae	4
Oecophoridae	2
Blastobasidae	13
Gelechiidae	45
Scythrididae	1
Cosmopterigidae	15
Psychidae	1
Tineidae	35
Gracillariidae	13
Yponomeutidae	1
Argyresthiidae	1
Heliodinidae	2
Choreutidae	1
Cossidae	1
Tortricidae	19
Opostegidae	1
Total	359

A synoptic collection, containing at least one specimen representing each form, was taken to the Smithsonian Institution (USNM), Cornell University (CU), and most importantly, to the Natural History Museum (BMNH), London, by the first author. The list below is a result of the identifications made by comparing this synoptic collection with identified material, especially type specimens (including important voucher specimens and types from Forbes 1930, 1931, Schaus 1940). The first author has compiled a synonymic list of Antillean Lepidoptera (Becker in prep.), which has provided further taxonomic background.

This report is aimed not only at lepidopterists, but also at biologists and students interested in the fauna of the Virgin Islands. For this reason we give a brief synopsis of each species to provide a context and to suggest what kind of observations should be undertaken. Information on each species is provided under the following headings: ID: Diagnostic characters allowing identification of the species in the context of the other species know from Guana Island; DIST: General distribution of the species, as represented in the literature and VOB and USNM collections; GUANA: The Guana Island specimens seen by us in preparing the manuscript (see the introduction for the dates sampled each year); BIO: Known host records, sometimes including notes on immature stages; COM: Any other comments.

SPECIES ACCOUNTS

SPHINGIDAE

Eighty five species of sphingids have been recorded from the Antilles (Becker in prep.), 22 (25%) of them were collected by us in Guana. Color illustrations of adults can be found in Hodges (1971) and D'Abrera (1986); color illustrations of larvae can be found in Moss (1912, 1920).

Sphinginae

Agrius cingulatus (Fabricius, 1775)
(Sweetpotato hornworm, Pink spotted hawk moth)

ID: Separated from other hawk moths by the pink dots on the abdomen.
DIST: United States south to Argentina, including Galapagos.
GUANA: 1 specimen, 1989.
BIO: The variable larvae (green to dark brown) feed on various plants belonging to Convolvulaceae, including sweet potato.

Cocytius antaeus (Drury, 1773)
(Giant sphinx)

ID: Distinguished from other sphingids on the island by the dark green wings and three pairs of yellow dots on the abdomen.
DIST: Southern United States to Argentina; not in Galapagos.
GUANA: 1 specimen, 1989.
BIO: Green larvae feed on various *Annona* species (Annonaceae) such as custard apple.

Manduca sexta (Linnaeus, 1763)
(Tobacco hornworm, Carolina sphinx)

ID: Distinguished from other sphingids on the island by the gray wings and six pairs of yellow dots on the abdomen.
DIST: Widespread in the New World, including Galapagos.
GUANA: 5 specimens, 1984, 1988, 1989.
BIO: Pest of cultivated solanaceous plants, such as tobacco, tomato, potato, etc. Mature larvae are green-yellow with seven pairs of white lateral bands, and red anal horn.

Manduca rustica (Fabricius, 1775)
(Rustic sphinx)

ID: Distinguished from other sphinx moths on the island by the dark grayish-brown forewing with transverse grayish-white waving bands, and three pairs of yellow dots on the abdomen.
DIST: Widespread New World species, present in Galapagos.
GUANA: 2 specimens, 1984, 1989.
BIO: Larva is greenish-gray, distinguished by its small white nodules on the thoracic segments, mainly on dorsum. They feed on various species of Bignoniaceae, Verbenaceae and Boraginaceae (Hodges 1971).

Manduca brontes (Drury, 1773)

ID: Distinguished from other species in the genus occurring on the island by the absence of yellow dots on the abdomen.
DIST: Antillean species occurring northward to Central Florida.
GUANA: 1 specimen, 1989.
BIO: The larva is similar to that of the tobacco hornworm but feeds on *Tecoma* (Bignoniaceae) (Hodges 1971).

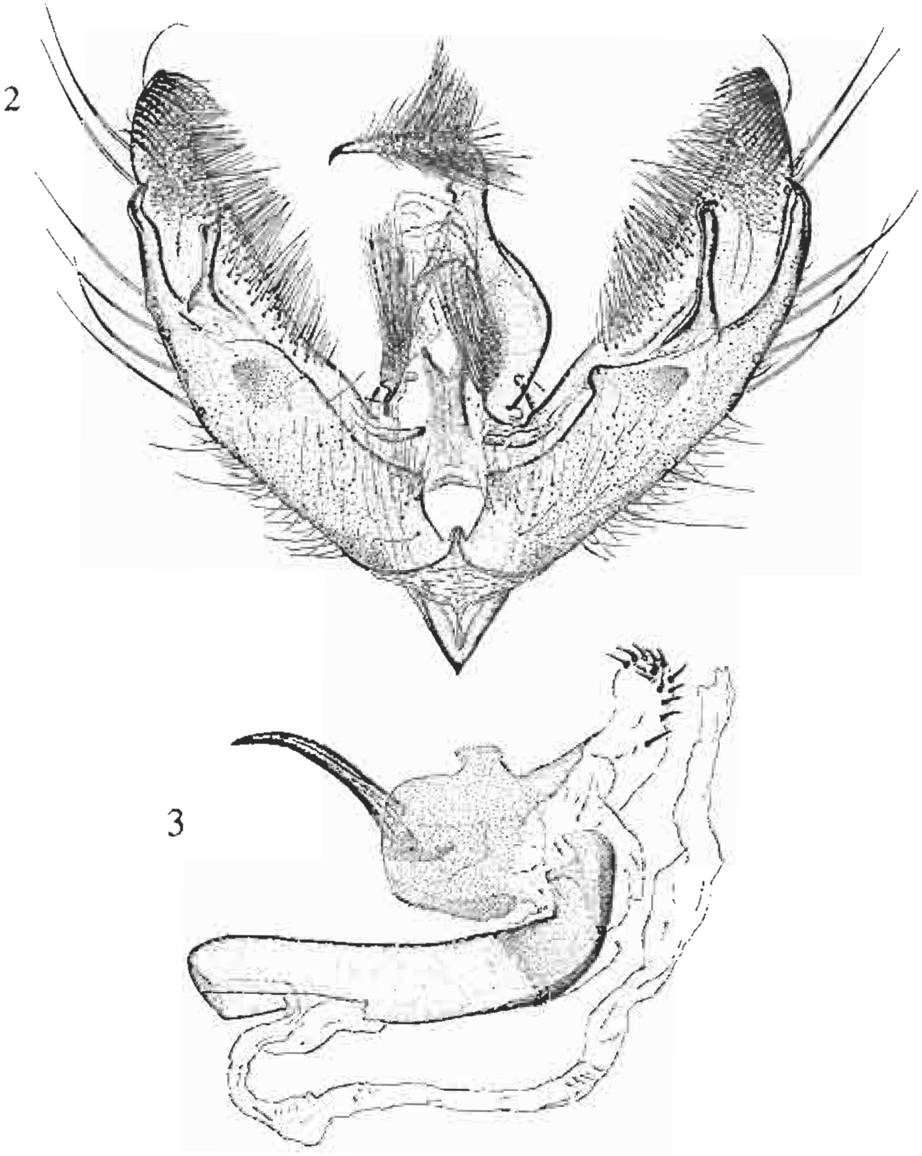
Macroglossinae

Pseudosphinx tetrio (Linnaeus, 1771)
(Frangipani hornworm)

ID: The largest sphinx on the island; pale gray with irregular darker markings.
DIST: United States throughout the Antilles to Argentina.
GUANA: 7 specimens, 1988, 1990.
BIO: The conspicuous bright caterpillars—banded black and yellow with reddish brown head and orange legs—are frequently seen defoliating frangipani (*Plumeria* spp., Apocynaceae) on the island.

Erinnyis alope (Drury, 1773)
(Papaya hornworm)

ID: Distinguished from other sphingids on the island by the combination of yellow basal half of hindwing and alternate pairs of light gray and black dots on the abdomen.
DIST: Widespread in the New World, including the Galapagos.
GUANA: 1 specimen, 1989.
BIO: Larvae on a variety of plants with milky sap, such as papaya (*Carica papaya* L., Caricaceae), *Jatropha* (Euphorbiaceae), and *Alamanda* (Apocynaceae).



FIGS. 2–3. Genitalia of *Catabenoides terminellus*. 2, male, ventral view, aedeagus removed; 3, aedeagus, lateral view.

Erinnyis ello (Linnaeus, 1758)
(Cassava hornworm)

ID: Sexually dimorphic. Male forewing dark gray with a blackish irregular band along the wing from near base to apex. Female forewing light gray with almost no markings. Abdomen with pairs of alternate light gray and black dots dorsally.
DIST: The most common species of the genus in tropical America; also in Galapagos.
GUANA: 5 specimens, 1984, 1990.
BIO: Larvae varying in color from yellowish to green and to brownish have been serious pests of cassava (*Manihot*) in tropical America; feeds on various Euphorbiaceae.

Erinnyis crameri (Schaus, 1898)

ID: Forewing more brownish than those of *E. ello*; basal area reddish brown and abdomen with indistinct markings.
DIST: Southern United States, through the Caribbean south to Brazil.
GUANA: 1 specimen, 1989.
BIO: Grayish brown larva, figured by Moss (1920: pl. 7, figs. 3a, b), has been reared on various members of the Apocynaceae (Hodges 1971).

Erinnyis domingonis (Butler, 1875)

ID: Same size as *E. obscura* (see below) but forewing mostly dark gray.

DIST: Same as *E. obscura*, except for Galapagos.
GUANA: 2 specimens, 1987.
BIO: Unknown.
COM: It is very likely that *E. obscura* and *E. domingonis* are only forms of the same species (Hodges 1971:102, Kitching and Cadiou 2000: note 162). This could be verified by rearing.

Erinnyis obscura (Fabricius, 1775)

ID: Similar to *E. ello*, which is also dimorphic, but easily distinguished by its smaller size and absence of dots on abdomen.
DIST: Southern United States throughout the Caribbean south to Brazil, including Galapagos.
GUANA: 4 specimens, 1984, 1987.
BIO: The pale yellowish or pale green larvae have been reared on various milk plants such as *Philibertia* and *Cynanchum* (Asclepiadaceae).

Pachylia ficus (Linnaeus, 1758)
(Large fig hornworm)

ID: Large, dull brown with stout body, quite distinct from other sphingids on the island. Easily recognized by the pale, inverted trapezoidal mark on costa near apex.
DIST: Widespread throughout the New World, but absent from Galapagos.
GUANA: 1 specimen, 1987.
BIO: Moss (1912) figured in color the several forms of the caterpillars, which feed on various species of *Ficus* (Moraceae). Some are green, banded yellow dorsally, while the others are gray brown ventrally and orange, banded black, dorsally.

Callionima falcifera (Gehlen, 1943)

ID: Recognized by the orange brown color and the metallic silvery mark near center of forewing.
DIST: Southern United States to Argentina.
GUANA: 4 specimens, 1987, 1990.
BIO: Unknown. Other species in the genus have been reared on some apocynaceous plants (Hodges 1971).
COM: Similar to, and frequently confused with, *C. parce* (Fabricius) (Kitching and Cadiou 2000: note 91). The specimen illustrated as *C. parce* in Hodges (1971: pl. 10, fig. 8) represents this species.

Perigonia lusca (Fabricius, 1777)

ID: Medium size dull brown sphinx, recognized by the bright orange area along the middle of hindwing.
DIST: Southern Florida to Argentina.
GUANA: 27 specimens, 1987, 1988, 1989, 1990.
BIO: Bluish green larva, figured in color by Moss (1912), was reared by him on coffee (Rubiaceae). Recorded from *Gonzalagunia spicata* (Lam.) Maza and other Rubiaceae in Puerto Rico by Torres (1992).
COM: Kitching and Cadiou (2000: note 448) review names associated with *P. lusca*.

Enyo lugubris (Linnaeus, 1771)

ID: Medium size, dark brown; distinguished from other hawk moths on the island by the dentate borders of both wings.
DIST: Southern United States, throughout the Antilles, south to Uruguay and Argentina, including Galapagos.
GUANA: 3 specimens, 1987, 1989.
BIO: Larvae on *Ampelopsis* spp., *Cissus* spp., and *Vitis* spp. (Vitaceae) (Hodges 1971).

Aellopos tantalus (Linnaeus, 1758)

ID: Small, dark gray, diurnal, sphinx moth distinguished by the conspicuous white bar across base of abdomen.
DIST: New York south to Argentina.
GUANA: One specimen captured in a Malaise trap, 1990.
BIO: Larvae on *Ixora venulosa* Benth. (Rubiaceae) (Biezanko et al. 1949).

Eumorpha vitis (Linnaeus, 1758)
(Vine sphinx)

ID: Forewing dark green crossed with grayish bands and dashes, and hindwing with anal margin pink. A beautiful and showy species.
DIST: United States throughout the Caribbean to Argentina (not in Galapagos).
GUANA: 2 specimens, 1987, 1990.
BIO: The larvae vary in color: some are dark pink, others are pale green or yellow green (Moss 1912). They feed on grape leaves (*Vitis* spp.).

Cautethia noctuiformis (Walker, 1856)

ID: The smallest sphingid in the New World, with a wing span slightly over 3 cm. Gray, with basal half of hindwing orange yellow.
DIST: Caribbean.
GUANA: 166 specimens, 1984, 1986, 1987, 1988, 1989, 1990.
BIO: Unknown, but larvae of *C. grotei* have been reared on *Chiococca alba* (L.) Hitch. (Rubiaceae) (Hodges 1971).
COM: Kitching and Cadiou (2000: note 96) discuss the taxonomy and place the Guana population in the subspecies *C. noctuiformis bredini* Cary, 1970.

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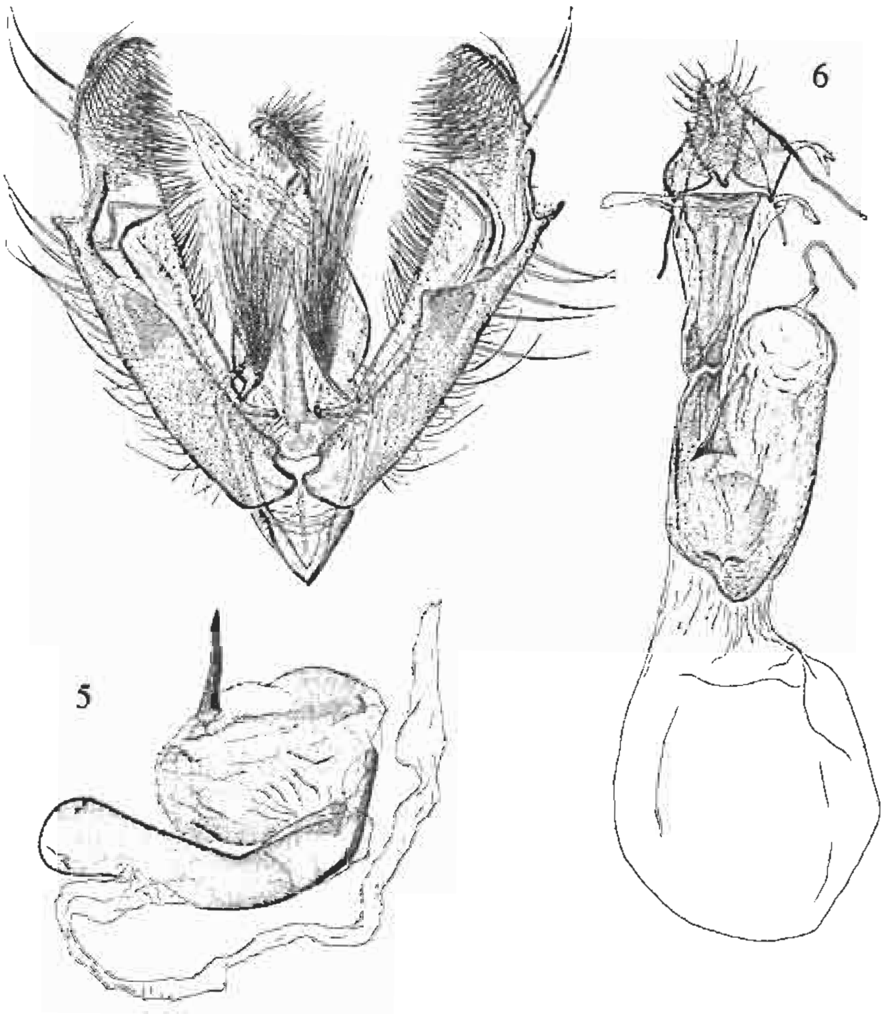


FIGS. 4–6. Genitalia of ***Catabenoides lazelli*, new species**. 4, male, ventral view, aedeagus removed; 5, aedeagus, lateral view; 6, female, ventral view.

Xylophanes chiron (Drury, 1770)

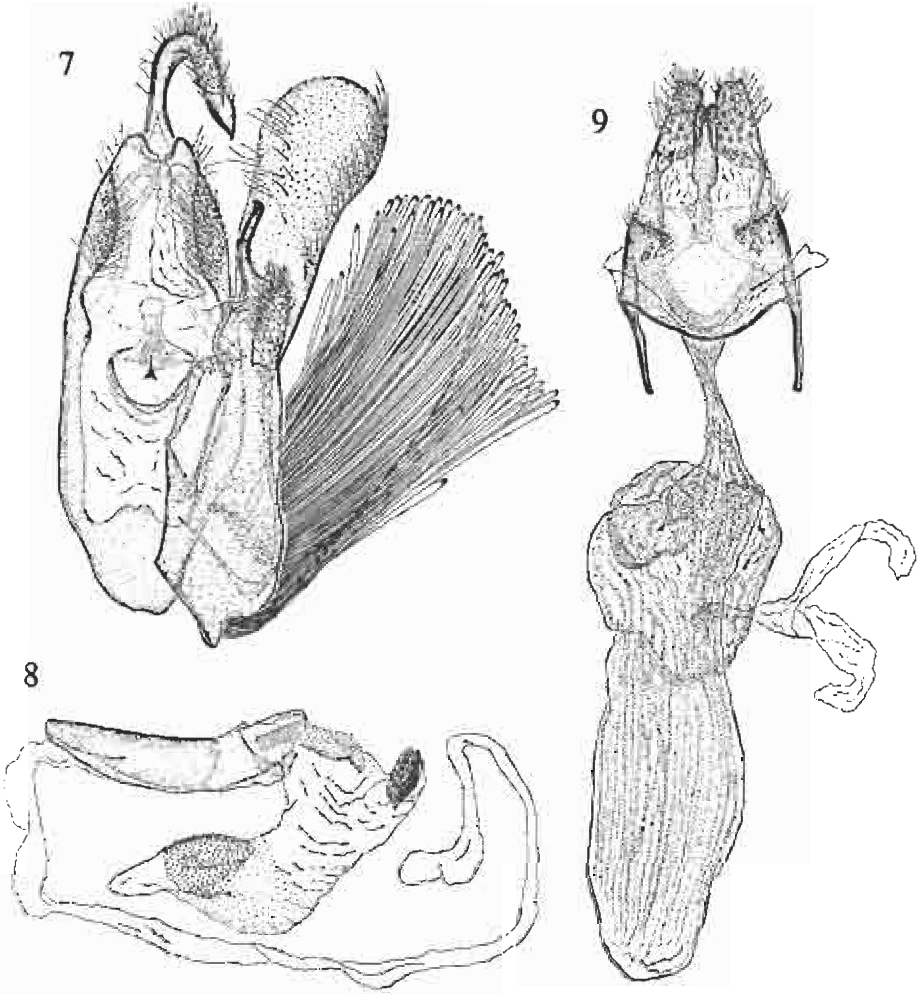
ID: Green with an oblique grayish brown irregular band on the forewing looking like a leaf with dead areas.
DIST: Mexico, throughout the Antilles to Argentina.
GUANA: 1 specimen, 1987.
BIO: The showy caterpillar, illustrated in color by Moss (1920: pl. 8, figs. 6a–f), was reared by him on *Palicourea*, *Psychotria*, and *Spermacoce* (Rubiaceae). They are glossy green, bearing pairs of red or white red-ringed eye spots on the first two abdominal segments.

Xylophanes pluto (Fabricius, 1777)

ID: Green with irregular transverse light and dark bands. Recognizable by the wide orange band on the hindwing.
DIST: Southern United States to Brazil.
GUANA: 8 specimens, 1987, 1988, 1989, 1990.
BIO: Torres (2000) described larvae from Puerto Rico, reared from *Hamelia patens* Jacq. (Rubiaceae). Gundlach (1881), mentioned by Hodges (1971), also described the larvae, which are of two color forms: one is basically green, the other is black, dark violet and red. Gundlach (1881) recorded the hosts as *Chiococca* (Rubiaceae) and *Erythroxylum* (Erythroxylaceae).

Xylophanes tersa (Linnaeus, 1771)

ID: Distinguished from its congeners on the island by the pale greenish gray forewing with several ill-defined, nearly parallel, longitudinal lines, running from base to apex; hindwing black with pale yellow marks in the vein interspaces parallel to the external margin.
DIST: Ontario, across the Antilles down to Argentina, including Galapagos.
GUANA: 4 specimens, 1986, 1987, 1989.



FIGS. 7–9. Genitalia of ***Perigea gloria*, new species**. 7, male genitalia, ventral view; aedeagus removed; 8, aedeagus, lateral view; 9, female genitalia, ventral view.

BIO: The larvae, beautifully illustrated by Moss (1912: pl. 14, figs. n–q), are yellowish brown with a pair of eye spots laterally on abdominal segments 1–7. The larvae feed on *Psychotria berteriana* DC, *Borreria verticillata* (L.) Meyer and *Diodia sarmentosa* Sw. (Rubiaceae) in Puerto Rico (Torres 1992).

Hyles lineata (Fabricius, 1775)
(White-lined sphinx)

ID: Resembles *E. vitis*, but is distinguished by its smaller size, shorter, clubbed antennae, and single wide fascia running from near base of dorsum to apex of forewing, crossed by whitish lines following the veins.
DIST: This powerful flyer, almost diurnal, has reached all continents, as well as remote islands such as Galapagos and Hawaii.
GUANA: 1 specimen, 1988.
BIO: Polyphagous. Most commonly used plants are species of *Portulaca* (Portulacaceae), but includes others such as *Fuchsia* (Onagraceae), *Boerhavia* and *Mirabilis* (Nyctaginaceae), *Xantium* (Asteraceae), and others. Larvae are highly variable in coloration and somewhat in maculation. Some specimens basically are black with a pattern of yellow; others are mainly yellow with some black pattern (Hodges 1971).

NOTODONTIDAE

Nystalea nyseus (Cramer, 1775)
(Fig. 15)

ID: Narrow winged, light gray, mottled with dark brown and black scales; recognized by the long scales on the base of antennae that forms a crest on top of the head when resting.
DIST: Mexico, throughout the Caribbean south to Brazil.
GUANA: 3 specimens, 1989.

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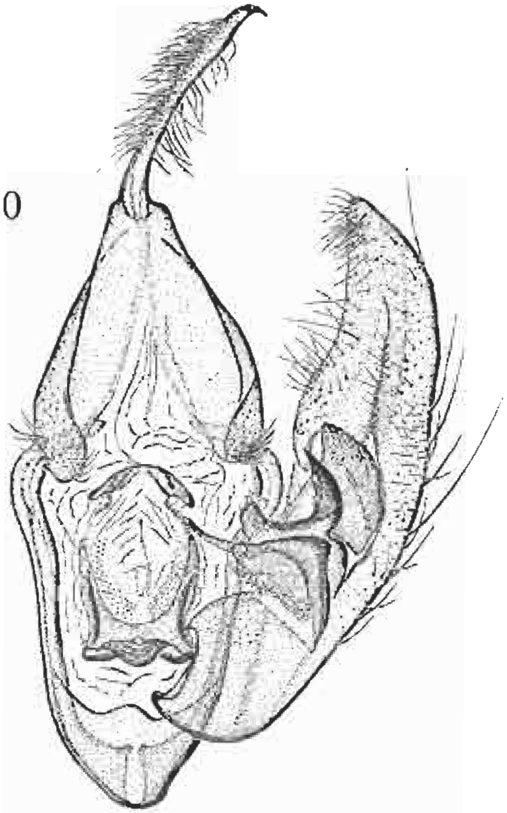

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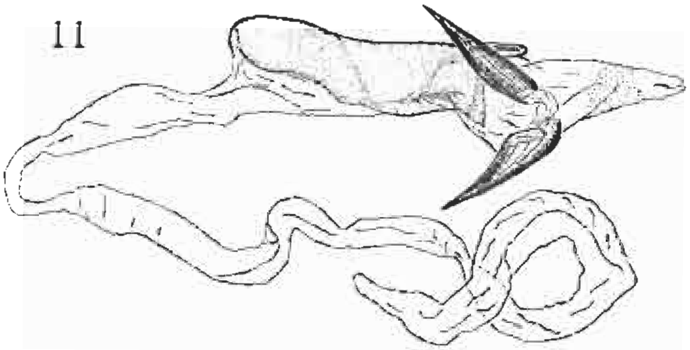


FIGS. 10, 11. Male genitalia of *Anaticimum affabilis*. 10, ventral view, left valva and aedeagus removed; 11, aedeagus, lateral view.

BIO: Larvae feed on various Myrtaceae especially on species of *Psidium* (Todd 1973:271).

COM: This is the only notodontid present on the island; less than 30 species have been recorded from the Antilles (Becker in prep.). Notodontidae typically occur in moister forests.

NOCTUIDAE

Heliothinae

Heliothis subflexa (Guenée, 1852)

(Fig. 16)

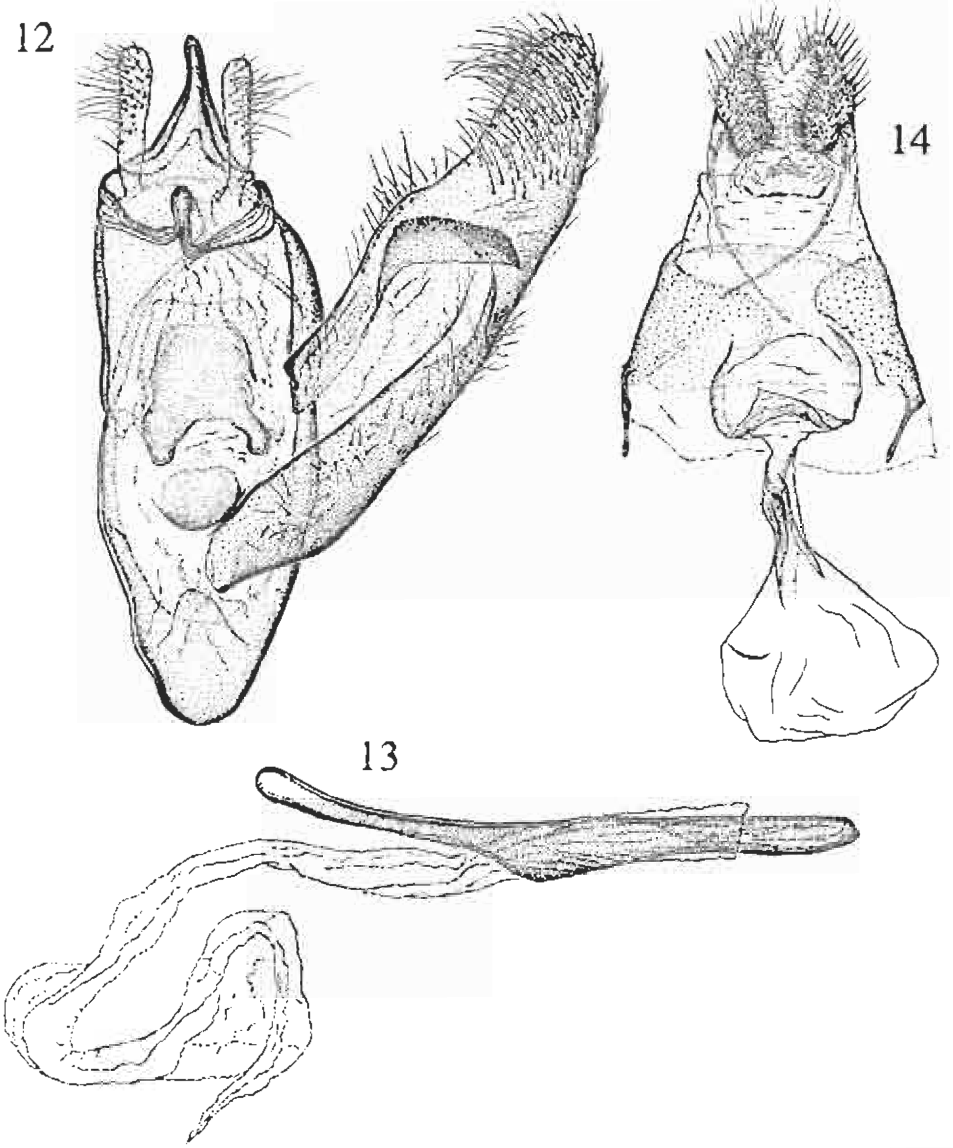
ID: Medium sized, pale olive green; forewing crossed with three olive bands, edged pale basad.

DIST: North America, throughout the Antilles, south to Argentina.

GUANA: 2 males, 1989.

BIO: Larvae on *Solanum nigrum* L., *Physalis* spp. (Solanaceae) (Poole et al. 1993).

COM: Easily confused with the tobacco budworm, *H. virescens* (Fabricius), not collected but certainly occurring on the island. Male *H. subflexa* have white hindwing, while in *H. virescens* they are bordered olive-gray. More details on both species can be found in Poole et al. (1993). Haile et al. (1975) discuss movement of *Heliothis* spp. among the Virgin Islands.



FIGS. 12–14. Genitalia of *Eucoma simplaria*. 12, male, ventral view, left valva and aedeagus removed; 13, aedeagus, lateral view; 14, female, ventral view

Noctuinae

Anicla infecta (Ochsenheimer, 1816)
(Fig. 17)

ID: Gray, with forewing reddish brown along external margin; hindwing hyaline. Recognized by blackish anterior border (patagia) of thorax.
DIST: Argentina through Central United States, including Galapagos and Bermuda.
GUANA: 6 specimens, 1986, 1989, 1990.
BIO: General feeder, cut worm. The larvae reach nearly 3 cm when fully grown. They are variable in color from gray to yellowish ferrugineous, olivaceous yellow and bright green, to a sordid brown, usually flecked with black.
COM: At least three other cut worms should be present in the island: *Agrotis ipsilon* (Hufnagel), *A. subterranea* (Fabricius) and *Peridroma saucia* (Hübner).

Hadeninae

Leucania humidicola Guenée, 1852
(Fig. 19)

ID: Medium sized, pale moth. Distinguished from other noctuids on the island by its forewing pattern: a long dark dash delimited above by a white line, running from base to middle.
DIST: Antilles to Brazil and probably Galapagos; the limits of the distribution of the species remain to be determined (Adams 2001).

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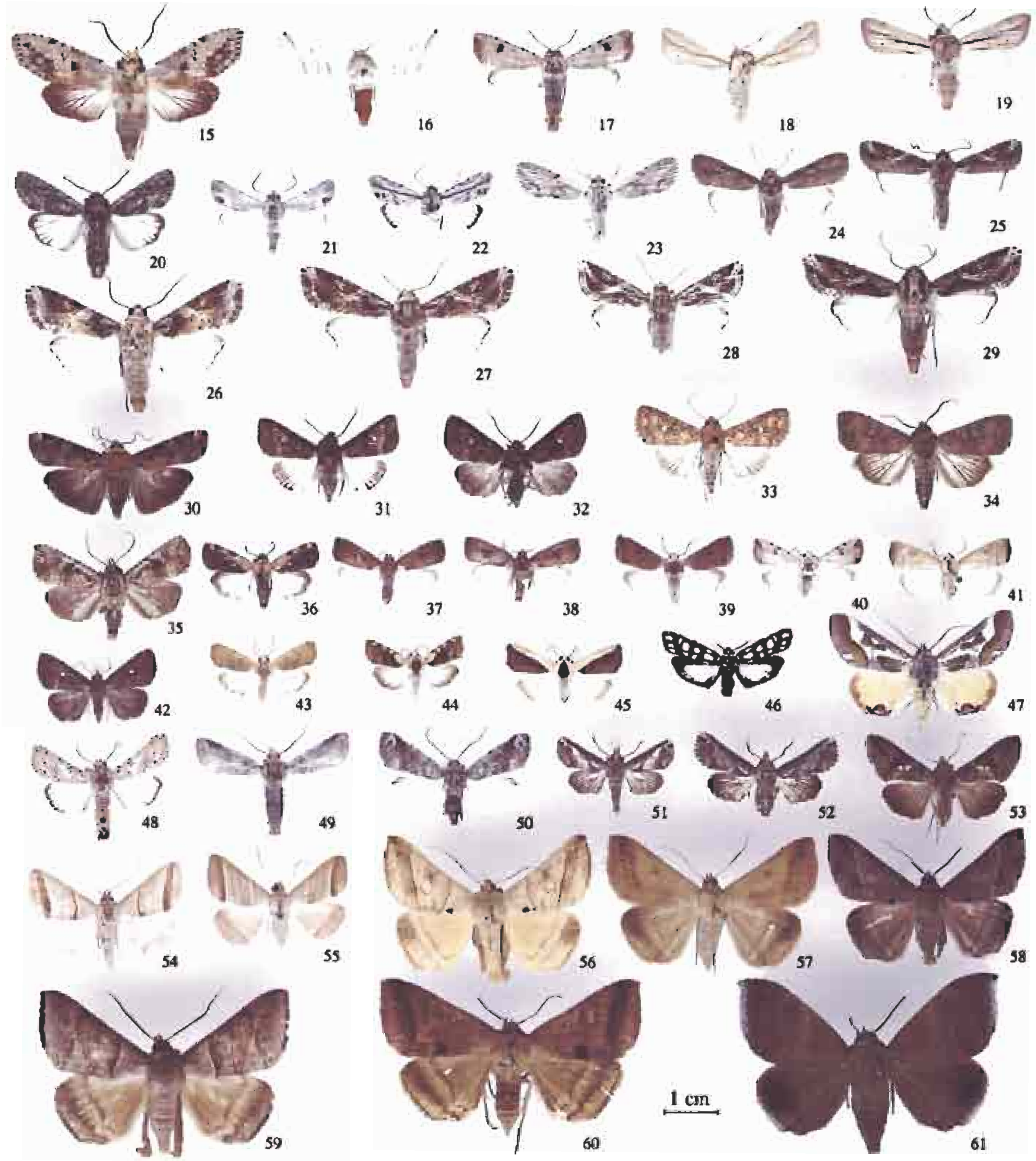


FIGS. 15–61. Natural size (1:1). Notodontidae (15) and Noctuidae (16–61) (species from Guana, unless stated otherwise). **15,** *Nystalea nyseus*, male; **16,** *Heliothis subflexa*, male (USA); **17,** *Anicla infecta*, male; **18,** *Leucania dorsalis*, female (Cuba); **19,** *L. humidicola*, male; **20,** *Neogalea sunia*, male; **21,** *Catabenoides lazelli*, holotype male; **22,** *C. terminellus*, female; **23,** *Spodoptera albulum*, male; **24,** *S. frugiperda*, female (Puerto Rico); **25,** *S. frugiperda*, male (Brazil); **26,** *S. latifascia*, male; **27,** *S. latifascia*, female (Cuba); **28,** *S. pulchella*, male; **29,** *S. dolichos*, male (Mexico); **30,** *Magusa orbifera*, female; **31,** *Condica albigera*, male; **32,** *C. albigera*, female; **33,** *C. nobilis*, male (Brazil); *C. sutor*, male (Brazil); **35,** *Perigea gloria*, holotype male; **36,** *Elaphria agrotina*, male; **37,** *E. nucicolora*, female; **38,** *E. nucicolora*, male (Cuba); **39,** *Micrathetis triplex*, female; **40,** *M. triplex*, male; **41,** *Bagisara repanda*, female; **42,** *Amyna axis*, female; **43,** *Ponometia exigua*, male; **44,** *P. exigua*, female; **45,** *P. exigua*, female (Mexico); **46,** *Cydosia nobilitella*, male (Cuba); **47,** *Caularis undulans*, male; **48,** *Motya abseuzalis*, male; **49,** *Collomena filifera*, male; **50,** *C. filifera*, female (Cuba); **51,** *Paectes obrotunda*, male; **52,** *P. obrotunda*, female; **53,** *Pseudoplusia includens*, female; **54,** *Ptichodis immunis*, male (Cuba); **55,** *P. immunis*, female; **56,** *Mocis antillesia*, male; **57,** *M. antillesia*, female; **58,** *M. latipes*, male; **59,** *M. repanda*, male (Cuba); **60,** *M. repanda*, female (Puerto Rico); **61,** *Ophisma tropicalis*, male.

GUANA: 2 specimens, 1989.
BIO: Hayes (1975) [as *L. solita*, see below] gives *Sporobolus virginicus* (L.) Kunth. (Poaceae) as foodplant.
COM: The Guana specimens were identified as *humidicola* by Morton S. Adams, who has subsequently published a revision of the group in the Caribbean (Adams 2001) although our specimens are not mentioned in his paper. The name *humidicola* (type-locality: FRENCH GUIANA) has been wrongly applied to a different species by most authors (see *dorsalis* below), following the misidentification by Hampson (1905). A specimen collected by the first author in COSTA RICA: Guanacaste, El Coco (VOB 33636), identical to those from Guana, matches the type of *solita* (type-locality: HONDURAS) in BMNH, and the specimen figured by Hayes (1975), from Galapagos. Therefore *L. solita* Walker 1856, **new synonym,** is a junior synonym of *humidicola*, not of *multilinea* Walker (sensu Hampson 1905, Poole 1989). We regard *multilinea* Walker 1856 as a valid species because we believe that Hayes (1975), who had the types of both *multilinea* and *solita* at hand, had good reasons to treat the latter as a valid species.

Leucania dorsalis Walker, 1856

(Fig. 18)

ID: Easily confused with *L. humidicola*; dash along middle of forewing not as conspicuous.
DIST: Antilles, northern South America, Central America, and southern Florida (Adams 2001).
GUANA: 1 specimen, 1988.
BIO: Unknown; presumably grasses as for its close relatives *L. infatuans* Franclemont and *L. extenuata* Guenée.
COM: This species belongs to a complex previously treated as *humidicola*, following a misidentification by Hampson (1905). See Adams (2001:199) for further discussion of the species complex.

Amphipyrinae

Neogalea sunia (Guenée, 1852)

(Fig. 20)

ID: Medium sized, inconspicuous gray moth resembling *Spodoptera albulum*, but darker. Usually distinguished from *S. albulum* by the dark marked veins and, for males, by the abdomen thickly clothed with long scales.
DIST: Florida to Argentina, including Galapagos.
GUANA: 6 specimens, 1987, 1989, 1990.
BIO: Larvae on *Lantana* (Verbenaceae) (Comstock and Dammers 1935). Introduced to Hawaii and Australasia to control *Lantana* (Biotte 1991, Holloway 1996:148).
COM: Immature stages described by Comstock and Dammers (1935, as *Catabene esula*). Although this genus was placed in Cuculliinae by Poole (1989), we place it in Amphipyrinae following the comments by Todd (1972b) and Poole (appendix to this paper) placing it with *Catabena* and *Catabenoides*, which Poole (1989) placed as Amphipyrinae. The proper placement of many genera formerly associated with Amphipyrinae and Cuculliinae requires review.

Catabenoides terminellus (Grote, 1883), **new combination**

(Figs. 2, 3, 22)

ID: This and the following species are closely related, almost impossible to distinguish with external characters (see *C. lazelli* below). They resemble small *S. albulum* but are distinguished from it by the gray, irregular dot on tornus of forewing. Females usually have a black line along middle, covering the length of the forewing.
DIST: Southern USA, Antilles.
GUANA: 4 specimens, 1984.
BIO: Unknown.
COM: In order to place this and the following species correctly, we include a description of the new genus *Catabenoides* by Robert Poole as an appendix to this paper.

***Catabenoides lazelli* Becker and Miller, new species**

(Figs. 4–6, 21)

Description. Light gray, 2.2–2.6 cm. This and the former are very closely related species, almost impossible to be distinguished from each other on external characters (see *terminellus* above). They resemble a small *S. albulum* but easily recognized from it by the gray, irregular dot on tornus of forewing. Females usually have a black line along middle, covering the whole extension of forewing. The only reliable external feature that distinguishes *lazelli* from *terminellus* is the color of patagia. In *terminellus* there is a transverse line of blackish scales, dividing the patagia along the middle, while in *lazelli* the line is ochreous. The genitalia are also distinct. In *terminellus* the distal processes of the sacculus are simple, nearly straight rods (Fig. 2), while those in *lazelli* are complex, branched (Fig. 4).
DIST: Guana, Anegada, St. Croix.
GUANA: 35 specimens, 1984, 1985, 1989, 1990.
MATERIAL EXAMINED: Holotype male: BVI: Guana Id., 1–14.vii.1984 (S. E. & P. M. Miller) (USNM). Paratypes: 13 males, 12 females: Same data as holotype (USNM, BMNH, BPBM, MCZ, VOB); 1

female: Same locality and collector, 5–23.vii.1985 (USNM); 2 males, 1 female: Same locality, x.1989 (V. O. Becker, 70710) (VOB); 2 males, 3 females: Same locality, 24.x–5.xi.1990 (S. E. Miller & T. M. Kuklenski) (BPBM). ANEGADA: 2 males, 1 female: 17–19.vii.1985 (S. E. & P. M. Miller) (USNM). ST. CROIX: 2 males, 2 females, Kingshill, x, xi.1944, v, vi.1945 (H. A. Beatty) (CU); 1 female, same locality, 6–16.vii.1967 (E. L. Todd) (USNM); 1 female, Christiansted, 19. xi.1941 (H. A. Beatty) (USNM); 1 male, 2 females, Mt. Eagle, 6–16.vii.1967 (E. L. Todd) (USNM); 4 males, 1 female, 1 mi W Airport, 6–16.vii.1967 (E. L. Todd) (USNM); 2 males, 1 female, Orangegrove, W End, 6–16.vii.1967 (E. L. Todd) (USNM); 1 male, Blue Mtn., 6–16.vii.1967 (E. L. Todd) (USNM); 2 males, Rust Up Twist, 6–16.vii.1967 (E. L. Todd) (USNM); 1 male, 1 mi N Great Pond, 6–16.vii.1967 (E. L. Todd) (USNM).

BIO: Unknown.

COM: This species belongs to a complex formerly considered the single species, *C. vitrinus* (Walker), a species not found in the Lesser Antilles. The genitalia of *C. lazelli* (Fig. 4, 5) are very similar, but show consistent differences, the most evident is the vesica armed with a single, strong cornutus, whereas in *vitrinus* the vesica bears a series of smaller cornuti. The complex will be treated in a forthcoming revision (Becker in prep.). This species is dedicated to our friend Dr. James "Skip" Lazell, who gave us the opportunity to study this interesting fauna.

Spodoptera albulum (Walker, 1857)
(Fig. 23)

ID: Plain, pale gray, medium sized species, readily distinguished by the presence, on the forewing, of a very fine black line running along the middle from base to one-fourth. Hindwing almost totally translucent whitish.

DIST: United States, throughout the Antilles, south to Argentina, but not including Galapagos and Bermuda.

GUANA: 5 specimens, 1989, 1990.

BIO: Larvae on *Amaranthus* sp. (Amaranthaceae) (Kimball 1965) and cotton (Bruner et al. 1975). Recorded from many crops in Puerto Rico by Armstrong (1994a).

COM: "This is the species previously identified as '*Spodoptera sunia* Guenée'. The real *Xylomyges sunia* Guenée 1852 is actually the species [formerly] known as *Neogalea esula* Druce" (Poole 1989) (see *N. sunia* above). *Spodoptera albulum* is easily confused with *S. eridania*, which has not been collected on Guana, but is likely to occur on the island. *Spodoptera eridania* is dusted brownish, and lacks the forewing line mentioned above. Todd and Poole (1980) give an illustrated key to the New World species of *Spodoptera* and distributions of *Spodoptera* species in the Caribbean are reviewed in Cock (1985:92).

Spodoptera frugiperda (J. E. Smith, 1797)
(Fall armyworm)
(Figs. 24, 25)

ID: Medium sized, sexually dimorphic, gray species. Males have an oblique whitish dash from middle of costa across the cell. Females have indistinct pattern, looking almost plain gray.

DIST: Widespread in New World, including Galapagos and Bermuda.

GUANA: 8 specimens, 1986, 1990.

BIO: Polyphagous on herbaceous plants and regarded as a serious pest of maize and other crops (Andrews 1980). In Puerto Rico, it has been recorded as a pest of various crops (Armstrong 1994b) and *Eucalyptus* seedlings (Myrtaceae) (Torres 1994).

Spodoptera latifascia (Walker, 1856)
(Figs. 26, 27)

ID: Medium sized, sexually dimorphic species. Male forewing with a diffuse pattern of reddish brown and gray on a whitish gray background. Female forewing darker, easily confused with *S. dolichos* and bearing an oblique elongate whitish mark from middle costa to end of cell, followed by three short whitish lines along veins.

DIST: Gulf States of the United States, throughout the Antilles, south to Costa Rica. The population from Costa Rica south to Argentina, previously included under *S. latifascia*, belongs to *S. cosmioides* (Walker), a closely related but distinct species (Silvain & Lalanne-Cassou 1997, M. Pogue pers. com.).

GUANA: 1 specimen, 1989.

BIO: Polyphagous on herbaceous plants, sometimes becoming a pest of vegetables and nursery seedlings.

Spodoptera pulchella (Herrich-Schäffer, 1868)
(Fig. 28)

ID: Wing pattern similar in both sexes; easily confused with the females of the former. It can be separated from similar species by the curved whitish line along dorsum, below the anal vein, from basal fourth to just before tornus.

DIST: Florida, Greater Antilles.

GUANA: 1 specimen, 1989.

BIO: Unknown.

COM: This seems to be the first record of this species to the Puerto Rican Bank. It has either been overlooked because of rarity, or because it was mistaken for the similar *S. latifascia*, a more common species.

Spodoptera dolichos (Fabricius, 1794)
(Fig. 29)

ID: About the same size as *S. latifascia*; both sexes showing similar pattern to that of female *S. latifascia*. Easily distinguished from the previous two species by the two conspicuous, parallel, dark gray bands along thorax.
DIST: Sympatric with *S. latifascia*, including in Galapagos.
GUANA: 1 specimen, 1989.
BIO: Larvae on a wide variety of plants, both crops and weeds (Ferguson et al. 1991).

Magusa orbifera (Walker, 1857)
(Fig. 30)

ID: An extremely polymorphic, medium sized (3–4 cm), gray to brown species. In the Guana population, some males have a wide pale area along dorsum of forewing, others have a very complex and contrasting maculation, while the females tend to be less marked and more brownish. One constant feature is the conspicuous round pale dot near the apex of forewing and the very broad dark fuscous hindwing. *Anateinoma affabilis* and *E. agrotina* also have the pale mark at end of apex of forewing but are at most half the size of *M. orbifera*.
DIST: Widespread throughout the New World, from Canada to Argentina (not reported from Galapagos, but *M. erema* Hayes (1975) may be a local variety of this species).
GUANA: 57 specimens, 1989, 1990.
BIO: Larvae on various legumes, including *Karwinskia* and *Condalia* (Fabaceae) (Kimball 1965).

Condica albigera (Guenée, 1852)
(Figs. 31, 32)

ID: Medium sized (2.5–3 cm wing span), dark fuscous; forewing with an irregular small white dot at end of cell, followed by a paler, almost straight transverse line.
DIST: Mexico, throughout Antilles, south to Paraguay.
GUANA: 3 specimens, 1989, 1990.
BIO: Unknown.
COM: Easily confused with *C. circuita* (Guenée), not collected but likely to occur on the island. In *C. circuita* the white dot on forewing is round and has a white lunule just under it.

Condica mobilis (Walker, [1857])
(Fig. 33)

ID: About same size as *C. albigera*, but more reddish brown and orange; white dot on cell usually larger than in *C. albigera*.
DIST: Southern United States, throughout Antilles, south to Argentina.
GUANA: 1 specimen, 1989.
BIO: Unknown.
COM: Commonly referred to in the literature as *Perigea apameoides* Guenée, which is a synonym of *C. sutor* (Guenée) (Hayes 1975).

Condica sutor (Guenée, 1852)
(Fig. 34)

ID: Same size as *C. albigera and C. mobilis*; fuscous with forewing showing little contrasting pattern. Distinguished from *albigera* and *mobilis* by the absence of the whitish mark on cell.
DIST: Southern United States, throughout the Antilles, south to Argentina, including Galapagos.
GUANA: 1 specimen, 1990.
BIO: Larvae on several species of herbaceous plants including *Wedellia*, *Tagetis* (Asteraceae), and celery (Kimball 1965).

***Perigea gloria* Becker and Miller, new species**
(Figs. 7–9, 35)

Description. Medium sized (3 cm wing span), pale moth; forewing shaded dark fuscous, with a series of small dark marks along costa and small black dots along termen, in the spaces between veins. Similar to *C. sutor* but with more contrasting pattern, and readily separated by the series of black dots along termen.
DIST: Guana, Tortola.
GUANA: 2 specimens, 1989.
MATERIAL EXAMINED: Holotype male: BVI: Guana Id., x.1989 (V. O. Becker, 70722) (USNM); Paratypes, 1 female, same data as holotype (VOB); 1 male Tortola, Mt. Sage, 460m, 13–15.vii.1987 (V. O. Becker & S. E. Miller, 66865) (VOB).
BIO: Unknown.
COM: Very similar in appearance to *P. berinda* (Druce), a species from the Greater Antilles and Central America, but with genitalia (Figs. 7–9) very different from those of *berinda*, being very similar to those of *P. glaucoptera* (Guenée). This species is dedicated to Ms. Gloria Jarecki, for her and her family's support of The Conservation Agency's biodiversity research on Guana Island over the years.

Elaphria agrotina (Guenée, 1852)
(Fig. 36)

ID: Small (2–2.5 cm wing span); forewing dark fuscous with a paler area along costa and a conspicuous pale dash near apex. Similar to *A. affabilis* (see below), but larger and with hindwing bordered whitish.
DIST: Florida, throughout the Antilles, south to Argentina.

GUANA: 5 specimens, 1987, 1989, 1990.
BIO: Larvae on cotton and beans (*Phaseolus*) (Fabaceae) (Silva et al. 1968).

Elaphria nucicolora (Guenée, 1852)
(Figs. 37, 38)

ID: Same size as *E. agrotina*; forewing dark fuscous, with a broad, ill-defined, darker triangular mark with base on middle of dorsum and vertex at end of cell. Hindwing whitish.
DIST: Throughout New World tropics including Bermuda. Immigrant to Hawaii.
GUANA: 1 specimen, 1989.
BIO: Larvae on various herbaceous plants (Ferguson et al. 1991).

Anateinoma affabilis Möschler, 1890
(Figs. 10, 11, 151, 152)

ID: Small (15 mm wing span); forewing reddish brown with transverse sinuate lines alternating pale and dark, and with a conspicuous whitish dash on apex. Similar to *E. agrotina* (see above) but smaller, and forewing lacking pale area along costa. *Magusa orbifera* also has a pale mark on apex, but is almost three times the size of *affabilis*.
DIST: Puerto Rico and Virgin Islands.
GUANA: 22 specimens, 1987, 1989, 1990.
BIO: Unknown.
COM: Despite the accurate color illustration presented by Möschler (1890), who described this species from Puerto Rico, Hampson (1910) treated *A. affabilis* as an unrecognized taxon in the Erastriinae [=Acontiinae], where it has remained. One of the reasons for this situation is because no material except for the types, which are supposed to be in MNHU, Berlin, has been available to subsequent authors working on the New World noctuid fauna. No material of this species was found in the BMNH or USNM; for this reason vouchers from the series studied here have been deposited there.

This species does not belong in Acontiinae, but is related to some species currently placed in *Elaphria* Hübner. However, at present we prefer not to synonymize *Anateinoma* under *Elaphria* as the group needs revision. The male genitalia is illustrated in Figs. 10, 11.

Micrathetis triplex (Walker, 1857)
(Figs. 39, 40)

ID: Small (1.5–2.2 cm wing span), slightly dimorphic, variable in color. Males have pale forewing speckled with darker small dots, termen dark brown, and a conspicuous dark brown dot at end of cell. Females are darker than males. Hindwing whitish, slightly bordered with dark gray. Easily recognized by the dot at the end of the cell and by the two rows of small blackish dots forming two arches, almost parallel to each other, from costa to dorsum.
DIST: Southern United States through South America.
GUANA: 14 specimens, 1987, 1989, 1990.
BIO: Unknown.

Agaristinae

Caularis undulans Walker, [1858]
(Fig. 47)

ID: Undoubtedly the most attractive noctuid on the island. Forewings white bordered and marked olive; hindwing golden yellow bordered reddish-brown with a lunular blackish mark on tornus. Male genitalia illustrated by Kiriakoff (1976).
DIST: Hispaniola, Jamaica, Puerto Rican Bank (Kiriakoff 1976).
GUANA: 9 specimens, 1989.
BIO: Unknown.

Bagisarinae

Bagisara repanda (Fabricius, 1793)
(Fig. 41)

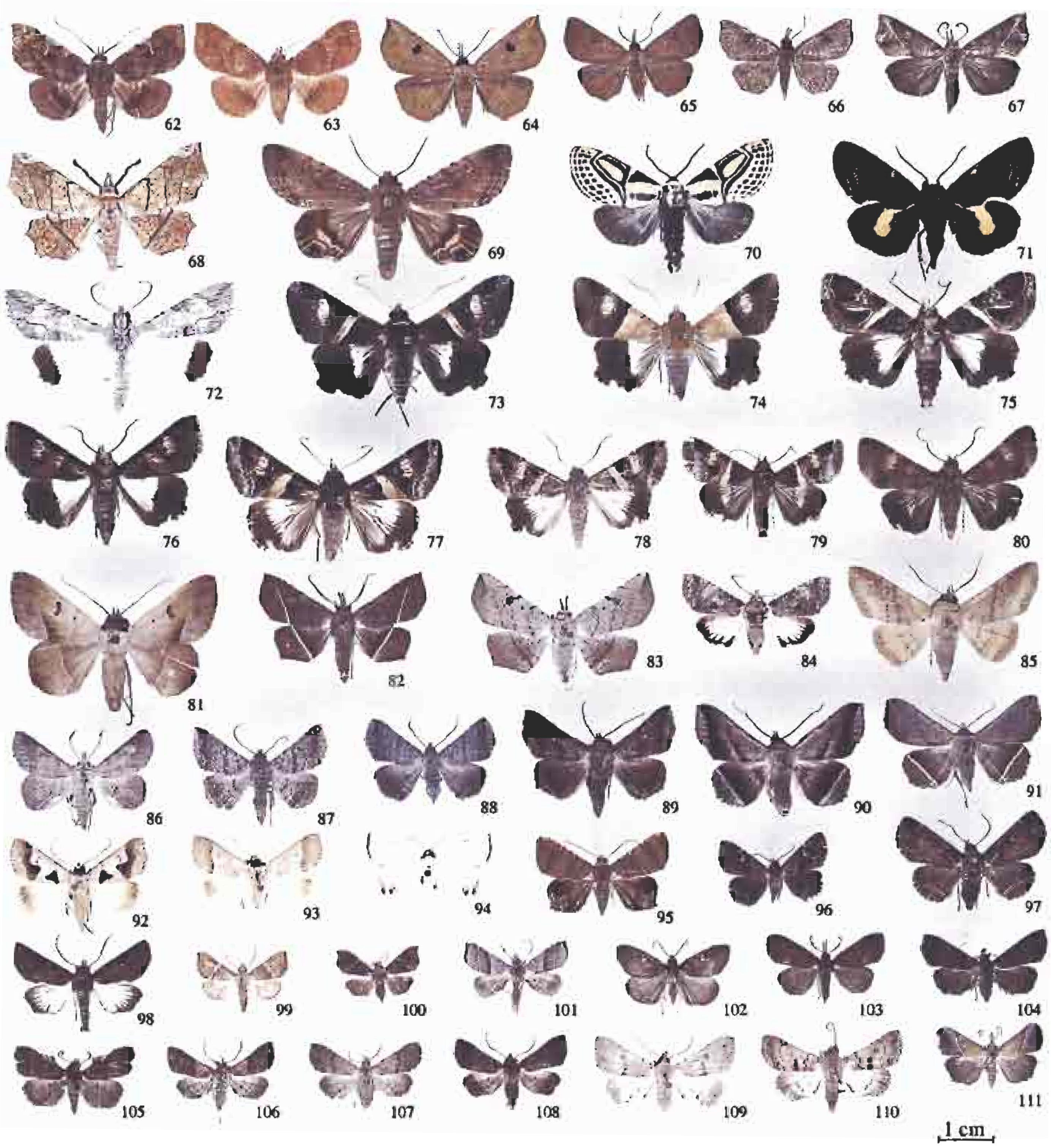
ID: Small, 2–2.5 cm wing span, pale yellow, dusted gray. Easily identified by the three pale lines crossing the forewing, more or less equidistant, parallel to each other, and bent basad near costa.
DIST: Widespread from Southeast United States to Paraguay, including Galapagos (Hayes 1975, Ferguson 1997).
GUANA: 4 specimens, 1987, 1989.
BIO: Larvae on *Sida glomerata* Cav. (Malvaceae) (Hayes 1975).
COM: Very common in disturbed areas where malvaceous weeds often occur.

Acontiinae

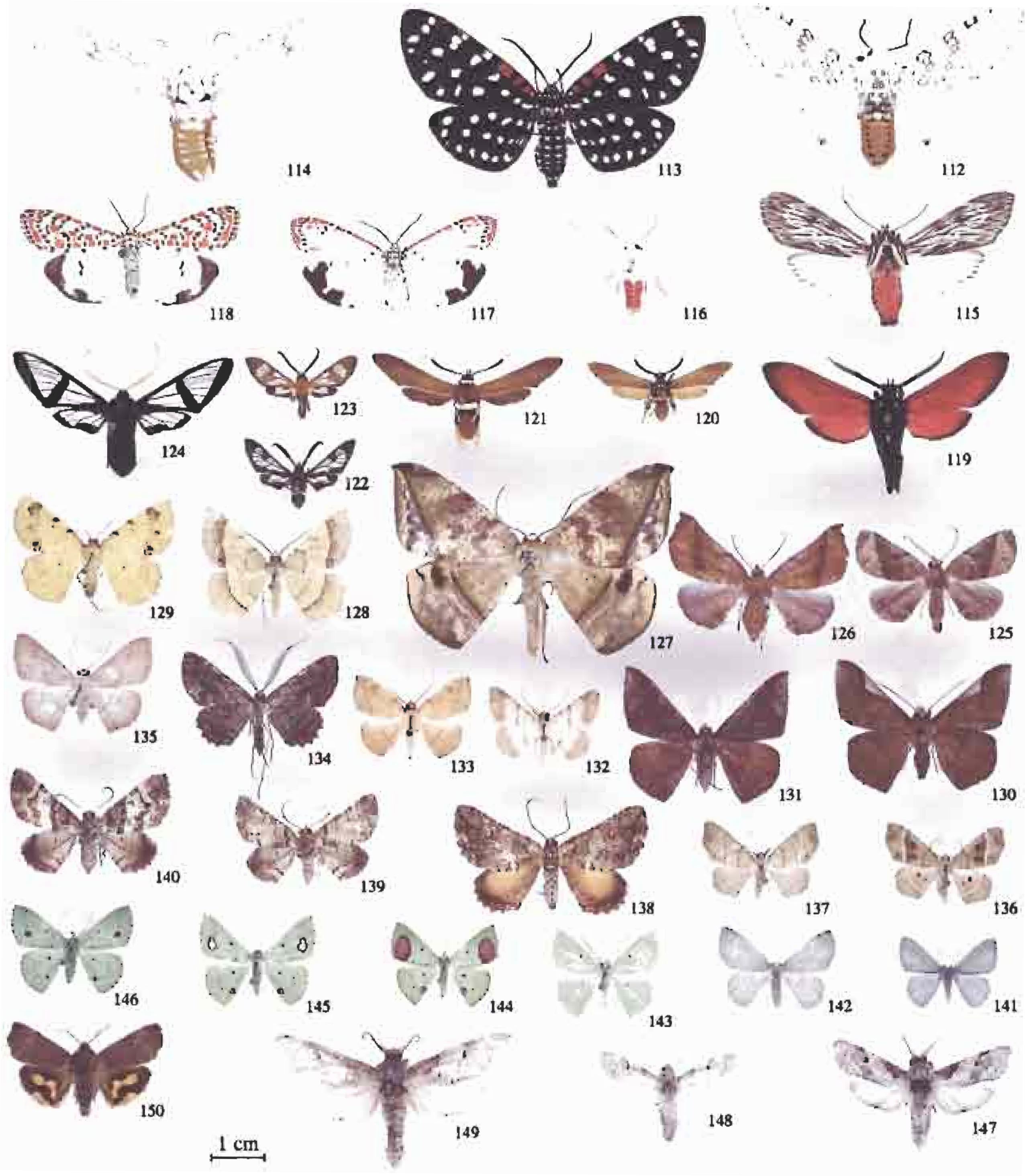
Amyna axis (Guenée, 1852)
(Fig. 42)

ID: Small, fuscous species, easily confused with some small *Condica* species. Males are distinguished from *Condica* by the presence of a round, semitranslucent area near base of forewing.
DIST: Pantropical, including Tahiti and Hawaii.
GUANA: 2 specimens, 1989.
BIO: Larvae on *Chenopodium* (Chenopodiaceae), *Cardiospermum* (Sapindaceae), *Parasponia* (Ulmaceae), and *Amaranthus* (Amaranthaceae) (Ferguson 1991).
COM: The large distribution and obscure pattern have contributed to long synonymy; it has been described

65



FIGS. 62–111. Natural size (1:1). Noctuidae (specimens from Guana, unless stated otherwise). **62,** *Azeta versicolor,* male; **63,** *A. versicolor,* female; **64, 65,** *Metallata absumens,* males; **66,** *M. absumens,* male; **67,** *Plusiodonta thomae,* male; **68,** *Syllectra erycata,* male (Cuba); **69,** *Litoprosopus puncticosta,* male; **70,** *Diphthera festiva,* male; **71,** *Gonodonta bidens,* male (Puerto Rico); **72,** *Melipotis acontioides,* female; **73,** *M. fasciolaris,* male; **74,** *M. fasciolaris,* female; **75,** *M. contorta,* male; **76,** *M. famelica,* male; **77,** *M. ochrodes,* male; **78,** *M. ochrodes,* female (Puerto Rico); **79,** *M. januaris,* male (Cuba); **80,** *M. januaris,* female (Cuba); **81,** *Epidromia lienaris,* male (Puerto Rico); **82,** *Ephyrodes cacata,* male (Cuba); **83,** *E. cacata,* female; **84,** *Concana mundissima,* female; **85,** *Massala asema,* male; **86,** *Manbuta pyraliformis,* male (Cuba); **87,** *Lesmone hinna,* male (Cuba); **88,** *L. hinna,* female (Cuba); **89,** *L. hinna,* male; **90,** *L. formularis,* male; **91,** *L. formularis,* female (Cuba); **92,** *Baniana relapsa,* male; **93,** *B. relapsa,* female; **94,** *Eulepidotis modestula,* male (Cuba); **95,** *E. addens,* female; **96,** *Toxonprucha diffundens,* male (Mexico); **97,** *Kakopoda progenies,* male; **98,** *Parachabora abydas,* male; **99,** *Cecharismena abarusalis,* male; **100,** *C. cara,* male; **101,** *Glympis eubolialis,* male; **102,** *Drepanopalpia lunifera,* male (Cuba); **103,** *D. lunifera,* female; **104,** *Lascoria orneodalis,* female; **105,** *L. orneodalis,* male (Cuba); **106,** *Bleptina caradrinalis,* male; **107,** *B. caradrinalis,* female; **108,** *B. hydrillalis,* male; **109,** *B. menalcasalis,* female; **110,** *B. menalcasalis,* male; **111,** *Hypena lividalis,* female.



FIGS. 112–150. Natural size (1:1). Arctiidae (112–124), Geometridae (125–146), Cossidae (147–149) and Hyblaeidae (150) (specimens from Guana, unless stated otherwise). **112,** *Hypercompe simplex*, male (Puerto Rico); **113,** *Composia credula*, male; **114,** *H. simplex*, female; **115,** *Calidota strigosa*, male; **116,** *Eupseudosoma involutum*, male (Puerto Rico); **117,** *Utetheisa ornatrix*, male; **118,** *U. pulchella*, female (Brazil); **119,** *Empyreuma pugione*, male; **120,** *Horama panthalon*, male; **121,** *H. pretus*, male; **122,** *Cosmosoma achemon*, male (St. Thomas); **123,** *Eunomia colombina*, male; **124,** *Nyridela chalciope*, female (Cuba); **125,** *Pero rectisectaria*, male; **126,** *P. rectisectaria* female; **127,** *Oxydia vesulia*, male; **128,** *Erastria decrepitaria*, male (Cuba); **129,** *E. decrepitaria*, female; **130,** *Sphacelodes fusilineatus*, male; **131,** *S. fusilineatus*, female; **132,** *Macaria paleolata*, male; **133,** *Patalene ephyrata*, male; **134,** *Almodes terraria*, male (Bahamas); **135,** *Semaeopus malefidarius*, male; **136,** *Leptostales noctuata*, male; **137,** *L. noctuata*, female; **138,** *Obila praecurraria*, female (Tortola); **139,** *Pterocypha defensata*, male; **140,** *P. defensata*, female; **141,** *Eueana simplaria* male; **142,** *E. simplaria* female; **143,** *Phrudocentra centrifugarium*, male; **144,** *P. centrifugarium*, female (Cuba); **145, 146,** *P. centrifugarium*, females; **147–149,** *Psychonoctua personalis*, males; **150,** *Hyblaea puera*, male (Cuba).

18 times (Poole 1989). Frequently referred to in the literature as *A. octo* (Guenée), a synonym based on the priority of names established by Nielsen et al. (1996: note 690).

Ponometia exigua (Fabricius, 1793)
(Figs. 43–45)

ID: Small, variable, sexually dimorphic species; males pale yellow with forewing crossed with diffuse, sinuate olivaceous bands. Female forewing dark fuscous with a wide, contrasting, pale fascia along costa. In some females this pattern is less contrasting.
DIST: Southern United States, throughout the Antilles, south to Brazil, including Galapagos.
GUANA: 9 specimens, 1989, 1990.
BIO: Larvae on *Waltheria ovata* Cav. (Sterculiaceae) (Hayes 1975).
COM: Commonly referred to in the literature by its junior synonym *P. indubitans* (Walker).

Cydosia nobilitella (Cramer, 1779)
(Fig. 46)

ID: Small showy moth; one of the most attractive noctuids on the island. Forewing with reticulated pattern with white areas enclosed by dark bluish metallic gray and red lines. Hindwing semitranslucent white in males, dark gray in females. Pattern resembles some species of *Atteva* (Yponomeutidae) and specimens are often found mixed in collections.
DIST: Southern United States, throughout Antilles, south to Argentina.
GUANA: 1 specimen, 1984.
BIO: Hampson (1910) mentioned "?*Spigelia anthelmia* L." (Loganiaceae) as hostplant, following Cockerell (1897). No species of this plant family known from the island (G. Proctor pers. com.), although the species occurs on other Virgin Islands (Acevedo-Rodriguez 1996). Cockerell (1897) and Dyar (1897) described the larvae.

Tripudia quadrifera (Zeller, 1874)
(Figs. 153, 154)

ID: The smallest noctuid on the island (0.7–1.2 cm wing span); resembling Olethreutinae (Tortricidae) and *C. metaspilaris* (see below). Dark gray; forewing with conspicuous quadrate mark on middle of dorsum.
DIST: Southern United States, throughout the Antilles, south to Brazil.
GUANA: 22 specimens, 1989, 1990.
BIO: Unknown.

Tripudia balteata Smith, 1900
(Fig. 155)

ID: Small, on average slightly larger than *T. quadrifera*. Dark gray. Easily identified by the broad, oblique, yellowish band on forewing.
DIST: Southern United States, Antilles, south to Brazil.
GUANA: 16 specimens, 1987, 1989, 1990.
BIO: Unknown.

Ommatochila mundula (Zeller, 1872)
(Fig. 156)

ID: Small, 1.5–2 cm wing span, dark gray, resembling some Olethreutinae species (Tortricidae). Forewing divided across the middle by a pale, almost straight line, the basal half much darker than outer half.
DIST: Southern United States, Antilles, south to Argentina.
GUANA: 14 specimens, 1986, 1989, 1990.
BIO: Unknown.

Cobubatha metaspilaris Walker, 1863
(Fig. 157)

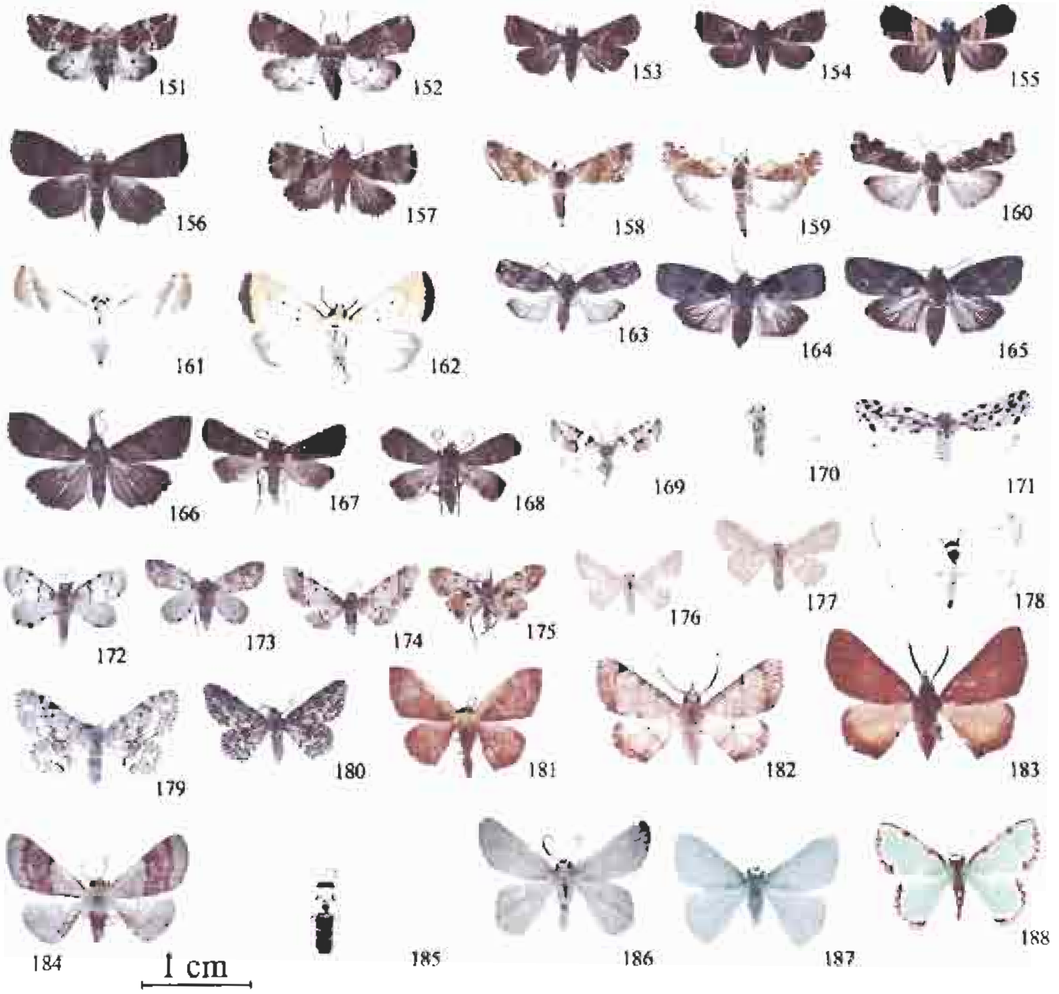
ID: Small, 1.5 cm wing span, gray; similar to, but larger than *T. quadrifera*. In the latter the mark on dorsum is quadrate whereas in *metaspilaris* it is trapezoidal.
DIST: Antilles.
GUANA: 3 specimens, 1990.
BIO: Unknown.

Eumicremma minima (Guenée, 1852)
(Fig. 158)

ID: Very small (1.2–1.5 cm wing span); forewing pale, crossed with olive and dark olive waiving bands, and with some very small, black dots along termen, the most conspicuous the one near apex and the other near tornus. In resting posture it looks like some species of Cochylini (Tortricidae).
DIST: Southern United States, Antilles, south to Argentina.
GUANA: 3 specimens, 1987.
BIO: Larvae on *Gnaphalium* (Asteraceae).

Eublemma rectum (Guenée, 1852)
(Fig. 161)

ID: Small, 1.5 cm wing span; pale yellow; forewing clouded with red brown with oblique pale fascia from middle of dorsum to near apex.
DIST: Southern United States, throughout the Antilles, south to Argentina, including Galapagos and Bermuda.
GUANA: 3 specimens, 1989.
BIO: Larvae on *Ipomoea* and *Convolvulus* (Convolvu-



Figs. 151–188. Twice natural size (2:1). Noctuidae (151–168), Arctiidae (169–171) and Geometridae (172–188) (specimens from Guana, unless stated otherwise). **151, 152,** ***Anateinoma affabilis***, males; **153,** ***Tripudia quadrifera***, female (Mexico); **154,** ***T. quadrifera***, female; **155,** ***T. balteata***, male; **156,** ***Ommatochila mundula***, female; **157,** ***Cobubatha metaspilaris***, male; **158,** ***Eumicremma minima***, male (Cuba); **159,** ***Spragueia margana***, male, (Brazil); **160,** ***S. margana***, female (Brazil); **161,** ***Eublemma rectum***, male; **162,** ***Thioptera aurifera***, male (Brazil); **163,** ***Characoma nilotica***, female; **164, 165,** ***C. nilotica***, females (Mexico); **166,** ***Hypena minualis***, female; **167,** ***Bleptina araealis***, male; **168,** ***B. araealis***, female; **169,** ***Afrida charientisma***, male; **170,** ***Progona pallida***, male; **171,** ***Lomuna nigripuncta***, female; **172,** ***"Idaea" monata***, male, **173,** ***Idaea monata***, female; **174,** ***Idaea eupitheciata***, female, **175,** ***I. eupitheciata***, male; **176,** ***I. minuta***, male; **177,** ***I. minuta***, female; **178,** ***Scopula laresaria***, female. **179, 180,** ***Idaea*** probably ***fernaria***, females; **181,** ***Leptostales phorcaria***, male; **182,** ***Cyclomia mopsaria***, male; **183,** ***C. mopsaria***, female; **184,** ***Leptostales oblinataria***, female; **185,** ***Acratodes suavata***, male; **186,** ***Chloropteryx paularia***, male; **187,** ***Synchlora frondaria***, male; **188,** ***S. cupedinaria***, male.

laceae) (Forbes 1954) [as *E. obliqualis* (Fabricius), a homonym].

Spragueia margana (Fabricius, 1794)
(Figs. 159, 160)

ID: The smallest of the two *Spragueia* species on the island; dimorphic. Similar to *S. perstructana* (see below). Males easily distinguished from the latter by the absence of orange, by the pale costa, and by the olivaceous shades and marks on forewing; females by the olivaceous thorax, which is edged pale yellow in *S. perstructana*.

DIST: Southern United States, throughout the New World tropics, including Galapagos.

GUANA: 4 specimens, 1987.

BIO: Larvae on *Abutilon* and *Sida* (Malvaceae) (Hayes 1975).

Spragueia perstructana (Walker, 1865)

ID: Similar to, but slightly larger than *S. margana* (see above); also dimorphic. Illustrated in color in Kimball (1965: Pl. IV, figs. 31, 37).

DIST: Southern United States, Antilles, south to Costa Rica.

GUANA: 1 specimen, 1989.
BIO: Unknown.

Thioptera aurifere (Walker, [1858]) (Fig. 162)

ID: Small, 1.5–1.8 cm wing span; yellow; forewing usually with two very small black dots, an ill defined reddish line beyond the cell from costa to dorsum, and termen edged with gray.
DIST: Southern United States, throughout Antilles, south to Brazil.
GUANA: 4 specimens, 1989, 1990.
BIO: Unknown, however Kimball (1965) gives *Digitaria ischaemum* [*Syntherisma impomoea*] (Poaceae) as the food plant for *T. nigrofimbria*, a closely related species.

Sarrothripinae

Characoma nilotica (Rogenhofer, 1882) (Figs. 163–165)

ID: Small, 1–1.2 cm wing span, highly variable, gray species. Rests flat, looking like some tortricids.
DIST: Described from Egypt, hence its name; now Pantropical, including Galapagos, Bermuda, and the Pacific Islands.
GUANA: 25 specimens, 1985, 1986, 1990.
BIO: Larvae on white mangrove, *Laguncularia racemosa* (L.) C.F. Gaertn. (Combretaceae) (Hayes 1975); willow, almond, azalea, and "black olive" (Ferguson 1991).

Collomena filifera (Walker, 1857) (Figs. 49, 50)

ID: Medium sized gray species, similar to female *S. frugiperda*. Distinguished by the whitish diffused band across the subterminal area of forewing and by the entirely whitish, semitranslucent hindwing (narrowly bordered gray in females).
DIST: Florida, throughout the Antilles, south to Brazil.
GUANA: 4 specimens, 1989, 1990.
BIO: Unknown.

Motya abseuzalis Walker, 1859 (Fig. 48)

ID: Slightly smaller than *C. filifera*; whitish gray. Easily recognized by the two, almost parallel, rows of small, black dots along termen, with the one near tornus conspicuously larger. The male abdomen has two paired black dots dorsally, near apex. Hindwing semitranslucent white, bordered gray.
DIST: Florida, throughout the Antilles, south to Brazil.
GUANA: 1 specimen, 1989.
BIO: Unknown.

Euteliinae

Paectes obrotunda (Guenée, 1852) (Figs. 51, 52)

ID: Medium sized, gray, irrorated brown; males have basal half of antennae strongly pectinate, and long slim abdomen; females have filiform antennae and short stout abdomen. Forewing with a conspicuous pale lunular mark near base, delimited externally by a narrow, double line.
DIST: Southern United States, throughout Antilles, south to Paraguay.
GUANA: 64 specimens, 1984, 1987, 1988, 1989, 1990.
BIO: Unknown, however, its larvae should be searched for on *Bursera simaruba* (L.) Sarg. (Simarubaceae), as a related species, *P. arcigera* (Guenée), was reared on *B. graveolens* (Kunth) Triana & Planch. in Galapagos (Hayes 1975).

Plusiinae

Pseudoplusia includens (Walker, [1858]) (Fig. 53)

ID: Medium sized, grayish brown with bronze luster. Recognized by the small silver markings near center of forewing.
DIST: United States to northern Chile and Argentina, including Galapagos and Bermuda (Lafontaine & Poole 1991:50).
GUANA: 2 specimens, 1989.
BIO: Polyphagous; Ferguson et al. (1991) lists plants belonging to 14 families as foodplants. Can be a minor pest of beans, soy beans, and other leguminous crops.
COM: Generally referred to in the literature as *P. oo* (Cramer), a homonym. Other species belonging to this subfamily, such as *Trichoplusia ni* (Hübner) and *Argyrogramma verruca* (Fabricius), are likely to be collected on the island in the future. These also bear silver marks on the forewing.

Catocalinae

Ptichodis immunis (Guenée, 1852) (Figs. 54, 55)

ID: Medium sized, 2.5–3 cm wing span, pale species. Forewing crossed with ill defined olivaceous lines, two of them highly contrasting: the antemedial and the postmedial, both bordered internally with lemon yellow.
DIST: Mexico, throughout the Antilles to Brazil.
GUANA: 6 specimens, 1987, 1989, 1990.
BIO: Unknown.

Mocis latipes (Guenée, 1852)
(Fig. 58)

ID: Medium sized, 3.5–4 cm wing span, broad winged, dark species. Highly variable in color and pattern. Ground color varies from pale brownish through fuscous to reddish brown. Females tend to have pattern less contrasting than males, and the paler forms could easily be confused with the darker forms of female *M. disseverans*, a Neotropical species recorded from the Greater Antilles. Smaller than *M. repanda* (see below). The males of the species belonging to this genus can be easily distinguished from other noctuids by the thickly hairy hind legs.

DIST: Southern United States, throughout the Antilles, south to Argentina, including Galapagos and Bermuda.

GUANA: 1 specimen, 1989.

BIO: Larvae on several species of grasses, sometimes a pest of grazing land.

COM: Generally referred to in the literature as *M. repanda*, a different species (see below).

Mocis antillesia Hampson, 1913
(Figs. 56, 57)

ID: Same size and easily confused with *M. latipes*. Ground color pale brownish to pale yellow. Clothing of hind legs usually yellowish in this whereas grayish in *M. latipes*. Smaller than *M. repanda* (see below).

DIST: Lesser Antilles, Bahamas.

GUANA: 4 specimens, 1989, 1990.

BIO: Unknown.

Mocis repanda (Fabricius, 1794)
(Figs. 59, 60)

ID: Larger than the former two species in the genus, 4.5–5.5 cm wing span. Smaller specimens of this species are larger than the largest specimens of both *M. latipes* and *M. antillesia*. Distinguished from congeners by shape of postmedial lines in both wings: in the forewing it is bent inwards after the angle near costa, and fades away before tornus, whereas in the former two it is straight and reaches tornus; in the hindwing it is strongly angled outwards before tornus whereas in the others it is straight.

DIST: Antilles and Guatemala.

GUANA: 2 specimens, 1987, 1990.

BIO: Larvae on *Mucuna deeringiana* (Bort) Merr. [as *M. megas*] (Fabaceae) (Martorell 1976).

COM: Generally known in the literature as *M. megas* (Guenée), a junior synonym (Poole 1989). Berio (1953) clarified the status of *M. repanda* and illustrated the male genitalia.

Ophisma tropicalis Guenée, 1852
(Fig. 61)

ID: Same size as *M. repanda*, but with stouter body. Extremely variable in pattern and color. Recognized by the small, conspicuous white dot on base of forewing.

DIST: Southern United States, throughout the Antilles, south to Argentina.

GUANA: 2 specimens, 1987.

BIO: Larvae on *Cupania americana* L. (Sapindaceae) (Martorell 1976).

Ophiderinae

Azeta versicolor (Fabricius, 1794)
(Figs. 62, 63)

ID: Medium sized, polymorphic species; ground color varies from ferrugineous to dark grayish brown. Recognized by the pointed forewing and transverse pale dash at middle of forewing costa.

DIST: Throughout the New world tropics from Florida to Argentina.

GUANA: 23 specimens, 1987, 1989, 1990.

BIO: Larvae on *Canavalia* (Fabaceae) (Kimball 1965).

COM: Commonly referred to in the literature by its junior synonym, *A. repugnalis* (Hübner).

Metallata absumens (Walker, 1862)
(Figs. 64–66)

ID: Medium sized, highly variable species. Ground color varies from reddish brown to gray. Similar to *E. cacata* but readily separated by the dark brown head and anterior border of thorax, by the nearly rounded border of hindwing, and by the filiform antennae in both sexes. Some specimens bear a black reniform mark at the end of forewing cell.

DIST: Southern United States, throughout the Antilles, south to Brazil, including Galapagos.

GUANA: 12 specimens, 1987, 1989, 1990.

BIO: Unknown.

Plusiodonta thomae (Guenée, 1852)
(Fig. 67)

ID: Medium sized, dark brown species with some shinning golden areas on forewing. Recognized by the single dentate expansion on middle of dorsum of forewing.

DIST: Described from St. Thomas, considered endemic to the Antilles.

GUANA: 4 specimens, 1987, 1989.

BIO: Unknown.

COM: It is very likely that the continental species, *P. clavifera* (Walker), is conspecific with *P. thomae*. There is some degree of variation in both the Antillean and the continental populations, and specimens from both regions intergrade into each other. *Plusiodonta clavifera* has been reported from Galapagos (Hayes 1975).

Syllectra erycata (Cramer, 1780)
(Fig. 68)

ID: Medium sized, reddish ferrugineous species. Forewing with three transverse lines, angled basad near costa, and with one or two small, round pale dots on outer side of postmedial line. Males distinguished by unique shape of antenna, which is uncommonly thick throughout its length except for the tip.
DIST: Florida, throughout the Antilles, south to Brazil.
GUANA: 3 specimens, 1986, 1987.
BIO: Unknown.

Litoprosopus puncticosta Hampson, 1926
(Fig. 69)

ID: Large, velvet fuscous species. The narrow wings and stout body resemble a small sphingid. Readily distinguished from other noctuids of same size on the island by the orbicular black mark at lower edge of hindwing.
DIST: Haiti, Virgin Islands.
GUANA: 1 specimen, 1989.
BIO: Unknown, however, a close relative, *L. futilis* (Grote & Robinson), has been found boring into the flower stalks of *Sabal* and *Serenoa* (Arecaceae) (Ferguson et al. 1991).

Diphthera festiva (Fabricius, 1775)
(Fig. 70)

ID: Medium sized, bright yellow, with an elaborate pattern of bluish gray lines and three parallel rows of dots parallel to external margin. Hindwing dark gray with pale cilia.
DIST: Widespread throughout the New World tropics, from Florida to Argentina.
GUANA: 2 specimens, 1987, 1989.
BIO: Larvae on *Casuarina equisetifolia* L. (Casuarinaceae), *Corchorus hirsutus* L. (Tiliaceae), *Schrankia portoricensis* Urb. (Fabaceae), and *Waltheria indica* L. (Sterculiaceae) (Martorell 1976, Torres 1994). Bright colored larvae reared in Brazil on *Sida* sp. (Malvaceae) (VOB), a common weed in disturbed areas on the island.
COM: Referred to as *Noropsis hieroglyphica* (Cramer), the junior synonym, in older literature. Its pattern may be aposematic. One male was tossed towards a gray kingbird, *Tyrannus dominicensis* (Gmelin), who caught it in the air, returned to its perch, tried to swallow the moth, then spit it out and cleaned its beak against the branch (VOB pers. obs.).

Gonodonta bidens Geyer, 1832
(Fig. 71)

ID: Showy, medium sized moth; cannot be confused with any other species on the island. Forewing velvet dark brown; basal and postmedial areas paler, crossed with waving dark and reddish brown lines. Hindwing dark gray with a bright elongate yellow area at middle. Head conspicuously white.
DIST: Florida, throughout the Antilles, south to Argentina.
GUANA: 1 specimen, 1990.
BIO: Larvae on *Guarea trichilioides* L. (Meliaceae), *Cupania* (Sapindaceae) and *Diospyrus* (Ebenaceae) (Todd 1972a). Adults have been reported to damage oranges in northern Mexico by piercing ripening fruits (Todd 1959).

Melipotis acontioides (Guenée, 1852)
(Fig. 72)

ID: Medium to large sized, 3.5–5 cm wing span, light gray species. Hindwings semitranslucent white with a broad gray band along external margin not reaching lower angle; often with a small gray dot just before lower angle.
DIST: Florida, Antilles, south to Brazil, including Galapagos.
GUANA: 4 specimens, 1989.
BIO: Larvae on *Delonix regia* (Bojer ex Hook.) Raf. (royal poinciana) and *Parkinsonia aculeata* L. (Fabaceae) (Martorell 1976, Torres 1994).
COM: Except for *M. acontioides*, species of *Melipotis* are difficult to distinguish because they look very similar to each other and there is a high degree of variation among specimens within each species. Most *Melipotis* species recorded for Guana also occur in southern United States and were reviewed by Richards (1939) and illustrated in color by Bordelon and Knudsen (1999).

The species of this genus are often the most abundant moths at lights in dry areas of the New World tropics. One of the reasons is that they feed on various leguminous plants such as *Acacia*, *Cassia*, *Prosopis*, and other species that are abundant in such habitats. During certain collecting trips, especially immediately after the beginning of rainy season, they came to light in such great numbers that the entire sheet was covered, making it impossible to collect any other moths. On some occasions the lights had to be disconnected and collecting discontinued (VOB pers. obs.).

Melipotis fasciolaris (Hübner, [1831])

(Figs. 73, 74)

ID: Medium to large sized, 3–4.5 cm wing span, variable species—the most variable species of the genus occurring on the island. In some specimens the pattern is less contrasting while in others the contrast is strong. Most specimens can be distinguished from those of other species on the island by the antemedial oblique, pale fascia of forewing. In *M. fasciolaris* the fascia is straight and uniform in width throughout. In some specimens the area basad of the fascia is pale olivaceous.
DIST: Southern United States, Antilles, south to Uruguay.
GUANA: 7 specimens, 1989.
BIO: Unknown, however Wolcott (1951) noted "Numerous caterpillars hiding under loose bark of trees of *Guaiacum officinale* L. (Zygophyllaceae), presumably after feeding at night on the foliage". This observation should be verified because this tree generally grows together with many leguminous species known as food plants of other species of *Melipotis*.

Melipotis contorta (Guenée, 1852)

(Fig. 75)

ID: Same size as larger specimens of *M. acontioides* and *M. fasciolaris*, but not as variable. Very similar to *M. famelica* with which it shares the white basal area of hindwing, and pale head and dorsal area of thorax. Easily separated from *M. famelica* by the irregular pale area at the end of cell. In the latter this is nearly rounded, whereas in *contorta* its lower end extends broadly towards the external margin.
DIST: Florida, Antilles.
GUANA: 4 specimens, 1989, 1990.
BIO: Unknown.

Melipotis famelica (Guenée, 1852)

(Fig. 76)

ID: Very similar to *M. contorta* in size and pattern. Color pattern not highly variable but sexually dimorphic. Females have pattern less contrasting than males. Some males have antemedial fascia tinged reddish brown.
DIST: Southern United States, Antilles, south to Venezuela, including Bermuda (Ferguson et al. 1991).
GUANA: 9 specimens, 1987, 1989, 1990.
BIO: Larvae on *Leucaena latisiliqua* (L.) Gillis & Stearn (Fabaceae) (Martorell 1976).

Melipotis ochrodes (Guenée, 1852)

(Fig. 77, 78)

ID: Easily confused with *M. indomita*, a neotropical species also recorded from the Greater Antilles but not collected on Guana. Highly variable. Basal area of hindwing semitranslucent gray, not whitish as in *M. contorta* or *M. famelica*, or almost dark gray as in *M. januaris*.
DIST: Antilles, Mexico, south to Brazil.
GUANA: 1 specimen, 1989.
BIO: Larvae on *Prosopis juliflora* (Sw.) DC. and *Schrankia portoricensis* Urb. (Fabaceae) (Martorell 1976).
COM: The specimen illustrated here, identical to the one collected on Guana, matches the series at BMNH identified as *M. ochrodes* (type specimen in MNHN, Paris, not examined). This species could represent only a smaller form of *M. indomita*.

Melipotis januaris (Guenée, 1852)

(Figs. 79, 80)

ID: On average slightly smaller than other *Melipotis* species on the island; sexually dimorphic. Males have forewing with very contrasting, dark brown pattern; females little contrasting, reddish brown. Easily distinguished from all other species on the island by almost entirely dark gray hindwing.
DIST: Southern United States, throughout Antilles, south to the Guianas and Colombia.
GUANA: 1 specimen, 1987.
BIO: Larvae on *Inga laurina* (Sw.) Willd. [as *I. fagifolia*] (Fabaceae) (Martorell 1976).

Ascalapha odorata (Linnaeus, 1758)

(Witch moth, black witch)

ID: Distinguished by very large size and broad wings showing bluish hue. Sexually dimorphic: males blackish gray, females lighter in color, with more contrasting pattern, and with three close, parallel, zig-zag, white lines crossing the wings.
DIST: Originally South American, now Pantropical.
GUANA: 3 specimens, 1982 (J. Lazell), 1988, 1989.
BIO: Larvae on various leguminous trees, including *Acacia*, *Cassia* and *Piptadenia* (Hayward 1969, Hayes 1975). Comstock (1936), Schreiter (1936) and Bourquin (1947) describe its life history and immature stages.
COM: Illustrated in several works, including Covell (1984), Ferguson et al. (1991), Hayes (1975), and Kimball (1965).

Epidromia lienaris (Hübner, 1823)

(Fig. 81)

ID: Large, 5 cm wing span; highly variable, gray fuscous species; forewing with conspicuous reniform black mark at middle and a postmedial, almost straight, pale line.
DIST: New World tropics.

GUANA: 1 specimen, 1990.
BIO: The larvae (reported as *E. pannosa* Guenée) were found on *Psidium longipes* (O. Berg) McVaugh (Myrtaceae), and were fed in the laboratory on *P. guajava* L., *Eugenia axillaris* (Sw.) Willd. (Myrtaceae), *Metopium toxiferum* (L.) Krug & Urb., and *Rhus copallina* L. (Anacardiaceae) (Dickel 1991).
COM: This is a widespread and highly polymorphic species, described more than 10 times (Becker 2001), and is commonly known in the literature as *E. zetophora* Guenée (Hayes 1975) and *E. pannosa* (Solis 1986, Dickel 1991).

Manbuta pyraliformis (Walker, 1858)
(Fig. 86)

ID: Medium sized, gray species. Forewing speckled with small black dots and with an oblique postmedial yellowish fascia; basal area of this fascia light gray, distal area dark gray. Males with pectinate antennae.
DIST: Florida and Antilles.
GUANA: 1 specimen, 1986.
BIO: Unknown.
COM: Poole (1989) listed this species under *Epidromia* Guenée, however, its genitalia and pectinate antennae are similar to those of species currently placed in *Manbuta* Walker (Becker 2001).

Ephyrodes cacata Guenée, 1852
(Figs. 82, 83)

ID: Resembling *M. absumens* in size and coloration (see above). Variable in color, from reddish brown to gray, mottled with black scales. Distinguished by the strongly angled termen of both wings, especially of the hindwing, forming a small tail. Male antennae strongly pectinate, female filiform.
DIST: Southern United States, throughout the Antilles, south to Colombia.
GUANA: 5 specimens, 1989.
BIO: Larvae on *Sesbania grandiflora* (L.) Pers. (Fabaceae) (Brunner et al. 1975).

Concana mundissima Walker, [1858]
(Fig. 84)

ID: Medium sized, silky shining gray species; forewing with fine, broken, transverse lines and a dark dot near middle, closer to dorsum. Hindwing semitranslucent white, edged with gray.
DIST: Florida, throughout the Antilles, south to Brazil.
GUANA: 7 specimens, 1989, 1990.
BIO: Unknown.

Massala asema Hampson, 1926
(Fig. 85)

ID: Medium sized, 3.5 cm wing span, stout bodied, pale brownish species. Wings shaded brown with ill defined, irregular brownish lines, nearly parallel to each other, from costa to dorsum.
DIST: Antilles.
GUANA: 2 specimens, 1989.
BIO: Unknown.

Lesmone formularis (Geyer, 1837)
(Figs. 90, 91)

ID: Medium sized, gray, sexually dimorphic species; males have two wide ill-defined dark gray bands across the wings; in spread specimens the bands are continuous, crossing both forewing and hindwing. Females lack these bands, however, the edge of the postmedial band in the hindwing is replaced by a straight yellow fascia running from apex to tornus.

DIST: Southern United States, throughout the New World tropics, including Galapagos.

GUANA: 3 specimens, 1987, 1989.

BIO: Larvae on *Cassia* and *Mimosa* (Fabaceae).

Lesmone hinna (Geyer, 1837)
(Figs. 87–89)

ID: Same size and similar to *L. formularis*, but distinguished by the conspicuous round, pale dot on the forewing cell.
DIST: Southern United States, throughout the Antilles, south to Brazil.
GUANA: 5 specimens, 1989.
BIO: Unknown.

Baniana relapsa (Walker, 1858)
(Figs. 92, 93)

ID: Small to medium sized, pale ochreous, sexually dimorphic species. Male forewing with conspicuous triangular black patch near base, close to dorsum; postmedial area black, fading gradually towards termen. Females lack the triangular patch and have the distal area lighter gray, resembling *P. immunis*, but readily distinguished by the dark brown anterior edge of thorax.
DIST: Restricted to the Antilles.
GUANA: 18 specimens, 1986, 1987, 1989, 1990.
BIO: Unknown.

Eulepidotis addens (Walker, 1858)
(Fig. 95)

ID: Small, grayish brown; forewing with three straight lines across, the medial and postmedial double, en-

closing a conspicuous ochreous band. Hindwing with diffuse orbicular mark followed by a short tail on the lower part of external margin.
DIST: Antilles.
GUANA: 12 specimens, 1987, 1989, 1990.
BIO: Larvae on *Inga vera* Willd. (Fabaceae) (Martorell, 1976).

Eulepidotis modestula (Herrich-Schäffer, 1869)
(Fig. 94)

ID: Small, white tinged yellow species, with lines crossing the forewing and a short tail on the hindwing similar to those of former species.
DIST: Antilles.
GUANA: 1 specimen, 1989.
BIO: Larvae on *Ceiba pentandra* (L.) Gaertn. (Bombacaceae) (Martorell 1976).

Toxonprucha diffundens (Walker, 1858)
(Fig. 96)

ID: Small sized, 1.8–2.2 cm wing span, gray species. Highly variable; most specimens have pattern as in *Kakopoda progenies* (see below).
DIST: Antilles, south to Brazil.
GUANA: 1 specimen, 1990.
BIO: Unknown, however, other species in the genus have been reared on *Acacia* (Fabaceae) (Crumb 1956).

Kakopoda progenies (Guenée, 1852)
(Fig. 97)

ID: Medium sized, 2.5–3.0 cm wing span; broad winged, dark gray moth. Wings crossed with many fine waving lines alternating black and pale. Very similar to, and easily confused with, *T. diffundens* (see above), but readily separated by size. Smaller specimens of this species are always larger than the largest of the latter. Males are also separated from *T. diffundens* by the pale brush at the tip of abdomen.
DIST: Florida, throughout the Antilles to Brazil.
GUANA: 4 specimens, 1987, 1989.
BIO: Unknown.
COM: We consider *Kakopoda cincta* Smith, 1900, **new synonym,** described from Florida, to represent the same species.

Parachabora abydas (Herrich-Schäffer, [1869])
(Fig. 98)

ID: Small to medium sized, cupreous brown species; hindwing semitranslucent white, bordered with a wide, diffuse gray area, and veins contrastingly gray.
DIST: Mexico, throughout the Antilles, south to Brazil.
GUANA: 3 specimens, 1988, 1989.
BIO: Unknown.

Cecharismena abarusalis (Walker, 1859)
(Fig. 99)

ID: Small brown species with forewing tinged copper and ferrugineous; apex of forewing pointed. Very similar to the following, but easily separated by the oblique straight medial line.
DIST: Florida, throughout Antilles, south to Brazil.
GUANA: 9 specimens, 1987, 1989.
BIO: Unknown, however, *C. nectarea* Möschler has been reared in Puerto Rico on *Caperonia palustris* (L.) A. St.-Hil. (Euphorbiaceae) (Schaus 1940).

Cecharismena cara Möschler, 1890
(Fig. 100)

ID: Same size and easily confused with *C. abarusalis*. Forewing with violet hue. Readily distinguished from the former by the medial oblique line curved in *C. cara* and straight in *C. abarusalis*.
DIST: Antilles.
GUANA: 2 specimens, 1989.
BIO: Unknown (see *C. abarusalis*).

Glympis eubolialis (Walker, [1866])
(Fig. 101)

ID: Small gray species with forewing crossed, in the middle, with ill defined, straight dark brown band; area distad to this band usually darker than basal area. Shape, size, and color similar to *Bleptina* species (below). Easily distinguished from *Bleptina* by the porrect labial palpi, which are long and upturned in *Bleptina* (see below).
DIST: Antilles.
GUANA: 22 specimens, 1989, 1990.
BIO: Unknown, however, the larvae of *G. concors* were found feeding on *Sesbania grandiflora* (L.) Pers. (Fabaceae) in Puerto Rico (Martorell 1976).

Herminiinae

Drepanopalpia lunifera (Butler, 1878),
new combination
(Figs. 102, 103)

ID: Small to medium sized, 1.5–2 cm wing span, dimorphic, dark fuscous species. Males have very long labial palpi thickly covered with long scales, reflexed over the head to the posterior margin of thorax. Females have long, porrect palpi. Male forewing with a reniform, pale mark at end of cell; in females this mark is reduced to small dot.
DIST: Antilles.

GUANA: 9 specimens, 1987, 1989.
BIO: Unknown.
COM: The series in VOB, including specimens from Guana Island, Tortola, Puerto Rico and Cuba, was compared with material in BMNH. Males match the type of *Drepanopalpia polycyma* Hampson 1898, **new synonym,** and females match the type of *Hypena lunifera* Butler 1878. *D. polycyma* is also curated in BMNH as a synonym of *Mastigophorus latipennis* Herrich-Schäffer. There is no specimen of *M. latipennis* in Coll. Gundlach (IES, Havana) where the type material of the Cuban species described by Herrich-Schäffer is supposed to be deposited. It is possible that some material is in MNHU, Berlin. It is possible that both *M. lunifera* and *M. polycyma* are junior synonyms of *M. latipennis*.

Lascoria orneodalis (Guenée, 1854)
(Figs. 104, 105)

ID: Small to medium sized, 1.5–2 cm wing span, dark fuscous species, resembling *D. lunifera*. Males have labial palpi as in the former species, but the forewing has a strong indentation at middle of external margin. Females have long upcurved palpi as in *Bleptina*.
DIST: Florida, Antilles.
GUANA: 3 specimens, 1987.
BIO: Larvae on tomato leaves (Solanaceae) (Martorell 1976).

Bleptina hydrillalis Guenée, 1854
(Fig. 108)

ID: Dark brown, 1.8–2.0 cm wing span; forewing crossed by three, well defined, pale lines: a straight line near base, and two sinuate lines, one after the reniform mark on cell, the other before external margin. Reniform mark usually pale, but black in some specimens.
DIST: Southern United States, Central America, Antilles.
GUANA: 34 specimens, 1986, 1989.
BIO: Unknown.

Bleptina caradrinalis Guenée, 1854
(Figs. 106, 107)

ID: About same size as *B. hydrillalis*, pale, variable. In those specimens with a dark band across forewing, the band is closer to the middle.
DIST: Southern United States, throughout the Antilles, South to Brazil.
GUANA: 6 specimens, 1989.
BIO: Larvae reported on dead leaves (Kimball 1965).

Bleptina menalcasalis Walker, [1859]
(Figs. 109, 110)

ID: Medium sized, 2.2–2.7 cm wing span, pale species. Forewing diffusely crossed with ill defined, irregular lines. Distinguished from other noctuids of same size by the long, upcurved labial palpi.
DIST: Antilles, south to Venezuela.
GUANA: 27 specimens, 1986, 1987, 1989, 1990.
BIO: Unknown, but likely dead leaves (see *B. caradrinalis*).

Bleptina aracalis (Hampson, 1901)
(Figs. 167, 168)

ID: Very small, 1–1.3 cm wing span, variable, fuscous to dark fuscous species. Forewing often with a dark gray fascia on basal fourth; area basad to fascia paler than rest of wing. Easily distinguished from other small species on the island by the very long upcurved labial palpi and by three very small, round, pale dots on forewing, the first just outside the basal band and the two others close together at end of cell.
DIST: Antilles and Florida (Dickel 1991). The first author recently collected one male and one female in Mexico: Tamaulipas, El Encino.
GUANA: 12 specimens, 1987, 1990.
BIO: Unknown (see previous species).

Hypeninae

Hypena lividalis (Hübner, 1790)
(Fig. 111)

ID: Small, gray; forewing with straight, white postmedial line; area basad of line olive, area distad gray.
DIST: South Palearctic, Pantropical.
GUANA: 2 specimens, 1989, 1990.
BIO: Larvae on *Urtica* and *Parietaria* spp. (Lödl 1994:502).
COM: In a revision of the genus, Lödl (1994) listed six synonyms under *H. lividalis*, two of them originally described from material collected in the Antilles.

Hypena minualis (Guenée, 1854)
(Fig. 166)

ID: Small, dark gray species with little contrasting markings. Forewing with a slightly paler basal area, separated from the external dark area by an ill defined oblique, dark gray line from near base of costa to middle of dorsum; a faint dash near apex. The palpi resemble those of female *D. polycyma*, but readily separated from the latter by the absence of the pale dot on cell.
DIST: Antilles, south to Brazil.
GUANA: 3 specimens, 1989.
BIO: Larvae on *Sida rhombifolia* L. (Malvaceae) (Ferguson et al. 1991).

ARCTIIDAE

Arctiinae

Hypercompe simplex (Walker, 1855)

(Figs. 112, 114)

ID: Large, white; forewing with outer half translucent, basal half with a series of annulate black edged spots. Abdomen orange with subdorsal pairs of dark bluish dots. Females much larger than males; spots on the abdomen white.
DIST: Puerto Rico, Virgin Islands and Lesser Antilles.
GUANA: 6 specimens, 1987, 1989.
BIO: Martorell (1976) lists over a dozen hostplants, including *Cedrela* (Meliaceae), *Cissus* (Vitaceae), *Erechtotes* (Compositae), *Erythrina* (Fabaceae), *Ipomaea* (Convolvulaceae), tomato, banana, beans, guava, eggplant and *Solanum torcum* Sw. (Solanaceae).
COM: Commonly found in the literature, including in Martorell (1976), as *Ecpantheria icasia* (Cramer), a similar species from continental South America.

Calidota strigosa (Walker, 1855)

(Fig. 115)

ID: Large, gray moth with pink abdomen. Forewing with veins darker than ground color, shortly interrupted with pale. Cannot be confused with any other moth from the island.
DIST: Antilles and Southern United States.
GUANA: 28 specimens, 1984, 1987, 1989, 1990.
BIO: Dyar (1901:270) reared this species on *Guettarda elliptica* Sw. (Rubiaceae) and described its larvae; Martorell (1976) lists the same plant as its host in Puerto Rico.
COM: Franclemont (1983) and Watson & Goodger (1986) resurrected, respectively, *C. laqueata* (Edwards 1887) (type-locality: USA) and *C. cubensis* (Grote [1866]) (type-locality: Cuba) from the synonymy of *strigosa*. We believe they are only geographical forms of the same species.

In the resting position, the adult looks cryptic but when touched it opens the wings exposing the bright pink abdomen that seems to be aposematic. A specimen was picked from the collecting sheet by a pearly-eyed thrasher, *Margarops fuscatus* (Vieillot), and rejected. The same specimen was placed back on the wall where the bird often perched. The same bird picked up the moth again and then dropped it again (VOB pers. obs.).

Eupseudosoma involutum (Sepp, [1855])

(Fig. 116)

ID: Medium sized, white moth, with red abdomen. Cannot be confused with any other species in the island.
DIST: Southern United States, throughout Antilles, south to Argentina.
GUANA: 4 specimens, 1987.
BIO: Larvae on guava (*Psidium guineense* Sw.), *Eugenia*, *Eucalyptus*, and other Myrtaceae.

Utetheisa ornatrix (Linnaeus, 1758)

(Fig. 117)

ID: Medium sized, variable white moth. Most specimens have the forewing white, tinged pink, and a pink costa interrupted regularly by dark gray dots. In other specimens most of the white is replaced by pink and the wing is crossed with transverse rows of dark gray dots. The proportion of gray in the hindwing also varies; in some specimens it is restricted to the borders, while in others it covers most of the area.
DIST: Southern United States, throughout the Antilles, south to Argentina.
GUANA: 5 specimens, 1984, 1988, 1989, 1990.
BIO: Larvae on various species of *Crotalaria* (Fabaceae).
COM: Commonly found flying during the day in open, disturbed areas where its host plants often grow. Pease (1973) discussed the variation of this moth in the Virgin Islands.

Utetheisa pulchella (Linnaeus, 1758)

(Fig. 118)

ID: Easily confused with the dotted form of *U. ornatrix* (see above); easily separated by the dots on dorsum of thorax. *Utetheisa ornatrix* has three pairs; *U. pulchella* has only three dots.
DIST: Africa and Asia, now established in the New World tropics, but very rare in collections. The first author collected two specimens in Brazil, one at Pipa Beach, south of Natal, Rio Grande do Norte, and one in Planaltina, DF, near Brasília, which is the southern most record for the species in the New World.
GUANA: 1 specimen, 1990.
BIO: Larvae on *Myosotis* (Boraginaceae) and grasses (Hampson 1901).

Pericopinae

Composia credula (Fabricius, 1775)

(Fig. 113)

ID: Large, black, with body and wings dotted white; forewing with deep red markings on basal half below costa.
DIST: Endemic to the Antilles, this is the only species of the genus found on the Puerto Rican Bank.
GUANA: 10 specimens, 1984, 1986, 1987, 1989.
BIO: Unknown. Its closest relative, *C. fidelissima*

Herrich-Schäffer, from Cuba and Florida, has been reared on *Canavalia* (Fabaceae), oleander (*Nerium*), and *Echites* (Apocynaceae) (Kimball 1965).

COM: Commonly referred to in the literature by its junior synonym *C. sybaris* (Cramer). It is a crepuscular moth, commonly found flying along the trails before dark. Todd (1982) states it "occurs throughout the Greater Antilles, and south to Brazil" but that the "continental distribution needs to be studied." Previous authors (Forbes 1930, Bates 1933) considered it to be endemic to the Antilles. In the series in USNM there is only one non-Antillean specimen, an old specimen labeled only "Brazil," which we believe to be mislabeled. We are not aware of any other continental records for this large and colorful species, which would not be overlooked by collectors.

Ctenuchinae

Empyreuma pugione (Linnaeus, 1767)

(Fig. 119)

ID: Large, wasp-like moth with conspicuous red wings and black body. Wings bordered dark gray, and body tinged iridescent green.

DIST: Apparently restricted to the Puerto Rican Bank.

GUANA: 9 specimens, 1984, 1987, 1989, 1990.

BIO: Larvae on oleander, *Nerium oleander* L. (Apocynaceae) (Gundlach 1881).

COM: Day flying; very likely a Müllerian mimic of *Pepsis rubra* (Drury) (Hymenoptera: Pompilidae) (R. Snelling det.), as its larvae feed on a toxic plant. Similar to other arctiids, the larvae presumably sequester alkaloids from the host plant. Referred to in the older literature as *E. lichas* (Cramer).

Horama pretus (Cramer, 1777)

(Fig. 121)

ID: Large, wasp-like, ochreous brown species, distinguished by the broad white band across base of abdomen.

DIST: Antilles.

GUANA: 36 specimens, 1984, 1985, 1987, 1989, 1990.

BIO: Larvae on *Cassine xylocarpa* Vent. [as *Elaeodendron xylocarpum*] (Celastraceae) (Wolcott 1951).

COM: Day flying, commonly seen visiting flowers. Presumably a Müllerian mimic of *Polistes major* Palisot de Beavois (Hymenoptera: Vespidae) (R. Snelling det.).

Horama panthalon (Fabricius, 1793)

(Fig. 120)

ID: Similar but smaller than *H. pretus*. Distinguished by pattern on abdomen: only a small white dash across base, followed by alternating ochreous and black bands.

DIST: Southern United States, throughout the Antilles, south to southern Brazil.

GUANA: 13 specimens, 1986, 1989, 1990.

BIO: Unknown.

COM: Dietz and Duckworth (1976) divided the species into three subspecies, assigning the Antillean population to the nominal form. Very likely a Müllerian mimic of *Polistes crinitus* (Felton) (Hymenoptera: Vespidae) (R. Snelling det.).

Cosmosoma achemon (Fabricius, 1781)

(Fig. 122)

ID: Small, wasp-like moth with unique combination of colors. Mostly orange with vertex of head and subdorsal sides of abdomen metallic bluish green; forewing with translucent areas.

DIST: Antilles south to Brazil.

GUANA: 10 specimens, 1989, 1990.

BIO: Unknown.

Eunomia colombina (Fabricius, 1793)

(Fig. 123)

ID: Medium sized, wasp-like moth with black body and translucent wings. Forewing bordered black with a dark, red mark at end of cell connected with costa. Thorax striped white; abdomen with a carmine red band across the base, expanding laterally, followed by a white band, partially interrupted dorsally; the rest banded with alternating, narrow, red and white lines.

DIST: Antilles. Hampson (1898) gives also Honduras and Brazil, but the material studied by him should be checked.

GUANA: 1 specimen, 1989.

BIO: "Oruga en las convolvulaceas" (Gundlach 1881).

COM: Listed as *E. columbina*, a misspelling, by Wolcott (1951).

Nyridela chalciope (Hübner, [1831])

(Fig. 124)

ID: Medium sized, wasp-like, black moth with transparent wings. Head, thorax dorsally, base of wings, legs, and abdomen dorsally and laterally with iridescent blue. Antennae yellow. Forewing bordered black with an oblique transverse band from middle of costa to tornus.

DIST: Described from Havana, occurs throughout the West Indies and Central America, south to Panama.

GUANA: 1 specimen, 1990.

BIO: Larvae on *Cupania americana* L. (Sapindaceae) (Möschler 1890).

COM: Some authors regard the Central American

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population as belonging to a separate species, *N. xanthocera* (Walker).

Lithosiinae

Afrida charientisma Dyar, 1913
(Fig. 169)

ID: Very small, 8–12 mm wing span, slightly variable species. Forewing mostly grayish, slightly tinged with green, crossed by alternating, ill defined whitish and dark gray bands. Easily recognized by the antemedial whitish band across forewing, starting from costa and running obliquely outwards to middle, then bent to base towards dorsum.
DIST: Antilles.
GUANA: 27 specimens, 1985, 1986, 1990.
BIO: Unknown, however, most of the species of this subfamily are lichen-feeders (Hampson 1900).

Progona pallida (Möschler, 1890)
(Fig. 170)

ID: Small, pale species, with no markings. Forewing slightly dusted gray.
DIST: Previously known only from Puerto Rico.
GUANA: 6 specimens, 1986, 1990.
BIO: Unknown.

Lomuna nigripuncta (Hampson, 1900)
(Fig. 171)

ID: Small, 1.3–1.7 cm wing span, whitish moth. Forewing dusted gray, conspicuously spotted with small, dark gray dots.
DIST: Previously known only from Puerto Rico (Field 1952).
GUANA: 29 specimens, 1984, 1985, 1986, 1990, 1991.
BIO: Unknown.

GEOMETRIDAE

Oenochrominae

Almodes terraria Guenée, [1858]
(Fig. 134)

ID: Medium sized, gray species. Wings densely dusted with dark gray scales and crossed with pale and dark ill defined, irregular bands. Males easily recognized by the strongly pectinate antennae nearly the length of forewing. Females have a slight olivaceous tinge, and external margins of both wings more strongly dentate.
DIST: Southern United States, throughout the Antilles to Colombia.
GUANA: 2 specimens, 1990.
BIO: Unknown.

Ennominae

Pero rectisectaria (Herrich-Schäffer, [1855])
(Figs. 125, 126)

ID: Medium sized, sexually dimorphic, variable species. Males with ground color varying from pale to dark brown; forewing with antemedial band, when visible, strongly bent to the base near costa, postmedial band nearly straight, with area distad to it much paler than rest of wing. Females more reddish brown. Easily distinguished from other species of same size by the conspicuously scalloped forewing margin near apex.
DIST: Puerto Rico, throughout the Lesser Antilles.
GUANA: 42 specimens, 1986, 1987, 1988, 1989, 1990.
BIO: Unknown.
COM: Poole (1987), who revised this large genus, stated that "Either it is rare, or it occurs in areas not commonly collected." Judging from the long series collected by us, it is not rare. It was common in October 1989, just after hurricane Hugo, when the first author had dozens of specimens on the light and selected 10 males and 4 females.

Oxydia vesulia (Cramer, [1779])
(Fig. 127)

ID: Large, extremely variable species, with no two identical specimens. Ground color of both wings varying from pale yellow, through pale gray to brown, clouded and irrorated in various degrees by gray. Forewing with an oblique post medial band from apex to near middle of dorsum. Easily recognized by the white vertex of head.
DIST: Southern United States, Antilles, south to Argentina.
GUANA: 4 specimens, 1987.
BIO: Larvae on *Acalypha* (Euphorbiaceae), *Cinchona* (Rubiaceae), *Cissampelos* (Menispermaceae), *Citrus* (Rutaceae), *Persea* (Lauraceae), *Rosa* (Rosaceae), and *Securidaca* (Polygalaceae) (Martorell 1976, Torres 1992).

Erastria decrepitaria (Hübner, [1823])
(Figs. 128, 129)

ID: Medium sized, yellow moth. Sexually dimorphic: males suffused olive, especially forming a wide bar along external margin; females more yellowish with the external olive area reduced to a faint irregular band, with a conspicuous dark spot on the band near the tornus.
DIST: Southern United States, throughout Antilles, south to Brazil.
GUANA: 4 specimens, 1987, 1989.
BIO: Unknown.

Sphacelodes fusilineatus (Walker, 1860), **revised status**
(Figs. 130, 131)

ID: Medium sized, dimorphic species. Males dark olive brown; forewing crossed with three equidistant, nearly parallel lines and with a subtriangular gray mark on costa between medial and postmedial line. Females brown with lines same as males, but mark on costa absent.
DIST: Antilles.
GUANA: 25 specimens, 1986, 1988, 1989, 1990.
BIO: Unknown.
COM: This species has been confused in the literature with *S. vulnerarius* (Hübner). The two differ in many features, the most obvious the color of antenna and costal mark of forewing. In *S. fusilineatus* the antenna and costal mark are light gray, whereas in *vulnerarius* the antenna is ochreous and the costal mark reddish brown. *Sphacelodes fusilineatus* was described from material with no locality label. There is a series in VOB collected in Guana, Tortola, St. Thomas, and Cuba. One of these was compared with and matches the type of *S. fusilineatus*. It is very likely that this is the species referred to by Kimball (1965:192) as "5221, 1 S. SP.", and listed by Ferguson (1983:95) as *S. haitiaria* Oberthür. The series of *S. vulnerarius* in VOB was collected in Cuba, Mexico, and Brazil. In Cuba, *S. fusilineatus* was captured at Pinares de Mayarí, Holguín, while those of *vulnerarius* at Viñales, Pinar del Río. The first locality is dry, similar to the conditions in St. Thomas and Guana, while the second is humid, similar to those areas on the American continent from where the series of *S. vulnerarius* came.

Macaria paleolata (Guenée, [1858])
(Fig. 132)

ID: Small, slightly variable, pale species. Wings crossed by two ill defined, nearly straight bands; area distad to postmedial band darker than rest of the wing. Distinguished by head and anterior margin of thorax ochreous.
DIST: Antilles.
GUANA: 24 specimens, 1989, 1990.
BIO: Unknown, however, other species of this large genus feed on leguminous species (Fabaceae).
COM: This species was transferred from *Semiothisa* to *Macaria* by Scoble (1999). It is very likely that other, similar species of the large genus *Macaria* occur on the island.

Patalene ephyrata (Guenée, [1858])
(Fig. 133)

ID: Small, variable, pale yellow to pale brown species. Forewing with antemedial band nearly evenly rounded, postmedial band straight to near apex then strongly angled basad to costa. Hindwing with a single, straight band near middle. Distinguished by pointed apex and the sinuate external margin of forewing.
DIST: Antilles (Herbulot 1984).
GUANA: 41 specimens, 1986, 1987, 1988, 1989, 1990.
BIO: Larvae on *Ficus* (Moraceae) and *Ricinus* (Euphorbiaceae) (Brunner et al. 1975).

Cyclomia mopsaria Guenée, [1858]
(Figs. 182, 183)

ID: Small, extremely variable species. Ground color often pale tinged reddish brown, to dark reddish brown. Forewing varying from unmarked to marked with transverse, ill defined, irregular lines. Hindwing pale to orange, often bordered with reddish brown. Similar to small noctuids such as *Eublemma* spp., but distinguished by the bipectinate antenna in males. Distinguished from other small geometrids by sharply pointed, porrect labial palpi, unusually long for a geometrid.
DIST: Antilles, south to Brazil.
GUANA: 11 specimens, 1987, 1989, 1990.
BIO: Unknown, however, *Erythroxylum havanense* Jacq. (Erythroxylaceae) has been listed as food plant of "*Cyllomia* sp. [presumably a misspelling] Un gusano medidor," in Cuba (Brunner et al. 1975).
COM: Its extreme variation led to its description several times. It is likely that after revision more names will be added to the six junior synonyms currently listed (Becker in prep.).

Geometrinae

Eueana simplaria Herbulot, 1986
(Figs. 12–14, 141, 142)

ID: Small to medium sized, bluish green species. Lines on wings almost indistinct. Vertex of head white; abdomen with traces of a whitish line dorsally. Genitalia (Figs. 12–14) very similar to those of *E. niveociliaria* (Herrich-Schäffer), illustrated in Ferguson (1985: fig. 25a–e).
DIST: Guadaloupe.
GUANA: 17 specimens, 1986, 1989.
BIO: Unknown, but Scoble (1999) records *E. niveociliaria* from Rhamnaceae.
COM: Of all "greens" from the island this is the only bluish species, and it is slightly larger than the other species. The subfamily was revised for North America by Ferguson (1985) and for the neotropics by Pitkin (1996).

Phrudocentra centrifugarium (Herrich Schäffer, 1870)
(Figs. 143–146)

ID: Medium sized, extremely variable, bright green species. Some specimens, usually males, have only

small, dark brown dots on wings, one on cell and the others along what would be the antemedial and postmedial lines; others have larger marks, of various sizes and shapes, whitish or brownish, above tornus. Abdomen has a series of minute, white dots dorsally, one on each segment.
DIST: Florida, throughout Greater Antilles to Puerto Rico (Ferguson 1985).
GUANA: 4 specimens, 1990.
BIO: Larvae on *Myrica cerifera* L. (Myricaceae) (Scoble 1999).

Chloropteryx paularia (Möschler, 1886)
(Fig. 186)

ID: Small, olivaceous species. Wings with antemedial and postmedial rows of minute whitish dots forming irregular lines. This is the only species of the green Geometrinae with this color.
DIST: Florida, throughout the Antilles.
GUANA: 11 specimens, 1987, 1989, 1990.
BIO: Larvae on *Myrica cerifera* L. (Myricaceae) in Florida (Ferguson 1985).

Synchlora frondaria (Guenée, [1858])
(Fig. 187)

ID: Small, bright green species. Distinguished from *S. cupedinaria* by the concolorous fringes.
DIST: United States, throughout the Antilles, south to Argentina.
GUANA: 29 specimens, 1986, 1988, 1989, 1990.
BIO: Larvae on *Stilingia* (Euphorbiaceae), *Pluchea*, *Bidens*, *Chrysanthemum*, *Helianthus* (Asteraceae), *Rubus* (Rosaceae), *Glycine max* (L.) Merr., and *Prosopis* (Fabaceae) (Ferguson 1985).

Synchlora cupedinaria (Grote, 1880)
(Fig. 188)

ID: Small, bright green species. Wings thickly bordered with brown. Thorax and abdomen brown dorsally; abdomen usually with white dots dorsally. Easily distinguished from the other green Geometrinae by the brown thorax and abdomen.
DIST: Florida, throughout Greater Antilles to Virgin Islands, to Nevis (Herbulot 1984).
GUANA: 41 specimens, 1985, 1986, 1988, 1989, 1990.
BIO: Larvae on *Lantana camara* L. (Verbenaceae) (Scoble 1999).

Sterrhinae

Of all the moths treated in this paper, the Sterrhinae have proven to be most difficult to identify. We have tried to reflect the species concepts as represented in the BMNH and USNM collections, and have followed the generic placements in Scoble (1999). Our dissections of types, as well as Guana specimens, indicate that many problems exist in the existing classification, and full resolution of the names is beyond the scope of this paper.

Semaeopus malefidarius (Möschler, 1890)
(Fig. 135)

ID: Medium sized, pale moth densely irrorated with reddish brown scales. Wings crossed with ill defined, hardly contrasting, irregular bands, slightly darker than ground color.
DIST: Puerto Rico, Virgin Islands.
GUANA: 14 specimens, 1989, 1990.
BIO: Unknown.
COM: Closely related to *S. castarium* (Guenée) from the Greater Antilles.

Leptostales noctuata (Guenée, [1858])
(Figs. 136, 137)

ID: Small to medium sized, pale species, densely irrorated with olive scales. Forewing with antemedial and postmedial bands darker than ground color, termen sinuate, apex pointed. Males show a dark mark on cell; in females this mark is reduced and faint.
DIST: Antilles.
GUANA: 19 specimens, 1986, 1987, 1988, 1989, 1990.
BIO: Unknown.

Acratodes suavata (Hulst, 1900)
(Fig. 185)

ID: Small, white species; wings crossed with three ill defined, little contrasting, grayish bands; medial and postmedial closer together. The only white geometrid on the island with no contrasting marks on wings.
DIST: Southern United States, Antilles.
GUANA: 31 specimens, 1985, 1986, 1987, 1988, 1989, 1990.
BIO: Larvae on *Randia aculeata* L. (Rubiaceae) (Kimball 1965).
COM: It is very likely that *A. virgotus* (Schaus), described from Jamaica, is a synonym. Our series matches the type of *A. virgotus* in USNM.

Lobocleta nymphidiata (Guenée, [1858])

ID: Small, white species with wings crossed with 4–5 narrow, irregular dark brown lines, consisting of rows of dark dots.
DIST: Antilles.
GUANA: 1 specimen, 1985.
BIO: Unknown.

Scopula laresaria Schaus, 1940
(Fig. 178)

ID: Small, pale whitish, irrorated with scattered gray scales; forewing crossed with poorly defined, irregular, narrow pale yellowish lines. Same size and color as *L. nymphidiata*, but readily distinguished by the blackish vertex of head, white in *L. nymphidiata*.
DIST: Puerto Rican bank.
GUANA: 9 specimens, 1985, 1988, 1989.
BIO: Unknown.

Idaea sp., probably *I. fernaria* (Schaus, 1940), **new combination**
(Figs. 179, 180)

ID: Small, light gray, densely irrorated with dark gray scales; wings crossed with three, ill defined, irregular, narrow, dark gray lines more or less interrupted, giving the impression that they are densely dotted; both wings with black dot on cell. Females slightly lighter than males.
DIST: Antilles.
GUANA: 27 specimens, 1985, 1986, 1988, 1987, 1989.
BIO: Unknown.
COM: Based on the structure of male genitalia and eigth sternite of a male paratype, this species does not belong in *Scopula*, so we are provisionally transferring it to *Idaea fernaria*, **new combination,** following the generic concept of Holloway (1997). The Guana specimens are very similar to the type series of *Idaea fernaria*, but differ in the size of the long expansion on the juxta. In Guana specimens it is much longer than in a paratype of *I. fernaria*, nearly the size of the valvae, expanding beyond the uncus. *Idaea fernaria* is externally similar to *I. amnesta* (Prout, 1922), from Jamaica, but the male genitalia are very different.

"*Idaea*" *monata* (Forbes in Ramos, [1947])
(Figs. 172, 173)

ID: Very small, gray species; antemedial and postmedial lines dark gray, strongly contrasting, especially in the males; in some males the area between the two lines are dusted dark gray, forming a wide band across the wings.
DIST: Antilles.
GUANA: 29 specimens, 1985, 1986, 1989, 1988, 1990.
BIO: Unknown.
COM: This species is very similar to *Idaea insulensis* (Rindge, 1958), from Florida, but differs in the base of the valvae being more expanded in *I. insulensis* than in *I. monata*, although study of extensive series could show this to be interspecific variation. Based on the structure of the male genitalia (Rindge 1958:fig. 9), neither *I. monata* or *I. insulensis* are properly placed in *Idaea* (cf. Holloway 1997), but recognition of the proper generic placement is beyond the scope of this paper. Weakly patterned individuals of *I. monata* are similar externally to *Lobocleata nataria* (Walker, 1866), but the male genitalia do not match the type of *L. nataria* in BMNH.

Idaea minuta (Schaus, 1901)
(Figs. 176, 177)

ID: Very small, 8–10 mm wing span, pale species. Wings crossed with several, narrow, ill defined, irregular, light brown lines. One of the smallest geometrid species on the island.
DIST: Antilles, USA.
GUANA: 19 specimens, 1985, 1987, 1988, 1989.
BIO: Unknown.
COM: Specimens belonging to this series were identified as *I. minuta* by C. Covell, and also matched the type of *Ptychopoda curtaria* Warren 1904, **new synonym,** from Jamaica, in BMNH.

Idaea eupitheciata (Guenée, [1858])
(Figs. 174, 175)

ID: Very small, sexually dimorphic, pale species, with wings crossed with irregular reddish brown bands. Males paler than females; forewing with small tuft of dark scales near dorsum; hindwing with a small tail near tornus. Females darker than males and without the tufts and tails.
DIST: Antilles.
GUANA: 16 specimens, 1985, 1988, 1989, 1990.
BIO: Unknown.

Leptostales phorcaria (Guenée, [1858])
(Fig. 181)

ID: Small, reddish brown; wings crossed with narrow, ill defined, irregular, yellowish lines; thorax dorsally and forewing costa yellow. Cannot be confused with any other species on the island.
DIST: Antilles.
GUANA: 2 specimens, 1989.
BIO: Unknown.

Leptostales oblinataria Möschler, 1890
(Fig. 184)

ID: Small, olivaceous species, with a broad reddish brown band across the forewing, delimited by medial and postmedial bands. Some specimens with this band faded. Cannot be confused with any other species on the island.

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DIST: Southern United States, Antilles, into South America (Covell 1969).
GUANA: 15 specimens, 1988, 1989, 1990.
BIO: Unknown.

Larentiinae

Obila praecurraria (Möschler, 1890)
(Fig. 138)

ID: Large species with velvet moss green forewing and orange ochreous hindwing. Forewing crossed with numerous alternating pale and dark gray waving bands. Hindwing with a wide gray band extending inwards, along internal margin, to the base. Female with middle of forewing crossed with a wide, irregular whitish band.
DIST: Antilles.
GUANA: 1 specimen, 1989.
BIO: Unknown.
COM: Our specimen matches the type of *Pterocypha xantholiva* Warren, 1895, synonymized with this by Schaus (1940:326).

Pterocypha defensata Walker, 1862, **revised status**
(Figs. 139, 140)

ID: Medium sized, variable, moss gray. Similar to *O. praecurraria*, but slightly smaller and lacking the orange ochreous hindwing color.
DIST: Southern United States, Antilles.
GUANA: 20 specimens, 1986, 1987, 1989, 1990.
BIO: Unknown.
COM: Commonly referred to in the literature, including Scoble (1999), by its synonym *P. floridata* (Walker), but *P. defensata* was described in 1862 and *P. floridata* in 1863, so *defensata* has priority.

HYBLAEIDAE

Hyblaea puera (Cramer, 1777)
(Fig. 150)

ID: Medium sized, fuscous species with hindwing beautifully decorated with yellow to orange patches. Abdomen dorsally crossed with narrow lines behind each segment.
DIST: Pantropical.
GUANA: 2 specimens, 1989, 1990.
BIO: Larvae on *Crescentia cujete* L., *Spatodea campanulata* P. Beauv., *Tabebuia heterophylla* (DC.) Britton (Bignoniaceae), and *Petitia domingensis* Jacq. (Verbenaceae) (Martorell 1976). Considered as a minor pest of forest trees in Puerto Rico (Torres 1994). Immature stages described by Singh (1995).

COM: Taxonomy of the related species discussed by Berio (1967), but *H. puera* apparently represents a species complex (Shaffer & Nielsen 1996).

COSSIDAE

Psychonoctua personalis Grote, 1865
(Figs. 147–149)

ID: Medium to large, 2–4.5 cm wing span, narrow winged, gray species. The short, strongly pectinate antennae, and abdomen thickly clothed with long scales makes it easily recognized from any other large moths on the island.
DIST: Antilles and Mexico.
GUANA: 5 specimens, 1990.
BIO: The larvae are wood borers in many trees, sometimes causing severe damage to orange, coffee, white mangle, sea grape, etc. (Wolcott 1951).

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APPENDIX

Catabenoides Poole, new genus

[The following new generic description was intended to appear in a fascicle of the series *Moths of America North of Mexico*. Because this fascicle will not be published in the foreseeable future, the author has permitted us include the new generic name here, in order to allow us to describe *Catabenoides lazelli* in the proper place.]

Type-species: *Adipsophanes terminellus* Grote, 1883

Catabenoides contains the majority of the species previously placed in *Catabena*. The genus appears to be an outlier of a large group in southern South America, primarily Paraguay and Argentina. The genus is postulated to be closest phylogentically to *Catabena* and *Neogalea*, but it has a number of curious synapomorphies making its affinities somewhat problematical. The principle identifying characters are in the male and female genitalia. In the male valve the bottom margin of the sacculus in both the right and left valves is produced into a long process separate from the clasper. The ventral margins of the valvae have strong elongate setae. The sacculus is lightly chitinized proximal to the clasper separating off a much more heavily sclerotized plate.

In addition to the three species known from North America (the type species, *C. vitrina* (Walker), **new combination,** and *C. divisa* (Herrich-Schäffer), **new combination**), there is one previously described species: *Catabenoides scorsa* (Todd) (*Catabena scorsa* Todd), **new combination,** from the Galapagos Islands. There are two undescribed species in the West Indies [one of these is described herein as *C. lazelli*], one undescribed species from central Mexico, and at least two unnamed species from Paraguay. The exact affinities of *Catabenoides*, *Catabena*, and *Neogalea* with the Argentina and Chilean faunas remain to be determined. The single remaining described species in "Catabena" of Poole (1989), *Laphygma terens* Walker, was described from "Venezuela." The type is rubbed and its abdomen is missing. I have not been able to match it with any specimens from the extensive Venezuela material in the USNM. It appears superficially to be a *Catabenoides*. Therefore for book-keeping purposes, I place it as *Catabenoides terens* (Walker), **new combination.**

Description. Head: Lashes absent; eyes large, naked; frons slightly swollen, very closely scaled; antenna simple, faintly ciliate; palpi unremarkable for the tribe; proboscis normal; two thin ridges of flattened scales between the bases of the antennae. **Thorax:** Patagia capable of being raised in a hood; vestiture of dorsum of thorax of flattened scales without hairs; slight metathoracic tuft; vestiture of wings of flattened scales; no sign of sexually modified scales in male. **Prothoracic leg:** Tibia with later ridge of hair giving it a flattened look; no tibial claw; tibia approximately as long as first three tarsal segments; first four tarsal segments with three rows of spines; tarsal claw without a tooth. **Mesothoracic and metathoracic legs:** Proximal third of tibia with tuft of long hairs and scales; tibia approximately as long as first three tarsal segments. **External tympanic region:** Approximately as in *Supralathosea* Barnes & Benjamin, however, first tergum much shorter than in *Catabena* and *Supralathosea* and with a strong definite proximal lip as in *Apharetra* Grote; hood strong. **Internal tympanic region:** Not examined. **Abdomen:** Very weak tuft on first tergite; male with basal hair pencils and accessory hair pencils in known species. Eighth sternum with strong row of hairs in middle of U-shaped pleurite. **Male genitalia** (Figs. 2, 3): Valvae characterized by production of ventral margin of sacculus into a process of various shapes; ventral margin of valvae with strong modified setae; a weak unsclerotized area before origin of clasper; uncus swollen with an apical tooth; juxta a single pointed plate; vesica in type species elongate-ovate, connected by a short neck to body of aedeagus; type species with a group of elongate, fused spines at apex of vesica and with groups of short, stubby spines near the middle and ventral margin of the vesica; vesica variable in other species. **Female genitalia:** Ovipositor lobes square, unmodified; ductus bursa well sclerotized, elongate, mushroom shaped in type species, separated by a distinct junction from the heavily sclerotized upper part of bursa; bursa bilobed, but lobes not distinctly separate; corpus bursae with stellate ridges, but no signum. **Larva and foodplants:** Unknown for North American species but recorded as *Lantana peduncularis* Andersson (Verbenaceae) in *Catabenoides scorsa* from the Galapagos.

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Family reassignments and synonymy of some taxa of Neotropical Microlepidoptera

Vitor O. Becker [1]

ABSTRACT. Fourteen genera and 23 species were misplaced and are assigned to their proper families, 11 genera and 10 species are synonymized, one genus and one species are ressurected from synonymy, and 18 species are new combinations.

KEY WORDS. Gelechioidea, Sesiidae, Yponomeutoidea, Neotropical, taxonomy

HEPPNER (1984: 57), listed 11 genera and 38 species of Heliodinidae for the Neotropical Region, leaving out 9 genera and 12 species formerly included in this family. As no references to the transfer of these taxa to other families were found, a list of the missing taxa was sent to him (BECKER 1984a). In a newsletter sent to the members of the project of the *Atlas of Neotropical Lepidoptera* (HEPPNER 1987: 3-7) all these taxa were transferred to the Stathmopodini [=Stathmopodinae] (Oecophoridae).

During a visit to the Natural History Museum, London, in 1988, where most of the type material belonging to these taxa is deposited, it was found that none of them belongs to the Oecophoridae. The only exception is *Machaerocrates tunicata* Meyrick, whose type-specimen is deposited in the Naturhistorisches Museum, Vienna, that belongs to the Ococophoridae. Being the author of all the gelechioid parts in the checklist (BECKER 1984a: 27-53) and having been acknowledged by HEPPNER (1987: 3) as one of the contributors who supplied the information he used in the newsletter, it is obvious that subsequent authors would wrongly credit these changes to BECKER. In order to rectify this, a discussion on the correct placement of the taxa involved is presented here.

In the process of studying type-specimens, and visiting various museums in order to identify material in VOB, several other misplaced taxa have also been found. Their placement is also discussed here.

The taxa are arranged in alphabetical order by genus and by species under each genus. The information about the original placement and the new assignments is given in the discussion under each taxon. For the taxa previously illustrated references are given here, the others are illustrated whenever possible.

Abbreviations used in the text: (BMNH) The Natural History Museum, London, England; (CU) Cornell University, Ittaca, New York, USA; (FOC) Fundação Oswaldo Cruz, Rio de Janeiro, Brazil; (MNHN) Muséum National d'Histoire Naturelle, Paris, France; (IML) Instituto Miguel Lillo, Tucumán, Argentina; (NM) Naturhistorisches Museum, Vienna, Austria; (UMO) University Museum, Oxford, England; (UNLP) Universidade Nacional de La Plata, Argentina; (VOB) Collection Becker, Brasília, Brazil.

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restricted to India and Indonesia. There is a series of specimens from BRAZIL: DF, GO, MT (19372, 19678, 22227, 59276, 89275) which were compared, and matched the type of *T. albicellata*.

Triclonella citrocarpa (Meyrick, 1931), **comb.n.**

Figs 21, 61-63

Scaeosopha citrocarpa Meyrick, 1931: 118. Holotype male, BRAZIL: [ES], [Baixo] Guandu, 1920 (*Hoffmann*) (NM) [examined].

This and *T. albicellata* are very closely related and could be only geographic forms of the same species. They show slight differences in the male genitalia (Figs 61-63) and in *T. citrocarpa* (Fig. 21) the fore wings have an orange mark at the end of cell. The type specimen is in a very poor condition, with the head and left fore wing missing. There is a series of specimens from BRAZIL: MS, SC in VOB (11496, 11557, 13092, 13176, 17258, 52003) which were compared, and matched, the type.

With the transfer of these two species to *Triclonella*, the genus *Scaeosopha* has no representative in the New World fauna.

Triclonella mediocris (Walsingham, 1897), **comb.n.**

Fig. 4

Pigritia mediocris Walsingham, 1897: 94. Syntypes: VIRGIN IDS: St. Thomas, 12.III (*Gudmann*) (BMNH) [examined].

Triclonella rhabdophora Forbes, 1930: Holotype, VIRGIN IDS: St. Thomas, Coaling Dock, 24.III.1927 (CU) [not examined]. **syn.n.**

Pharmacoptis breviramis Meyrick, 1932: 277. Syntypes, VIRGIN IDS: St. Thomas, III.IV. (*Gudmann*) (NM) [not examined]. **syn.n.**

There is a series of 14 specimens in VOB from the BVI: Guana Id. (66819, 70967) (Fig. 4) and one from PUERTO RICO: Guanica (67852). The Puerto Rican specimen was compared with, and matches, the paratypes of *T. rhabdophora* in USNM, and the syntypes of *T. mediocris* in BMNH. *P. breviramis* had been synonymized with *T. rhabdophora* (HODGES 1978: 52). It Is very likely that the type-series of *T. breviramis* originally belonged to part of the type-series of *T. mediocris* as both were collected in St. Thomas by the same collector. The genitalia of both sexes of these Antillean specimens show no difference to those of *T. bicoloripennis* Hodges, from southern USA, as illustrated in HODGES (1978: 80, fig. 11b, 93, fig. 24g).

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The Genus *Podocerus* (Crustacea: Amphipoda: Podoceridae) from Guana Island, British Virgin Islands

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Abstract

A new species of *Podocerus* is described from Guana Island, British Virgin Islands. *Podocerus jareckii* n. sp. has dorsal carinations and an interramal spine on uropod 1. A second species of *Podocerus* collected from similar habitats lacks dorsal carinations and uropodal interramal spines; it is indistinguishable from *Podocerus fissipes* described from the coast of Brazil. The relationships of the species reported here to *Podocerus* found in Bermuda, and in the Caribbean and Mediterranean Seas, are discussed.

Keywords

Caribbean Sea, new species, *Podocerus fissipes*, new record, zoogeography.

Introduction

In general, the amphipod species of the Caribbean region are known from sporadic records and from descriptions of single species associated with specific areas or islands (Baldinger 2000). Other than an identification manual for the common marine amphipods of southern Florida (Thomas 1993), and a pictorial key to the families and genera of the tropical western Atlantic Ocean (Ortiz 1994), no monographs on the amphipods from the Caribbean have been published. Thomas (1993) recognized three podocerid amphipods from southern Florida: *Podocerus kleidus* Thomas and Barnard 1992, *Podocerus brasiliensis* (Dana 1853), and *Podocerus chelonophilus* (Chevreux and de Guerne 1888). In contrast, the amphipod fauna of the mid-Atlantic island of Bermuda has been relatively well studied (Kunkel 1910; Lazo-Wasem and Gable 1987, 1989; Gable and others 1988; Lazo-Wasem and others 1989; Gable and Lazo-Wasem 1990; Baldinger and Gable 1994, 1995; Ruffo and others 2000). *Podocerus*

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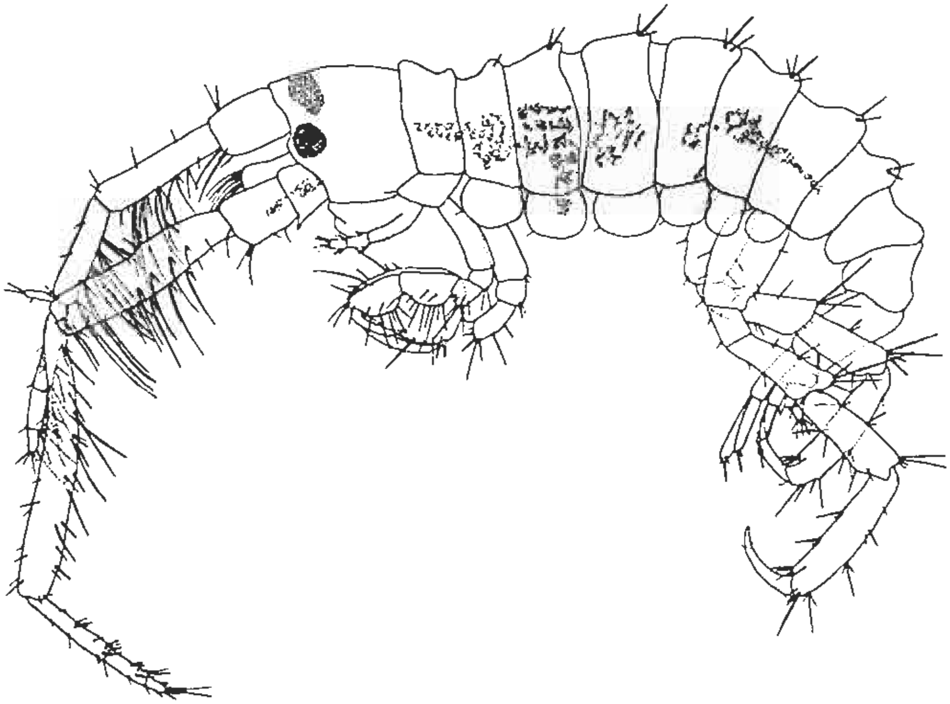

Figure 1

Podocerus jareckii. YPM 24061, female, 2.8 mm.

tachyrheo Baldinger and Gable 1994 and *Podocerus lazowasemi* Baldinger and Gable 1994 are considered endemic to Bermuda.

Examination of specimens found living in sponges or in association with coral rubble from Guana Island, British Virgin Islands, has added one new species, *Podocerus jareckii*, to the Caribbean amphipod fauna. A second species was found in habitats similar to those of *P. jareckii*. This second species is indistinguishable from *Podocerus fissipes* Serejo 1995, originally described from the coast of Brazil. Its occurrence in Guana represents a new distributional record for the Caribbean. Reanalysis of type material has revealed that some of Serejo's (1995) characters were inaccurately or incompletely described, and we discuss these discrepancies below.

Materials and Methods

Guana Island (lat 18°28′24″N, long 64°34′30″W) lies just north of Tortola in the British Virgin Islands, and is a small island of approximately 3 km^2, with a maximum elevation of 246 m. Amphipods from Guana Island were collected by E. A. Lazo-Wasem and A. J. Baldinger over a six-year period (1995 to 2001) from as many different microhabitats as possible. Specimens were either hand-picked from algal scrapings or screened from formalin washes of specific substrates in the field, and preserved in 70% EtOH. Samples were then sorted to the lowest taxonomic rank possible, and detailed investigations of selected specimens were made under a dissecting microscope. Mouthparts and appendages were dissected and mounted in glycerin on microscope slides. Morphological characters were described and illustrations were made with the aid of a camera lucida.

Type and voucher specimens are deposited at the Peabody Museum of Natural History, Yale University (YPM), and at the Museum of Comparative Zoology, Harvard University (MCZ). We also examined the types of *P. fissipes* deposited in the Museu Nacional UF Rio de Janeiro (MNRJ).

In the figures, body parts are marked by the following abbreviations:

A	antenna
Gn	gnathopod
UL	upper lip
LL	lower lip
Md	mandible
Mx	maxilla
Mxpd	maxilliped
P	pereopod
Pl	pleopod
T	telson
U	uropod
R	right
L	left

Gnathopods are numbered Gn1 and Gn2; pereopods are numbered P3 through P7.

Systematic Descriptions

Podocerus jareckii, new species

Figures 1 through 5.

Material examined. YPM 24069, male holotype, 2.1 mm, British Virgin Islands, Guana Island, Monkey Point, west side; formalin wash of purple-brown sponge; depth 2 m; collector E. A. Lazo-Wasem and A. J. Baldinger, 14 October 1999 [GUA 99-08]. YPM 24061, female paratype, 2.8 mm, same data as holotype. YPM 24062, male paratype, 2.2 mm, same data as holotype. YPM 24063, male paratype, 2.7 mm, same data as holotype. YPM 24064, 3 paratypes, same data as holotype. YPM 24066, male? paratype, 1.7 mm, same data as holotype. YPM 24067, male? paratype, 2.1 mm, same data as holotype. YPM 24068, female paratype, 1.9 mm, same data as holotype. YPM 24065, male paratype, 2.4 mm, British Virgin Islands, Guana Island, Crab Cove; formalin wash of large pieces of coral rubble; depth 3 m; collector E. A. Lazo-Wasem and A. J. Baldinger, 13 October 1999 [GUA 99-01]. MCZ 37444, 5 paratypes, British Virgin Islands, Guana Island, Monkey Point, west side; formalin wash of purple-brown sponge; depth 2 m; collector E. A. Lazo-Wasem and A. J. Baldinger, 14 October 1999 [GUA 99-08]. YPM 24251, 2 males, 1 female (ovigerous), 1 juvenile, British Virgin Islands, Guana Island, Bigelow Beach; on green algae attached to *Diploria* sp.; depth 1 m; collector A. J. Baldinger, 23 October 2000 [GUA 00-06]. YPM 24252, 2 males, 3 females (2 ovigerous), British Virgin Islands, Guana Island, Bigelow Beach; on flattened, light green sea rod; depth 1 m;

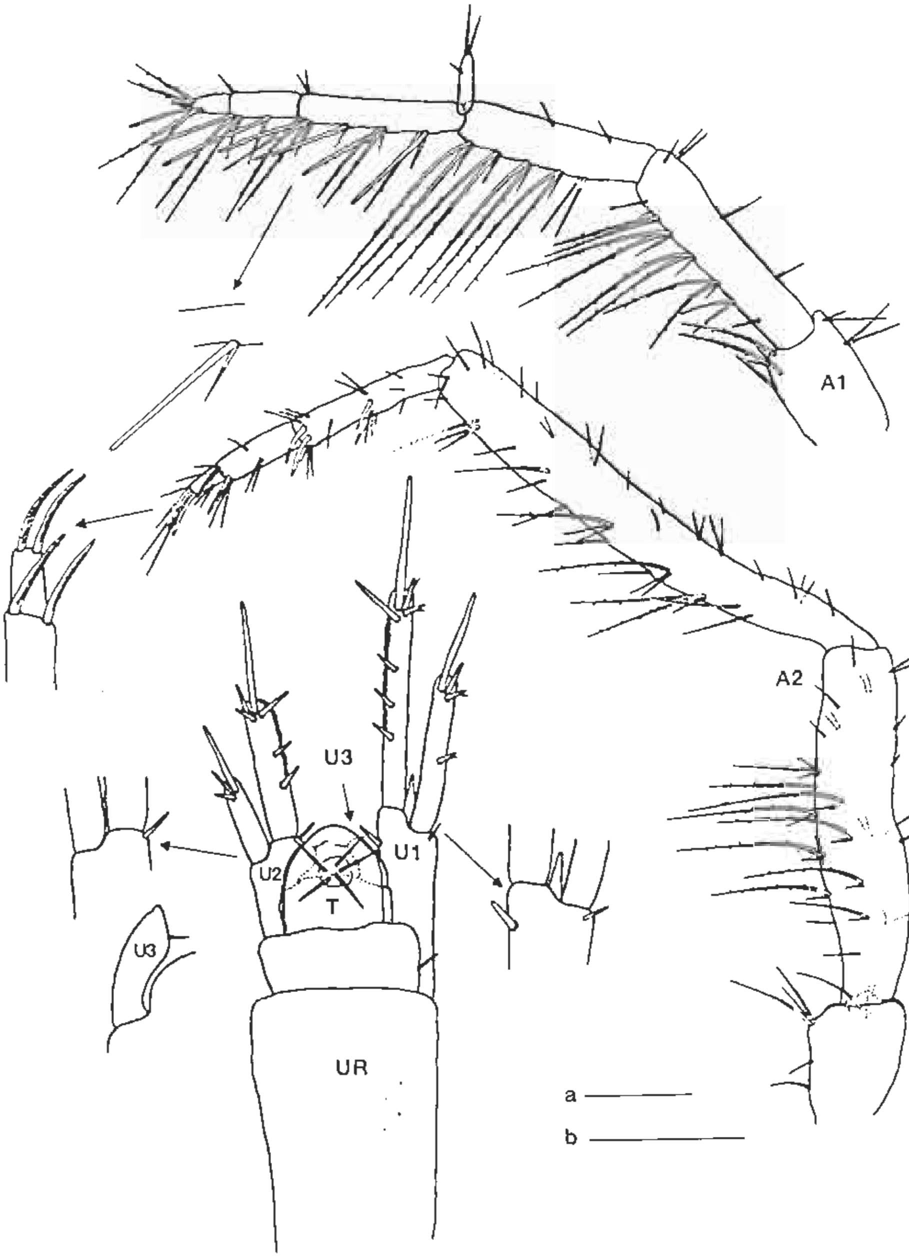

Figure 2

Podocerus jareckii. YPM 24062, male, 2.2 mm. Scale: a (A1, A2), 0.1 mm; b (UR), 0.1 mm.

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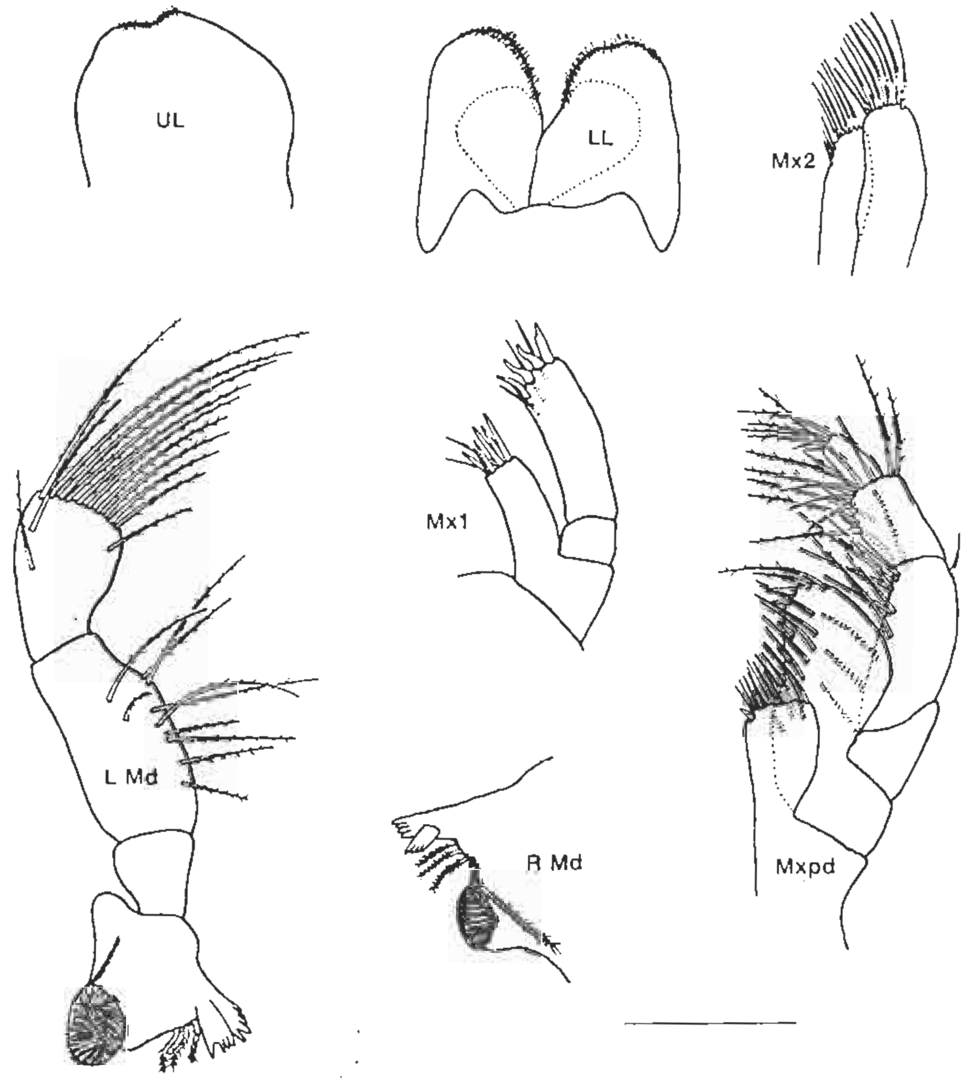

Figure 3

Podocerus jareckii. YPM 24062, male, 2.2 mm. Scale 0.05 mm.

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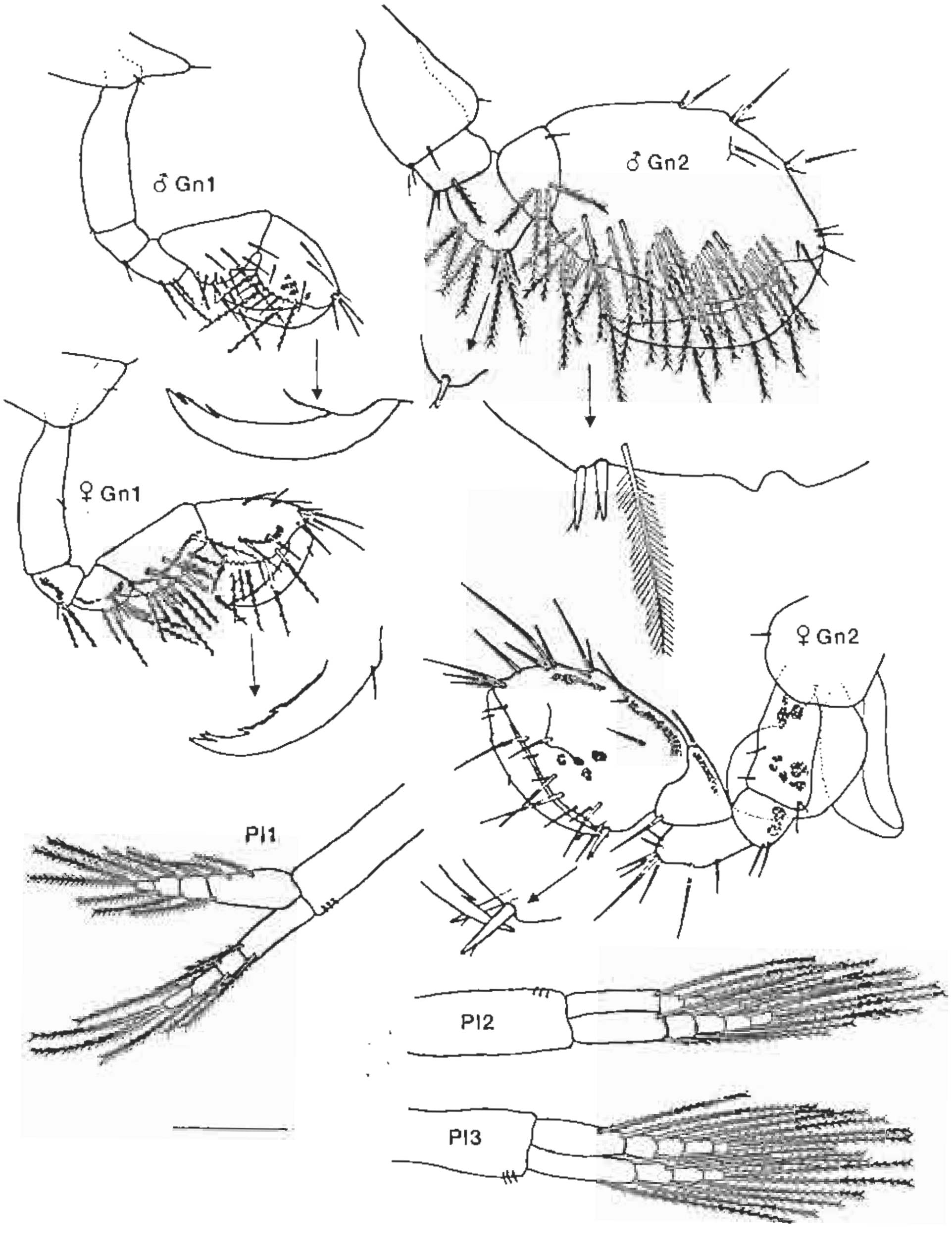

Figure 4

Podocerus jareckii. YPM 24062, male, 2.2 mm, Pl 1–3. YPM 24061, female, 2.8 mm. Scale 0.1 mm.

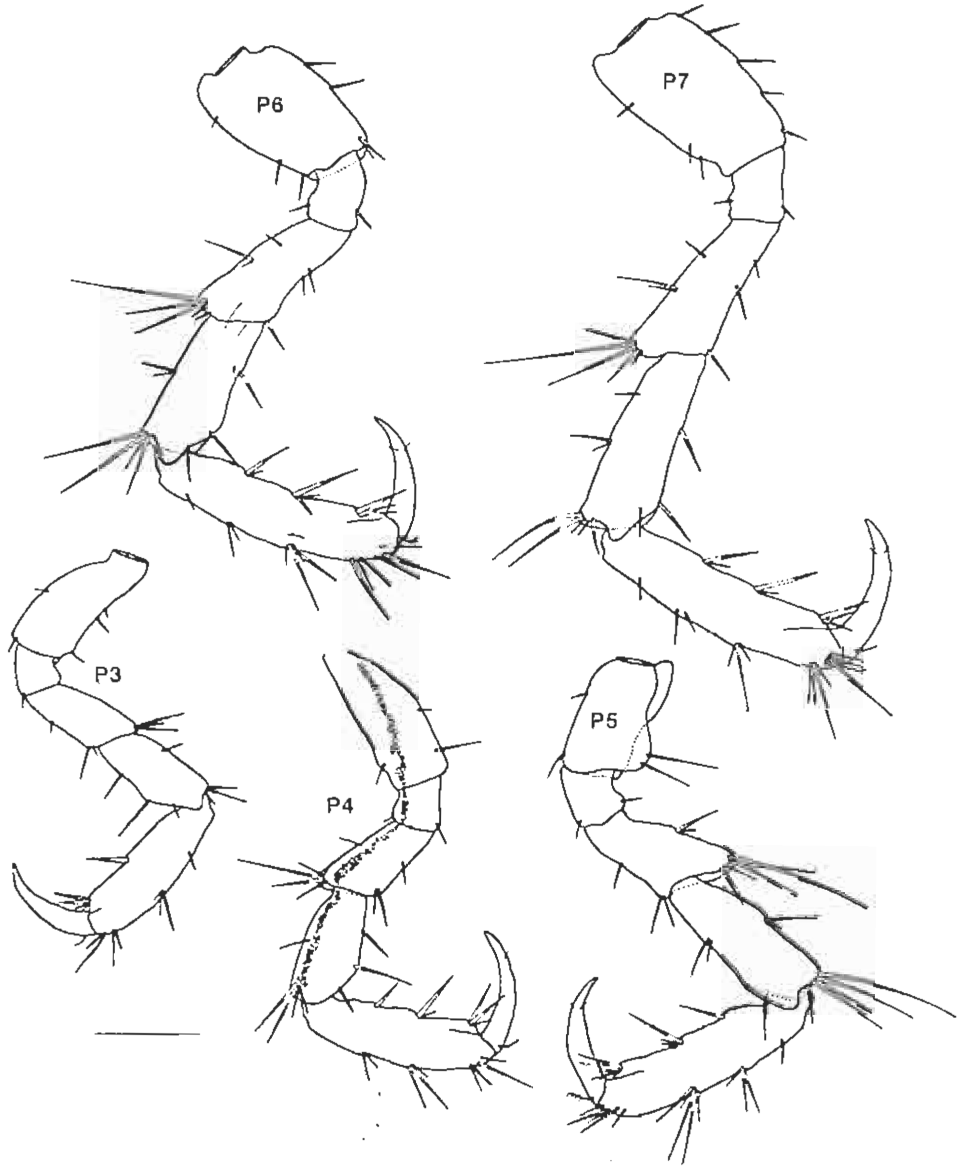

Figure 5
Podocerus jareckii. YPM 24062, male, 2.2 mm, P4–P7. YPM 24069, male, 2.1 mm, P3. Scale 0.1 mm.

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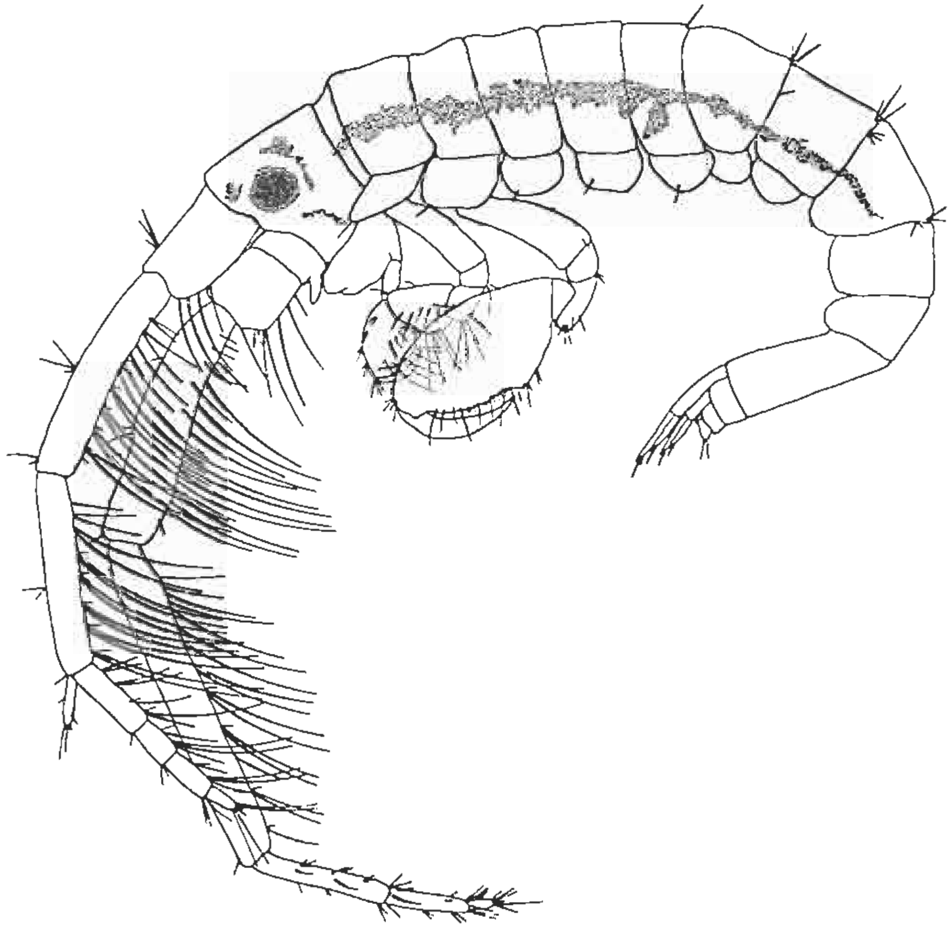

Figure 6

Podocerus fissipes, from Guana Island. YPM 24074, male, 3.0 mm.

collector A. J. Baldinger, 23 October 2000 [GUA 00-07]. YPM 24253, 1 male, British Virgin Islands, Guana Island, Bigelow Beach; on yellow-orange sponge; depth 1 m; collector A. J. Baldinger, 23 October 2000 [GUA 00-08].

Diagnosis. Body with dorsal carinations. Pereonites 2 through 7 and pleonite 1 with dorsal spines. Antenna 2 flagellum 3-articulate, each article with distinct spines. Uropod 1, peduncle with distal interramal spine. Dorsal lobe of telson with 5 long spines.

Description. *Male:* 2.2 mm in length. Body with dorsal carinations (Figure 1). Pereonites 2 through 7 and pleonite 1 with dorsal spine groups. Head cuboidal, slightly longer than pereonites 1 and 2.

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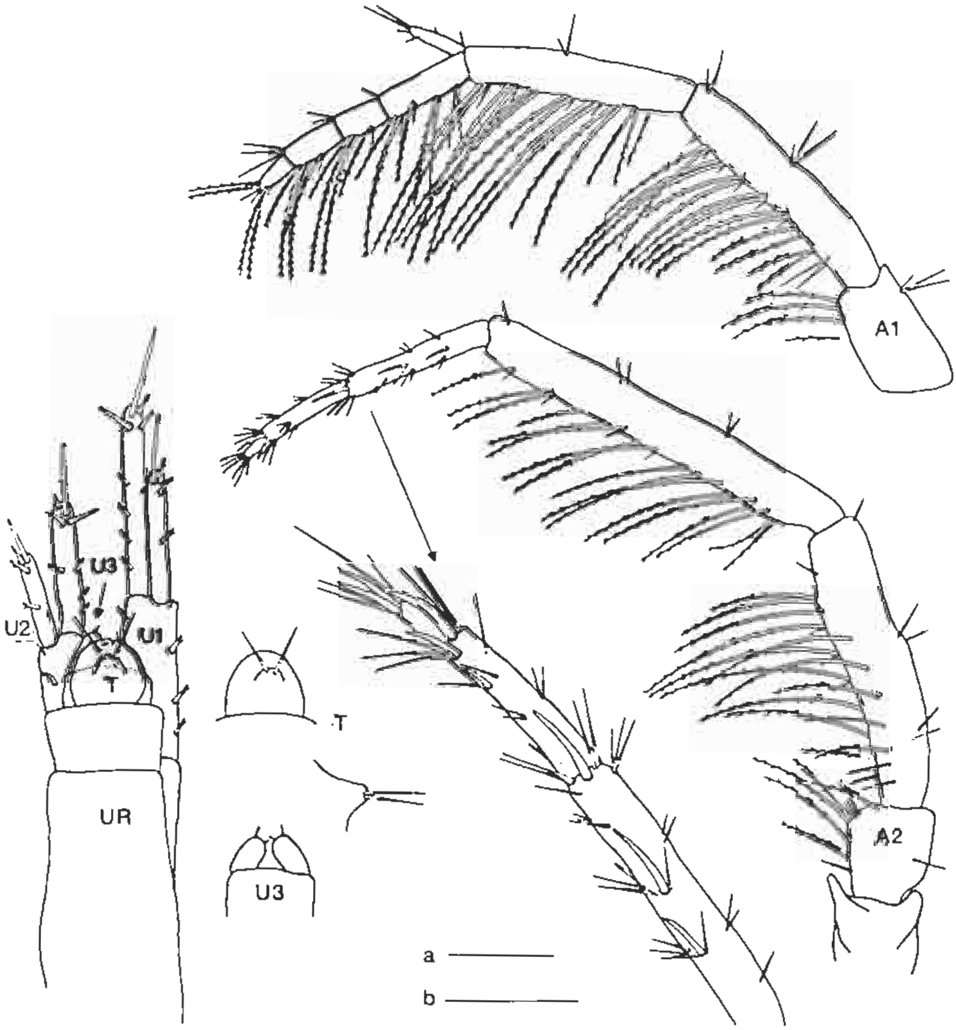

Figure 7

Podocerus fissipes, from Guana Island, YPM 24075, male, 3.0 mm. Scale: a (UR), 0.1 mm; b (A1, A2), 0.25 mm.

Eyes pigmented. Coxae reduced, with serial discontiguity.

Antenna 1 (Figure 2), 60% of total body length, peduncular ratio 1:2:1.7; peduncle article 3 with plumose setae equal to or longer than article length; flagellum 3-articulate, each article bearing setae and aesthetascs; accessory flagellum 1-articulate. Antenna 2 (Figure 2) greater than antenna 1 in length, article 4 of peduncle 66% the length of article 5; flagellum 3-articulate, each article with distinct spines.

Upper lip (Figure 3) rounded, anterior

Table 1

Morphological variation in males of four species of *Podocerus*.

Type locality	*P. jareckii* 2.2 mm Guana, BVI	*P. kleidus* 4.5 mm Florida Keys, USA	*P. lazowasemi* 3.3 mm Bermuda	*P. schieckei* 2.5 mm Mediterranean Sea
Interramal spines on uropod 1	Present	Present	Present	Absent
Interramal spines on uropod 2	Absent	Present	Present	Absent
Number of spines on telson	5	9	4	2
Number of flagellar articles on antenna 1	3	6	5	?
Spines on flagellum of antenna 2	Present	Absent	Present	?
Morphology of coxal plate of gnathopod 1	Rectangular	Cleft	Rhomboidal	Rectangular
Number of spines on article 4 of gnathopod 2	1	3	0	1
Number of spines between palm and posterior margin of gnathopod 2	2	1	4	1–2

margin slightly concave with fine setae. Left mandible (Figure 3), molar triturative, with an accessory plumose seta, inner margin with 3 plumose setae, incisor with 5 teeth, lacinia mobilis with 4 teeth; palp 3-articulate, terminal article clavate, with facial and apical plumose setae. Right mandible similar to left, but incisor and lacinia moblilis both with 4 teeth. Lower lip (Figure 3) normal, anterior margins with fine setae. Maxilla 1 (Figure 3), inner plate absent; outer plate with 5 apical spines; palp 2-articulate, terminal article with 4 apical spines and submarginal setae. Maxilla 2 (Figure 3), plates subequal in width, both with apical setae. Maxilliped (Figure 3), inner plate with marginal and submarginal setae and a single inner marginal spine; outer plate with inner marginal spine row and submarginal setae; palp 4-articulate, articles 2 and 3 with marginal plumose setae, terminal

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article shorter than article 3, with apical plumose setae.

Gnathopod 1 (Figure 4), coxal plate rectangular, with a distoanterior seta; basis elongated; articles 5 and 6 subequal in length, posterior margin of article 5 expanded, with marginal and submarginal setae, some plumose; palm of article 6 with marginal setae, some plumose; dactyl extending to middle of article 5, bifurcate, with one subterminal marginal spine. Gnathopod 2 (Figure 4), robust and much larger than gnathopod 1; article 4, distoposterior margin with plumose setae and a single spine; articles 5 and 6 densely covered with plumose setae, palm of article 6 with irregular margin bearing a conical tooth, hind margin demarcated distally by two bifurcate spines. Pereopod 5 (Figure 5), basis forming distal posterior lobe with 2 marginal setae, and a proximal posterior plate-like extension; pereopods 6 and 7 (Figure 5), bases each with a proximal posterior plate-like extension; pereopods 3 and 4 (Figure 5) anterior margins of article 6, and pereopods 5 through 7 posterior margins of article 6 with stout setae.

Pleopods 1 through 3 (Figure 4) long and slender, peduncles with 3 coupling hooks; rami with plumose setae. Uropod 1 (Figure 2), peduncle with short interramal spine; peduncle and rami with marginal and apical spines; inner margin of inner ramus minutely serrate. Uropod 2 (Figure 2), peduncle lacking interramal spine; peduncle and rami with marginal spines, rami with distinct apical spines; inner margin of inner ramus minutely serrate. Uropod 3 (Figure 2) vestigial, with single marginal setule. Telson (Figure 2) dorsally produced and armed with 5 long setae arranged in a circular pattern.

Female: 2.8 mm in length. All features same as male except as follows: gnathopod 1 (Figure 4), dactyl inner margin serrate, medially and subterminally bifurcate and not reaching middle of article 5; gnathopod 2 (Figure 4), article 4 lacking spine on distal margin; articles 5 and 6 not densely covered with plumose setae; palm straight.

Etymology. This species is named in honor of Henry Jarecki, owner and proprietor of Guana Island.

Remarks. *Podocerus jareckii* is similar to *P. kleidus* from the Florida Keys, the Bermuda endemic *P. lazowasemi* and the Mediterranean Sea endemic *Podocerus schieckei* Ruffo 1987 (see Table 1). Both *P. kleidus* and *P. lazowasemi* have an interramal spine on the peduncle of uropods 1 and 2. *Podocerus jareckii* has an interramal spine only on the peduncle of uropod 1, and *P. schieckei* lacks uropodal peduncular interramal spines. *Podocerus jareckii* can also be distinguished from *P. schieckei* by the spination of the urosome: *P. schieckei* has longer apical spines on the rami of uropods 1 and 2, and has 2 spines instead of 5 on the telson. Other differences are listed in Table 1.

PODOCERUS FISSIPES SEREJO 1995
Figures 6 to 12.

Serejo 1995: 49–57, figs. 1–3.

Material examined. YPM 24074, male, 3.0 mm, British Virgin Islands, Guana Island, probably Monkey Point; depth 0.1 m; collector E. A. Lazo-Wasem and A. J. Baldinger, 14–15 October 1999 [GUA

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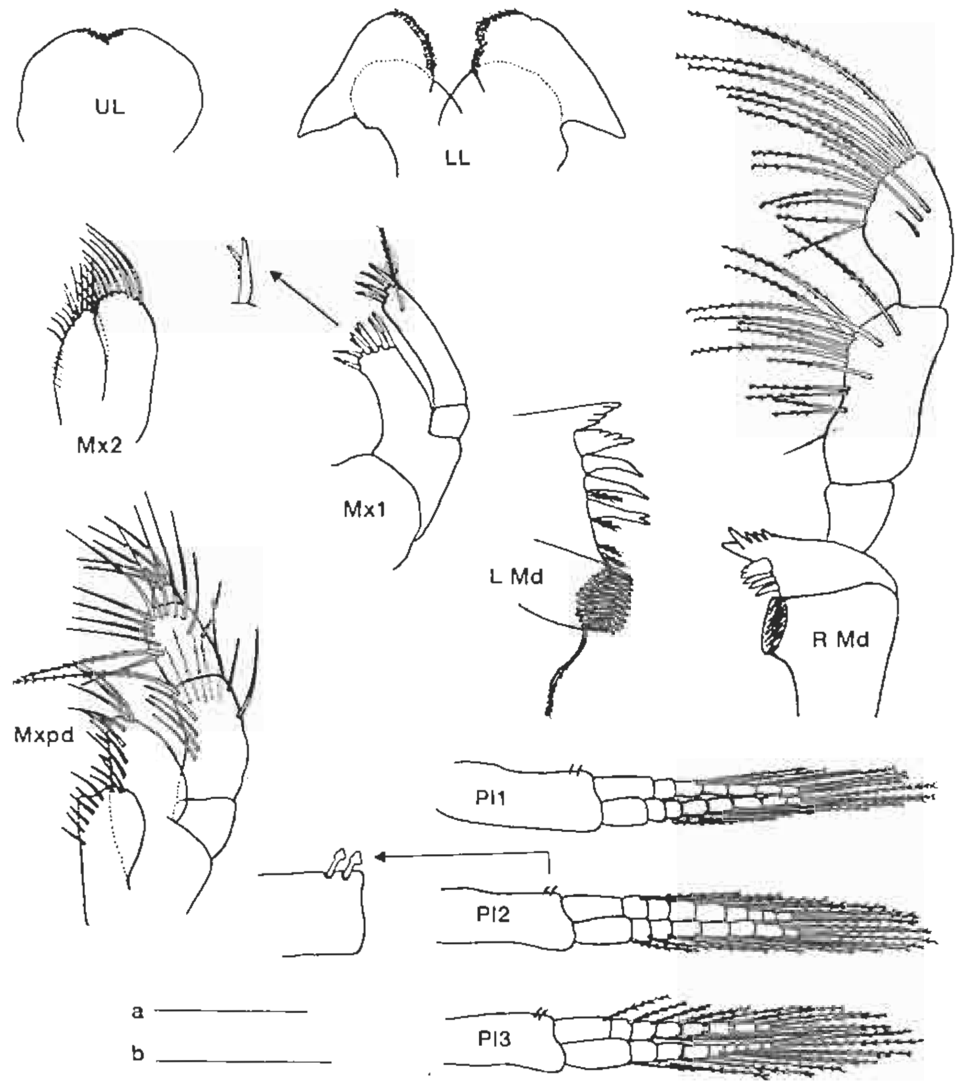

Figure 8

Podocerus fissipes, from Guana Island. YPM 24075, male, 3.0 mm. Scale: a (Pl 1–3), 0.25 mm; b (mouthparts), 0.1 mm.

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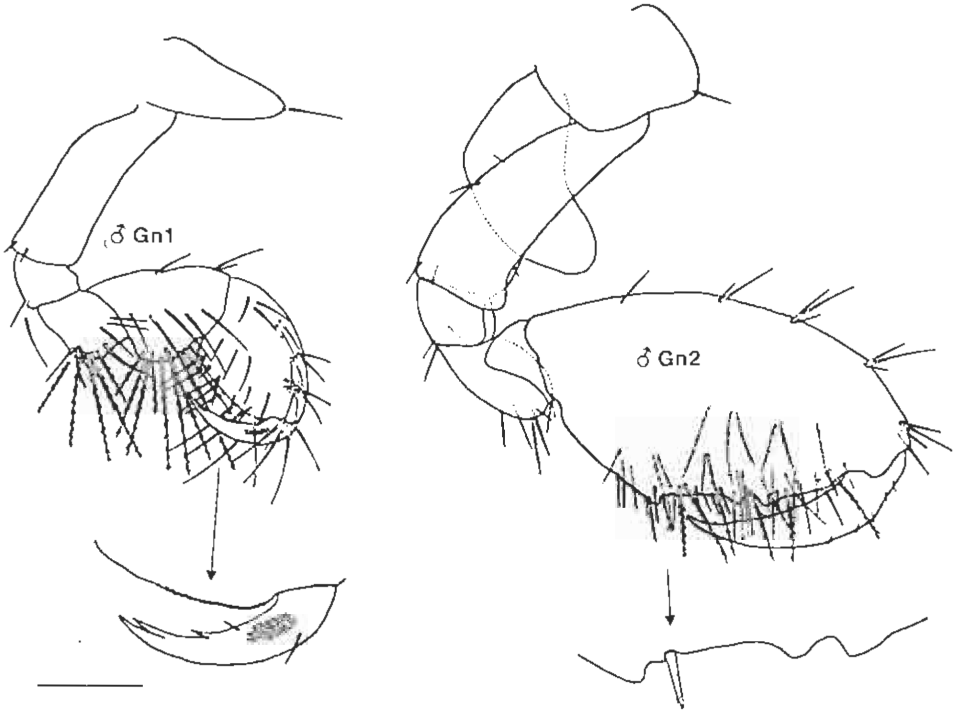

Figure 9
Podocerus fissipes, from Guana Island. YPM 24075, male, 3.0 mm. Scale 0.1 mm.

99-32]. All remaining specimens examined have the same collection data as YPM 24074, except as noted: YPM 24075, male, 3.0 mm; YPM 24073, female, 3.2 mm; YPM 24070, 60 specimens; YPM 24071, ovigerous female, 3.2 mm; YPM 24076, 3 males, 2.4 to 3.4 mm; YPM 24254, male, 2.8 mm; YPM 24255, male, 3.0 mm. MCZ 37445, 10 specimens, British Virgin Islands, Guana Island, probably Monkey Point; depth 0.1 m; collector E. A. Lazo-Wasem and A. J. Baldinger, 14–15 October 1999 [GUA 99-32]. MNRJ 6423, male holotype, 2.3 mm, Brazil, Rio de Janeiro, at Prainha in Arraial do Cabo; collector C. S. Serejo and L. Santi, 24 March 1994. MNRJ 6431, male paratype, 2.8 mm, same data as MNRJ 6423.

Diagnosis. Body smooth, without dorsal carinations. Pereonites 5 through 7 and pleonite 1 with dorsal spine groups. Antenna 2, flagellum 3-articulate, each article with distinct spines. Uropods 1 through 3 lacking interramal spines. Dorsal lobe of telson with 2 long spines.

Description. *Male:* 3.0 mm in length. Body smooth, without dorsal carinations (Figure 6). Pereonites 5 through 7 and pleonite 1 with dorsal spine groups. Head cuboidal, slightly shorter than length of

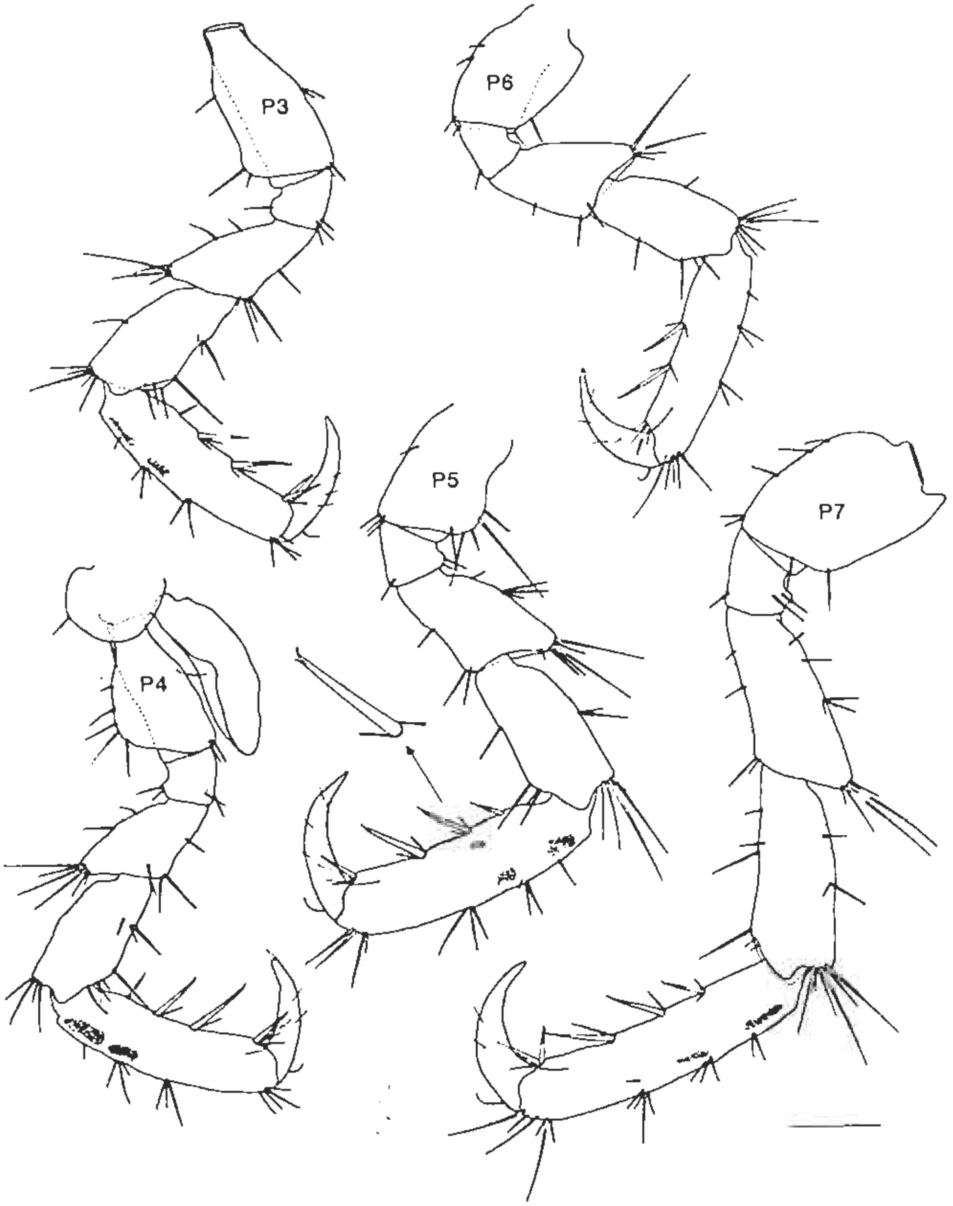

Figure 10

Podocerus fissipes, from Guana Island. YPM 24254, male, 2.8 mm, P3–P5, P7. YPM 24255, male, 3.0 mm, P6. Scale 0.1 mm.

pereonites 1 and 2 combined. Eyes pigmented. Coxae reduced with serial discontiguity.

Antenna 1 (Figure 7), 70% of total body length, peduncular ratio 1:2:1.7, peduncular articles 2 and 3 with plumose setae equal to or longer than length of each article, respectively; flagellum 4-articulate, with marginal plumose setae; accessory flagellum 1-articulate. Antenna 2 (Figure 7) longer than antenna 1, article 4 of peduncle 75% the length of article 5; flagellum 3-articulate, each article with distinct spines.

Upper lip (Figure 8) rounded, anterior margin slightly concave, with fine setae. Right mandible (Figure 8), molar triturative, inner margin with 3 stout spines; incisor with 5 teeth, lacinia mobilis with 3 teeth; palp 3-articulate, terminal article clavate, with facial and apical plumose setae. Left mandible similar to right, but incisor with 4 teeth and molar with an accessory plumose seta. Lower lip (Figure 8) normal, anterior and inner margins with fine setae. Maxilla 1 (Figure 8), inner plate absent; outer plate with 6 apical spines, center two spines bifurcate; palp 2-articulate, terminal article with 4 spines and a submarginal plumose seta. Maxilla 2 (Figure 8), plates subequal in width, both with apical setae; inner margin of inner plate with 4 small spines and fine setae. Maxilliped (Figure 8), inner plate with submarginal setae; outer plate with inner marginal spine row and submarginal setae; palp 4-articulate, articles 2 and 3 with marginal and submarginal setae, terminal article one-third the length of article 3, with apical setae.

Gnathopod 1 (Figure 9), coxal plate rhomboidal with distoanterior seta; basis elongated; article 5 subequal in length to article 6, posterior margin of article 5 expanded, with marginal and submarginal setae, some plumose; article 6, anterior margin setose, palm serrate with marginal setae, some plumose; dactyl bifurcate medially and terminally and not reaching hind margin of article 6. Gnathopod 2 (Figure 9), robust and larger than gnathopod 1; coxa rectangular, distoanterior corner with single seta; basis with distal anterior lobe; palm of article 6 with irregular margin bearing two medial conical teeth, hind margin demarcated by a tooth and one bifurcate spine. Pereopods 5 through 7 (Figure 10), bases with posterior, plate-like extensions; pereopods 3 and 4 (Figure 10), anterior margins of article 6, and pereopods 5 through 7 posterior margins of article 6 with stout setae.

Pleopods 1 through 3 (Figure 8), long and slender, peduncles with 2 harpoon-like coupling hooks, rami with plumose setae. Peduncles of uropods 1 and 2 (Figure 7) lacking interramal spines. Uropod 1 (Figure 7), outer margin of peduncle with 3 spines; outer margin of outer ramus with 1 medial spine, outer margin of inner ramus with 1 medial spine, inner margin of inner ramus with 4 spines. Uropod 2 (Figure 7), outer margin of outer ramus with 1 medial spine, outer margin of inner ramus with 1 medial spine. Uropod 3 (Figure 7) vestigial, with two marginal setules. Telson (Figure 7) dorsally produced and armed with 2 long setae. *Female:* 3.2 mm in length. All features same as male except as follows: gnathopod 1 (Figure 11), article 6, anterior margin with plumose setae, hind margin and palm demarcated by a single bifurcate spine, dactyl terminally bifurcate; gnatho-

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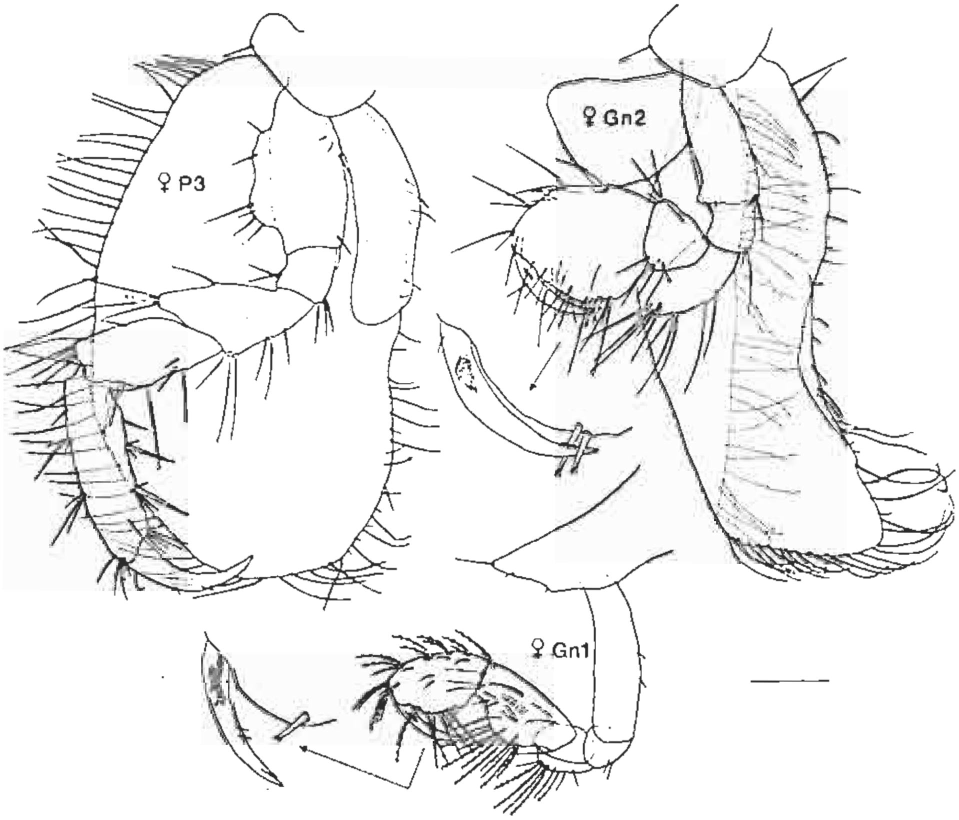

Figure 11
Podocerus fissipes, from Guana Island. YPM 24073, female, 3.2 mm. Scale 0.1 mm.

pod 2 (Figure 11), with large oostegite, article 4 forming a large posterior lobe with long setae, hind margin of article 6 demarcated by two bifurcate spines, palm straight.

Remarks. Serejo (1995) provided a list of the 39 described species in the genus *Podocerus*, and mentioned three species from the coast of Brazil. These are *P. fissipes* and *P. brasiliensis* collected in association with sponges, and *Podocerus fulanus* Barnard 1962 taken from the surface of intertidal animal colonies. Other than minute differences in the number of marginal setae on antenna 2 and the number of spines on the rami of uropods 1 and 2, the specimens of *P. fissipes* from Guana Island are indistinguishahle from *P. fissipes* in Brazil.

Reanalysis of type material of *P. fissipes* has revealed discrepancies in the characters used and illustrated by Serejo (1995). The flagellum of antenna 2 is 3-articulate rather than 4-articulate, and each article of the flagellum has distinct

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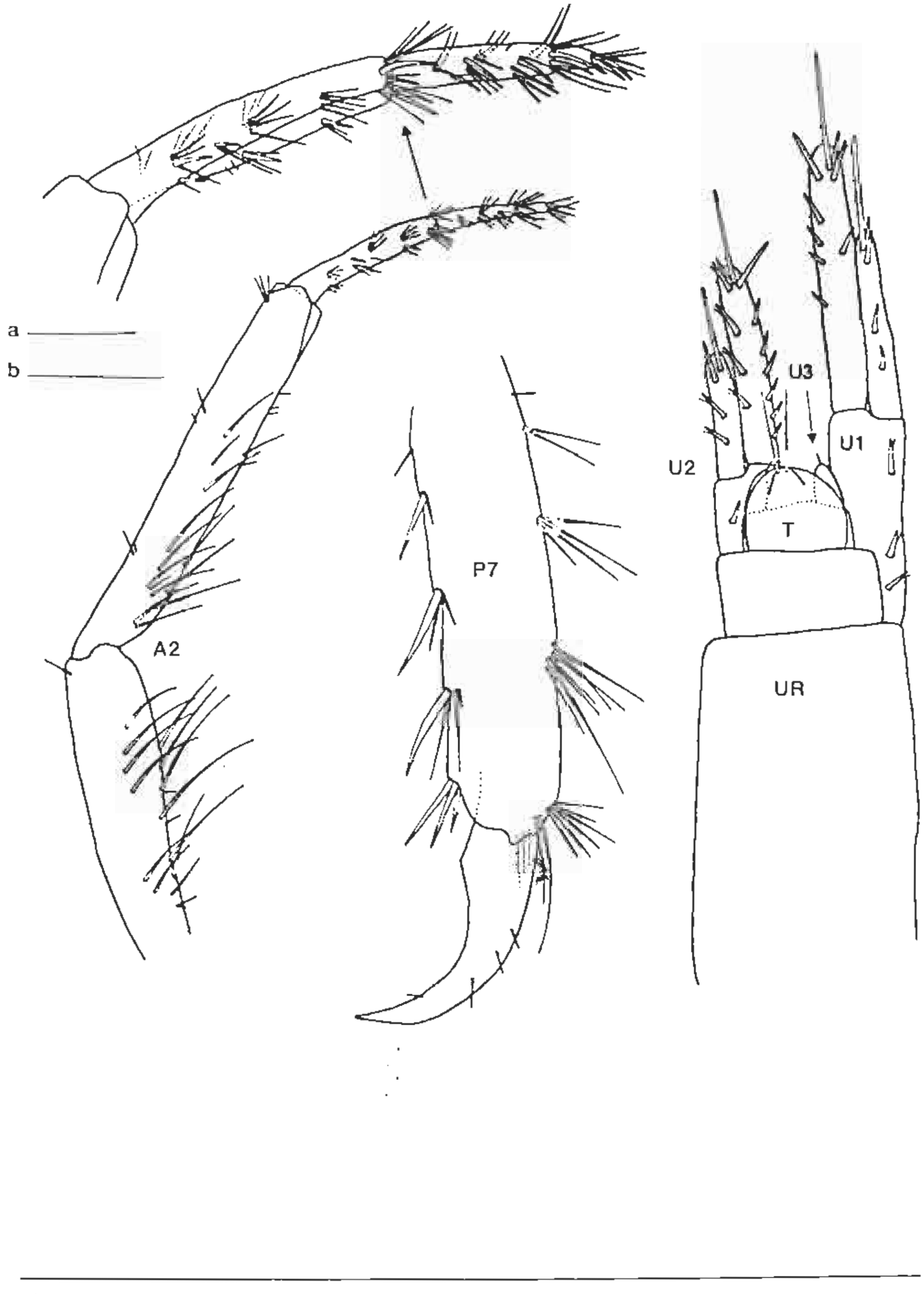

Figure 12

Podocerus fissipes, from Brazil. MNRJ 6431, male, 2.8 mm. Scale: a (A2), 0.1 mm; b (UR, P7), 0.05 mm.

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Table 2
Morphological variation between *Podocerus tachyrheo* and *P. fissipes.*

Type locality	*P. tachyrheo* Bermuda	*P. fissipes* Brazil
Number of flagellar articles on antenna 1	5	4
Number of spines demarcating hind margin of article 6 of the male gnathopod 2	2	1
Number of marginal spines on peduncle of uropod 1	4	3
Number of spines on outer margin of outer ramus of uropod 1	2	1–2
Number of spines on outer margin of inner ramus of uropod 1	3	1
Number of spines on inner margin of inner ramus of uropod 1	6	4
Number of spines on outer margin of outer ramus of uropod 2	2	1–2
Number of spines on outer margin of inner ramus of uropod 2	3	2–3
Number of spines on inner margin of inner ramus of uropod 2	6	3–6
Number of apical spines on telson	4	2

spines (Figure 12). Unfortunately, only one specimen with antenna 2 from Brazil is available for study. Article 5 of male gnathopod 2 is missing from the illustrations (Serejo 1995: figs. 1b, 2g, 3a) and male gnathopod 1 and 2 are more setose.

Serejo (1995) mentioned that *P. fissipes* is similar to *P. tachyrheo,* a species endemic to Bermuda. Reanalysis of type material of both species has revealed further discrepancies in many of the characters Serejo (1995) used to differentiate these species. The primary differentiating character is "a notch on article 6 of pere-

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opods 3–7" that is present in *P. fissipes* and not in *P. tachyrheo.* Superficially this character appears to be a notch (Figure 12), but closer examination reveals that the "notch" is likely a muscle attachment point for the dactyl within article 6. Furthermore, the bifurcate spines on the uropods (Figure 12), described as absent in *P. fissipes,* are actually present in both species. However, there are other features that serve to separate the two species; the most significant differences are shown in Table 2.

Summary

Baldinger and Gable (2000) first reported the presence of *Podocerus* from Guana Island, and in the Caribbean *P. jareckii* and *P. fissipes* are currently known from only Guana Island. The biogeographic distribution of *Podocerus* from islands surrounding Guana and throughout the Caribbean will not be known until further studies are completed. The occurrence of a species from Guana (*P. fissipes*) that exists outside the Caribbean suggests that the amphipod fauna of the Caribbean may be related to adjacent faunas, such as those of Bermuda, the Gulf of Mexico, and the Atlantic coast of South America.

Acknowledgments

A. J. Baldinger is grateful to the Jarecki family, the owners of Guana Island, for their dedication to conserving the flora and fauna of the island, and for affording him the opportunity to conduct this study. He also thanks E. A. Lazo-Wasem at the Peabody Museum of Natural History, Yale University, for the invitation to assist him with field collecting, for helpful comments and discussions on amphipod biogeography, and for reviewing this manuscript. This paper also benefited from reviews by C. O. Coleman, Museum für Naturkunde, Berlin, Germany, and R. Vonk and S. Konenmann, both from the Zoological Museum, Amsterdam, The Netherlands. All errors are the sole responsibility of the authors. We thank C. Serejo of the Museu Nacional UF Rio de Janeiro for the loan of *P. fissipes,* and A. B. Johnston of the Museum of Comparative Zoology, Harvard University, for sharing a departmental microscope. This study has been supported in part by a Museum of Comparative Zoology Barbour Funds grant to A. J. Baldinger, by a CSU-AAUP grant to M. F. Gable, and by the Conservation Agency, through grants from the Falconwood Foundation.

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Fungi

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The true fungi belong to a separate kingdom from plants and appear to share a common ancestor with animals, though their relationship is now very distant. Like animals, all fungi are heterotrophic, deriving their energy from other organisms, living or dead. Around 100,000 species have been named to date, but it is thought this figure may only represent a small minority of the true total.

Three fungal phyla have been recorded so far on Guana Island. The most ancient of these in evolutionary terms (Triassic, over 200 million years ago, MYA) are the *Glomales* (phylum *Zygomycota*), which form symbiotic relationships with living plant roots called 'arbuscular endomycorrhizae'. The term 'endo-' in endomycorrhiza means 'inside', and refers to the fungal penetration of the host plant's root cells, while 'arbuscular' means 'tree-like' or 'arborescent', and refers to the highly branched organ formed by the fungus inside the root cells. The arbuscles are structures formed for nutrient exchange between the partners. A mycorrhiza is the product of a mutually beneficial partnership between a fungus and a plant, analogous to that found in lichens. Endomycorrhizal symbionts are ubiquitous, and about 95% of higher plant species are dependant to some degree on species in the Zygomycota for the uptake of mineral nutrients and water from soil. The oldest fossils of these fungi that have been dated are more than 200 million years old. The earliest land plants other than algae were mosses, ferns and their allies, and the earliest fossils of these plants contain fungi of the Zygomycota. While mosses and ferns have root-like structures called rhizoids, rather than true roots, they also form symbiotic relationships with fungi in the Zygomycota. It has been hypothesized that symbiotic relationships with fungi enabled plants to colonize land. The spores of endomycorrhizal fungi are too large to be dispersed by wind, but are ubiquitous in all types of soil and can be transported to 'new' islands in (for example) the mud on the feet of birds.

The next most ancient phylum, making up the majority of fungal species worldwide, is the *Ascomycota*. These typically have both sexual and asexual stages, the latter including common molds (such as *Penicillium*, one of the common bread molds and a source of antibiotics) and many of the yeasts. The sexual stages include cup fungi, dead man's fingers (*Xylariaceae*), many leaf-spotting plant parasites, and some hyperparasites on other fungi. Molds, yeasts, and leaf spots certainly exist on Guana Island, but the ascomycetes have not yet been systematically surveyed.

The third, and most conspicuous phylum is the *Basidiomycota*. This group includes the mushrooms, shelf fungi, jelly fungi, coral fungi, earthstars, earth fans, puffballs, and stinkhorns. The majority of species decompose wood, leaf litter, and organic matter in the soil, playing a critical role in releasing and recycling nutrients. This is important for animals as well as plants. For example, most termites, including *Nasutitermes* on Guana Island (see Termites below), and many other invertebrates need basidiomycetes to precondition the wood by softening and enriching it in order for it to be palatable. The remaining basidiomycetes on Guana are mostly ectomycorrhizal symbionts forming a mutually beneficial relationship with the roots of certain trees and shrubs (seagrape, *Coccoloba*, and blolly, *Pisonia* on Guana). The term 'ecto-'in ectomycorrhizal means 'outside', and refers to the fungi remaining outside of the host root's cells. Hyphae of ectomycorrhizal fungi form a sheath on the surface of the host's fine roots and also surround (but do not invade) the root's outermost cells.

Though fungal mycelium (in soil and rotten wood) is always present on the island, the fungal fruitbodies only appear after heavy rain and may not come up at all in some years, making systematic surveys challenging. Nonetheless, around 120 species have been recorded from Guana to date and (if it were possible to make complete inventory) it is likely that the total actually present on the island would be well in excess of 2,000 species. The majority of these would be widespread, having a cosmopolitan, pantropical, or neotropical distribution. However, some of the basidiomycetes, especially those forming ectomycorrhizal symbioses with woody plants, would be more restricted.

Two ectomycorrhizal mushrooms associated with *Coccoloba, Amanita arenicola* and *Lactarius coccolobae*, have recently been described from Guana Island as species new to science (Miller et al., 2000) though both are known to occur on other nearby islands (including Puerto Rico). Other ectomycorrhizal fungi that have been found fruiting under *Coccoloba* and *Pisonia* include various mushrooms (*Inocybe, Lactarius*, and *Russula* species), boletes (*Xerocomus*), earth fans (*Thelephora*), and earthballs (*Scleroderma*). Conspicuous wood-rotting fungi on logs and dead standing trees include a number of shelf fungi (notably the pantropical, orange to scarlet *Pycnoporus sanguineus*), some jelly fungi (including the edible *Auricularia cornea*), and several mushroom-like species. One of the large shelf-fungus species, *Ganoderma nitidum*, was reported for the first time for the Caribbean region from Guana Island (Ryvarden 2000). Conspicuous wood-rotting fungi on Guana Island include stinkhorn relatives (*Clathrus crispus* and *Lysurus* cf. *gardneri*, cf. *L. cruciatus*) whose foul-smelling fruitbodies attract flies that disperse the spores.

From: "Rachel Finley" <goby@uri.edu>
To: <wenhua@etal.uri.edu>
Sent: Friday, April 18, 2003 6:39 PM
Attach: figures for Guana.ppt; Guana_text.doc
Subject: email for Skip

Hi Wenhua
I was hoping you could pass along this message to Skip as I do not have his email address.
Thanks, Rachel

Hi Skip
I'm writing to find out if I can come crash your science month again. It was great to be down at Guana for two months last year, since I am trying to finish up the bulk of my field research for my dissertation this summer I would greatly benefit from being on Guana again in October this year. I plan on being on Guana from mid/late July until the end of August, then am trying to work something out with Clive to work and stay on Tortola during September.

Attached is a copy of a proposal I have put together that summarizes my results from past work, and the work I plan on doing this year. I will be looking at the spatial patterning of the parasitic copepods in the fish population as it relates to fish density. I am trying to determine how clusters of high parasite prevalence form in the population - parasites may be transmitted most efficiently at high densities (as the epidemiology models predict) and they may be maintained in the fish population because of continued settlement of juvenile fish or dissipate because high mortality is associated with the infection. I really need to be down for a good chunk of time to get a the observations; we will be surveying and mapping populations weekly in order to apply the epidemiology models to the data.

I have attached the proposal as a Word document and the figures in a Powerpoint document. Lianna had trouble opening the PDF file, and these formats seemed to work better for her. Let me know if you have trouble with the documents and I will try another format (I can always resort to parcel post!).

I will probably only have one assistant with me again this year - either my husband or another graduate student of Graham's. Let me know what you think about me being on the island again this year.

Hope all is well!
Rachel

P.S. I hear from Jen periodically - she seems to be enjoying working on St. Thomas with Sibilla doing the ecotourism job!

~~~~~~~~~~~~~~~~~~~~~~~~~~

Rachel Finley
Ph.D. Candidate
~~~~~~~~~~~~~~~~~~~~~~~~~~

Rachel Finley, 18 April 2003

The role of ectoparasites in a benthic reef fish population

In marine benthic systems, explanations for population dynamics and community organization have focused on the effects of variable influx of pelagic larvae coupled with predator-prey and competitive interactions among adults in the benthic habitat (Roughgarden *et al.* 1988; Sale 1991; Hixon & Beets 1993; Caley *et al.* 1996; Bertness *et al.* 2001). The ability of macroparasites to regulate host population dynamics was first demonstrated mathematically by Anderson and May in the late 1970's (May & Anderson 1979; Anderson & May 1979) and examples confirming these models, for vertebrate hosts, have been demonstrated experimentally in some avian and mammalian systems (Gulland *et al.* 1993; Hudson *et al.* 1998). Yet only a handful of researchers have addressed the role parasites play in marine populations despite recent outbreaks of virulent pathogens (Lessios *et al.* 1984; Lavigne & Schmitz 1990; Harwood & Grenfell 1990; Goreau *et al.* 2000; Harvell *et al.* 1999; Jolles *et al.* 2002).

Work on reef fishes reflects the general lack of attention to potential impacts of parasitism on host population dynamics in marine systems (Sale 1991; Caley *et al.* 1996;Sale 2002). Despite lack of study, there is clear potential for parasites to affect fish populations because fish support diverse parasite communities (Poulin 1995; Raibaut *et al.* 1998), many of which have pathogenic effects (Sindermann 1987; Adlard & Lester 1994). Theoretical studies (Dobson & May 1987), as well as lab experiments (Sindermann 1987) and post-mortem examinations (Rousset & Raibaut 1984; Sasal *et al.* 2001) attest to potential impact of parasites to the individual fish hosts, though the applicability of these results to wild fishes and populations as a whole is uncertain. Reef fish may provide an ideal system to experimentally test the ability of macroparasites to regulate a vertebrate host population.

In 2001 we set out to investigate a marine host-parasite relationship to determine the potential for a gill copepod to impact a benthic reef fish, the bridled goby (Fig 1). We had 425 individually tagged fish in an area of continuous reef from which we determined growth and mortality rates. The average daily growth rate was 68% lower in fish that were parasitized, and mortality increased by a factor of 1.8 in fish that were parasitized during some or all of the study (Finley & Forrester 2003). Obviously the parasites exert a strong impact on the host but could they exert a regulatory force on the goby population? We may expect that the prevalence of infection (i.e. the percent of the population infected) would increase as density increased because the parasite may be transmitted more efficiently at high densities (May & Anderson 1979; May 1983). Central to the importance of the parasite to regulate a host population is for the impact of the parasite to be more severe with increasing host density. In addition to the observational tagging study we also censused the entire population on three occasions, and can use spatial analysis to look at processes creating density and disease patterns in the population at scales relevant to the individual.

Methods

We staked out a 600 square meter area of continuous reef in a 2 m x 2 m lattice (hereafter referred to as the grid) and censued the grid on three occasions obtaining an (x,y) coordinate, estimation of size, and infection status for each fish visible (Fig. 2a). Fish were assigned one of two infection statuses: healthy or parasitized. Parasitized fish showed obvious visual signs of infection while healthy fish did not show these signs (Fig. 1). The term healthy does not imply that the fish was not suffering from any other ailments or parasites, only that the fish did not have this gill copepod. Only fish larger than 15 mm standard length (SL) were used in the spatial analysis. Fish smaller than 15 mm SL are difficult to detect visually and could not be reliably censuses. Furthermore, fish that are most commonly infected with the gill copepod were 16 – 30 mm SL (Finley & Forrester 2003). The population size and prevalence changed dramatically over the course of the study. The population size was lowest at census 1, and highest at census 2, while prevalence remained fairly constant between the first two censuses and increased considerably at the third census (Fig. 2). To give a visual impression of the population distribution over the site, we carved up the area into 1m x 1m blocks and calculated the density m^{-2} (Fig. 2b). There are patches of high and low density in the population, but is the disease more common in areas where there is a high population density?

The spatial patterning of parasitized fish was looked at both on a local scale and global scale. Spatial analysis for local clustering identifies specific areas (location and size) where the placement of parasitized fish deviates from a random distribution. Global patterns will give a general idea of what each fish in the population is experiencing (i.e. crowding or prevalence experienced) but does not identify the specific location(s) in the population where abnormal conditions occur. We used Kuldorff's Spatial Scan Statistic (Kulldorff 2002) to identify local clusters of high and low parasite prevalence in the goby population. This analysis identifies areas that have a higher, or lower, number of parasitized individuals than would be expected if infected fish were randomly distributed throughout the population. A circular window is placed over each fish in the census, and the radius of the window varies in size from zero to some set upper limit. For this analysis we set the upper limit to encompass no more than 20% of the population. The most likely clusters are determined by comparing clusters in real populations to those generated in hypothetical populations with the same distribution but different placement of parasitized fish (Kulldorff & Nagarwalla 1995;Hjalmars *et al.* 1996). For a more quantitative assessment of crowding we used the (x,y) coordinates locations for each fish in a census to calculate the nearest neighbor distances and the infection status of those neighbors. Nearest neighbor analysis identifies global patterns in the population and may help distinguish whether conditions experienced by parasitized and healthy fish were similar or different.

Results and Discussion

Both high and low prevalence clusters were found in the goby population (Fig. 3a). High prevalence clusters, where a greater number of parasitized fish were found than would be expected under a random distribution, were located in all three censuses. Low prevalence clusters, where fewer than expected parasitized fish were found, were found only in the second and third censuses. Although there are identifiable areas of high prevalence in the population, parasitized fish were not confined to these clusters. Infected fish were found throughout the site. There is a consistency in the location of the clusters, especially between the second and third censuses (Fig. 3). Parasites may be directly transmitted between fish and not disperse over long distances. Within a site there may be habitat features that facilitate the formation of disease clusters such that: high prevalence clusters form in areas that have high density, and density may be dictated by the availability of suitable habitat. However, when we overlay the cluster locations on the density map we find no striking pattern of prevalence and density (Fig. 3b). High prevalence clusters do not necessarily occur in high-density areas; nor do low prevalence clusters occur in low-density areas.

A more quantitative assessment of crowding for parasitized and healthy fish was addressed by looking at the nearest neighbor relationships. The fish were the least crowded in census 1 and the most crossed in census 2 and 3. This makes sense because the population size was smallest in the first census and crowding will depend on the population size. More interestingly, in all three censuses parasitized fish were nearly twice as likely to have parasitized neighbors (Fig. 4). This is in agreement with our finding of high and low prevalence clusters: parasitized fish are found in high and low abundance throughout the population so they would naturally have more parasitized neighbors than healthy fish.

Finally, we looked for differences in the crowding experienced by healthy and parasitized fish. Since there are high and low prevalence disease clusters and the clusters do not seem to be associated with high or low-density areas, there may be no difference in the crowding conditions experienced by the healthy and parasitized fish. For the first and second census there was no difference in crowding experienced by healthy and parasitized fish, but when the disease was most prevalent in the third census parasitized fish were more crowded (Fig. 5). When the parasite is most common in the population, the parasitized fish are experiencing the most crowded conditions. When we look again at the prevalence clusters overlaid on the density distribution, we see at least one high prevalence cluster in an area of very high density (Fig. 6). **If the disease is transmitted most efficiently in high-density areas, there may be potential for parasites to exert a regulatory force on the goby population.**

Future Directions – Disease Cluster Formation

Clusters of high and low prevalence do occur in the population. Some clusters are consistent over time but the mechanisms creating and maintaining the patterns are currently unknown.

To identify the mechanisms creating and maintaining density aggregations and disease clusters we will manipulate prevalence in a goby population that varies naturally in density. The question this experiment will address is whether high prevalence clusters form only in high-density areas and not in low-density areas.

In an area of continuous reef, the goby population will be censused and mapped to identify high and low density aggregations. Areas of naturally high and low density will have parasitized gobies added or taken away to create artificial levels of prevalence. The population will be censused and mapped and spatial analysis will be used to identify the emergence of high and low prevalence disease clusters. The expectation is that high prevalence clusters will only form in areas of high density. We will further be able to identify whether high prevalence clusters are maintained in the population via the natural settlement of larval fish to high-density areas; or if they dissipate because of high mortality at high density and prevalence.

In addition to the manipulated population, we will continue to census and map an unmanipulated population. The natural emergence and dissipation of disease clusters is still not well understood. Observing them in an unmanipulated population may elucidate the correlation of clusters with other features of the population or habitat.

No direct connection between density and cluster formation is evident right now, but we may need to look at the establishment and behavior of spatial patterns in a natural and in a manipulated population on a much finer time scale.

In the 2001 experiment we mapped out the population on three occasions over a three-month period. This time frame was clearly not frequent enough to capture the dynamic changes in the population; rather it only gave snap-shots at three different times. Mapping out the natural and manipulated populations on a much finer time scale, i.e. weekly or bi-weekly, will allow us to better capture the formation of population aggregations (via settlement or migration) and disease clusters.

Furthermore, we excluded two components in our 2001 study that are likely critical to the complete understanding of the parasite's epidemiology: fish smaller than 15 mm in standard length, and an alternative goby host. Although the fish observed to be the most commonly infected by gill copepods are 15 – 30 mm SL, gobies are likely becoming infected shortly after settlement (at 6 – 8 mm SL) and may not show visible signs until they are slightly larger. Newly settled fish also may be the most susceptible to infection. In our previous study we were unable to detect whether the high prevalence clusters were maintained spatially because of direct transmission of the parasites to adult or juvenile neighbors.

A congener, the colon goby *Coryphopterus dicrus*, is also known to harbor the gill copepod. If the parasite is transmitted most efficiently above a threshold density, the presence of alternate hosts will lower the threshold density of the bridled goby because both gobies will constitute the population size susceptible to infection. Additional hosts need to be identified and all susceptible fish censused to understand the dynamics of parasite transmission.

We know that mortality is higher in parasitized gobies, but does mortality also correspond to density? And are fish more likely to become infected in areas of high and low prevalence?

The high prevalence clusters seem to correspond to fish density when the disease is most common. Parasitized fish have more parasitized neighbors and at high disease prevalence they are more crowded than healthy fish. A tag and resighting and recapture study will be done in the areas of high and low prevalence and density to determine if differences in growth, mortality, and incidence of infection correspond to the spatial patterns of the parasite and population.

Additional Experiments for 2003

Experimental infection in the lab

In 2002 we attempted to experimentally infect healthy fish in the lab and field to determine the likelihood of parasite transmission between a parasitized and healthy neighbors. Transmission of the parasite was confirmed in only one treatment tank (n = 16) while none of the control tanks became infected. The three fish that became infected in the treatment tank provided valuable information about the infection dynamics of *Pharodes tortugensis*. The adult stages of the copepod have been described, but no work has been done on the hatching or infective stages. We found that the hatching nauplii are strong swimmers and copepods do not become infective until the copepodite stage is achieved. We would like to repeat the experimental infection experiment again in 2003 using a slightly different protocol to increase the likelihood of infection in the hopes that more fish will become infected and we can discover more on the infection dynamics of *Pharodes tortugensis*.

Parasitized and healthy fish 16-30 mm SL will be collected from reefs near Guana Island using hand nets and SCUBA, and housed in tanks on the island. We previously had seawater constantly running through the tanks, this year we will eliminate water flow: water will be continuously aerated and changed periodically as needed. While the fish are held in aquaria they will be fed *ad libum* daily either a commercial fish food or, when possible, microcrustaceans collected from the field. Two parasitized fish carrying gravid female copepod will be kept in aquaria with two to four uninfected fish. Control tanks will consist of four to six healthy gobies held under the same conditions as the experimental infection fish. Water samples will be taken bi-weekly to look for infective stages of the parasite and the fish will be examined for developing infections.

Isolating the impact of parasites on growth and mortality

In 2001 we found growth rate were slower and the instantaneous rate of mortality higher in parasitized fish (Finley & Forrester 2003); however, these results were correlative because naturally infected and uninfected fish were compared. Factors other than infection status could have contributed to differences in growth and mortality. To isolate the impact of parasites on population dynamics, infection status must be controlled either by disinfecting parasitized fish or infecting parasite-free fish. A disinfection experiment cannot mimic natural shedding of parasites by hosts, but will provide a direct test for the impact of parasites on host growth. In a disinfection experiment, the growth rate will be compared between four groups of fish:

- Disinfected fish (parasites removed using aquarium disinfectant)
- Naturally parasitized fish
- Naturally parasite-free fish
- Parasite free fish that have been treated with the disinfectant as a procedural control

Fish will be collected and individually tagged in the field. Half of the fish (parasitized and healthy) will be treated with CopperSafe ® commercial aquarium treatment then returned to the site of capture. This disinfectant was successful in removing all parasites in a pilot study. To reduce variation in differences in growth because of differences in the size of fish, only *C. glaucofraenum* that are 15-25 mm SL will be used in this experiment. This size range is commonly infected with *P. tortugensis* and is still rapidly growing. Recapturing and measuring the fish several times in a 45-60 day period will assess growth rate. The null hypothesis of no difference in the average daily growth between the four groups will be compared.

Disinfect fish to determine if gill damage is reversed

Parasitized gobies suffer from extensive gill damage: the gill arches are distorted to accommodate the large female parasite attached to the lower gill cavity wall, while juvenile and male copepods damage the gill filaments either indirectly by irritation or directly by feeding on them. It is unclear if the parasites are naturally shed because there is no evidence of previous infection in any healthy fish I have examined. Parasitized fish will be disinfected using CopperSafe ® commercial aquarium treatment and allowed to recover for two to four weeks. The fish will then be examined for evidence of previous infection: scaring on the gill cavity wall, distortion of gill arches, and damage to gill filaments.

Density-prevalence transects (monthly)

Surveys of goby density and prevalence have been performed annually at five sites around Guana Island. The same sites will be visited during the summer of 2003 as part of the ongoing survey. Additionally, monthly surveys will be performed to determine smaller temporal changes in goby density and the prevalence of *Pharodes tortugensis.* Other sites in the BVI (e.g. bays on Tortola) will be surveyed if the opportunity arises.

Timeline for Summer 2003 Work

Week 1

- Mark out area to monitor population
- Check stake markers at 2001 study site – retag stakes as needed
- Map out populations at both sites to determine density patterning and location of disease clusters

Week 2

- Tag 100's of fish in both manipulated population and natural population sites
- At one site, adjust levels of prevalence in areas of different density
- Map natural and manipulated goby populations to determine disease cluster formation
- Set up tank experimental infection experiment
- Set up tank disinfection experiments

Week 3

- Map natural and manipulated goby populations to determine disease cluster formation
- Release disinfected fish in on Muskmelon Reef

Week 4 – 15 (end)

- Map natural and manipulated goby populations to determine disease cluster formation
- Check status of disinfected fish on reefs
- Tag in high and low prevalence clusters as needed
- Density-prevalence transects at established sites around Guana
- Visit other sites in BVI

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Figure 1. An infected goby (left) showing the swollen gill cavity which allows diagnosis of infection. A healthy goby is shown (right) for comparison (this fish is tagged XH4).

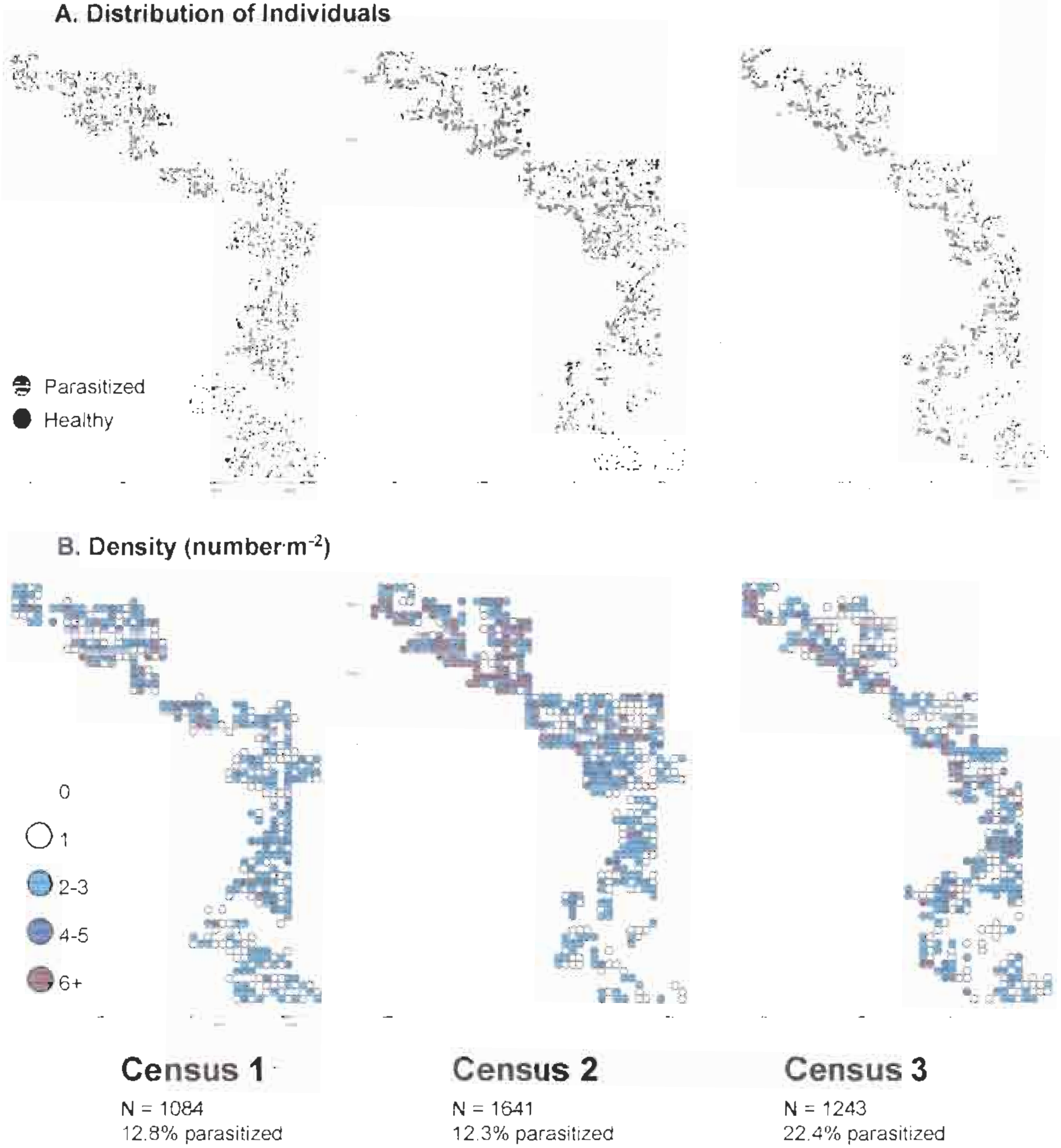

Figure 2. The location of healthy and parasitized fish in each census. Census 1 was performed on 4 – 6 July 2001, Census 2 on the 20 – 22 July 2001, and Census 3 on the 17 – 19 August 2001. The scale bars on each map are in centimeters, the distance between each mark is 1000 cm or 10 m. A) Black dots represent the location of healthy fish, while red dots are the location where parasitized fish were found. The censuses were performed along an area of continuous reef. The population is bounded on the left by a sand flat, and while we did try to include all goby habitat in the width of our site, fish can certainly be found to the right of the population that was mapped. The demarcations at the top and bottom of the maps are arbitrary and the population continues in both directions. B) The density m^{-2} of bridled gobies in each census. The intensity of the shade of blue increases with increasing density and a density of zero is indicated by areas outlined in gray.

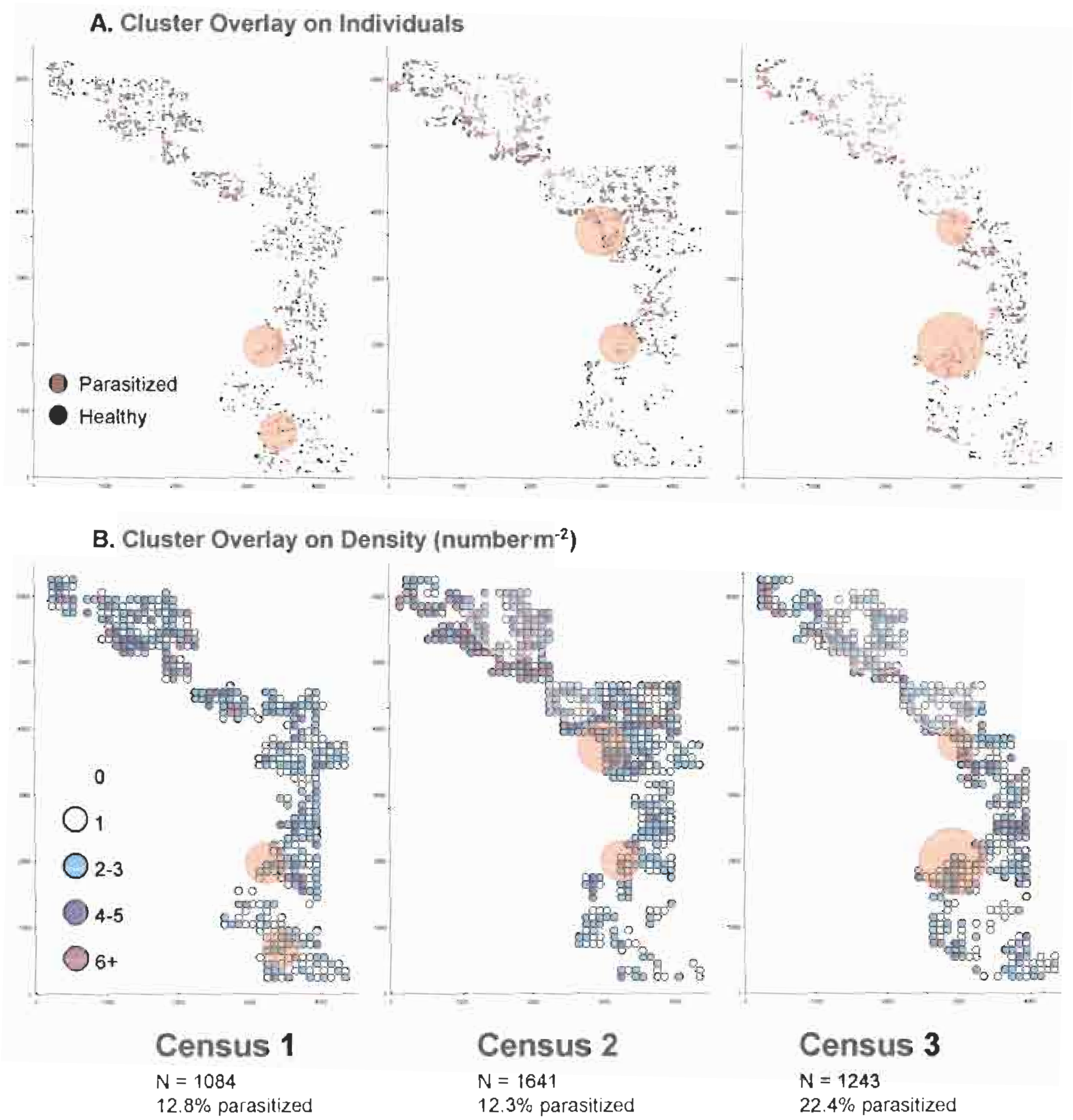

Figure 3. Location of high and low prevalence clusters in the population. High prevalence clusters (red shaded areas) were found in all three censuses, while low prevalence clusters (gray shaded) were only found in the second and third censuses. A) Cluster locations overlaid on the distribution of individual fish. Although there are identifiable areas of high prevalence, parasitized fish are not confined to the clusters and are found throughout the site. B) Cluster locations overlaid on the density distribution of fish. No striking pattern of prevalence and density is found: high prevalence clusters are not necessarily found in areas of high density, and low prevalence clusters are not necessarily found in areas of low density.

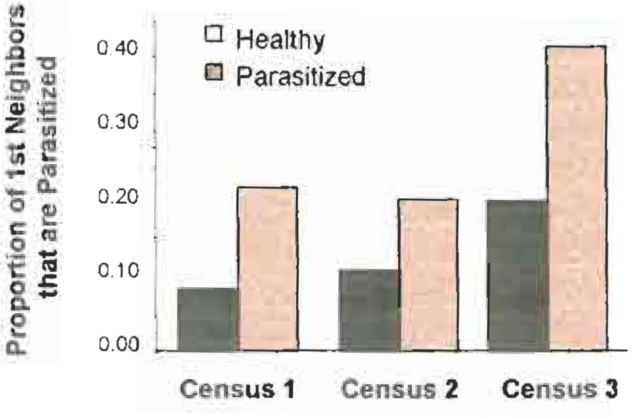

Figure 4. Proportion of neighbors that were parasitized. Parasitized fish were nearly twice as likely to have a 1st neighbor that was also parasitized. Results were similar for the 2nd and 3rd nearest neighbors.

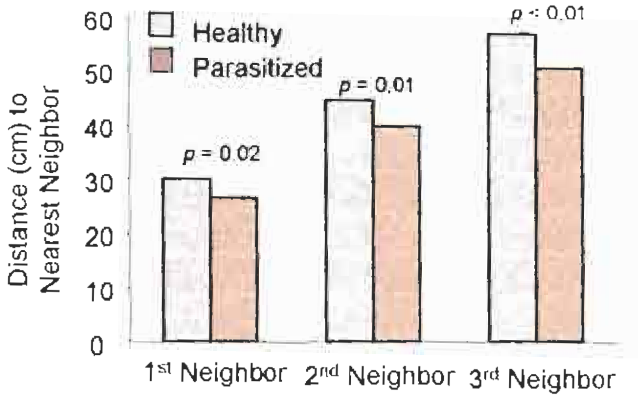

Figure 5. Nearest neighbor distance for Census 3. Parasitized fish were more crowded in this census than healthy fish because the average distance to the nearest neighbor was smaller. Error bars are too small to detect.

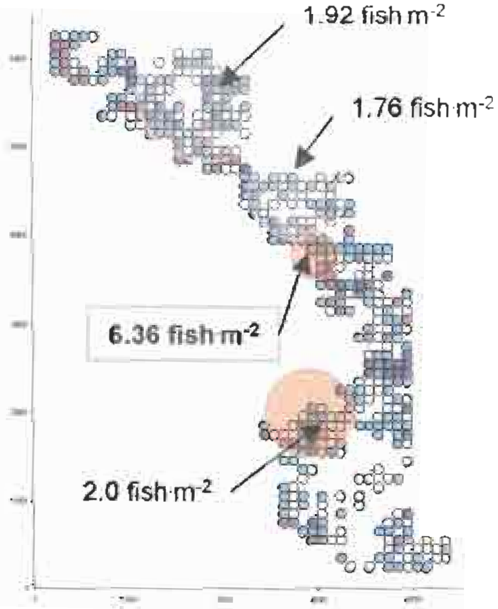

Figure 6. The density distribution and prevalence clusters for fish in census 3. Census three had the highest prevalence of parasitized fish, and the upper high density cluster is located in an area of very high density.

ELAPHE GUTTATA GUTTATA (Corn Snake). USA: US VIRGIN ISLANDS: St. Thomas: Crown Bay Cargo Port Area (18° 20.29' N, 64° 56.84' W). 3 October 1999 and two undated specimens from the 1990s. Judy Pierce and Donna Griffin. Both specimens verified by Jose Rosado. The dated specimen, an adult female, 66 cm SVL, 80 cm TL, was found at the industrial park near Victor's Hideout restaurant, approximately 600 m west of the Crown Bay cargo port area. It is preserved in the collection of the US Virgin Islands Division of Fish and Wildlife (address below). The two undated specimens are at the Museum of Comparative Zoology. MCZ 183544 is an adult male, SVL 83 cm, TL 103 cm; MCZ 183545 is a juvenile, SVL 31 cm, TL 37 cm.

Circumstantial evidence suggests these specimens may have arrived in cargo containers originating in Florida, a pattern which is consistent with other reports of introduced reptiles and amphibians in the Caribbean (e.g. Powell 2002. Herp. Rev. 33:321). Over the last few years, calls regarding corn snake sightings have been arriving at the office of the Division of Fish and Wildlife approximately once a year. Repeated sightings, as well as the capture of juveniles at the site, suggest a nascent population may be in the process of emerging. This is a first documented record for the Caribbean. However, although no specimens are available, corn snakes have also been reported from Curaçao and Bonaire. These too may have arrived from Florida, and juveniles have been reported on Curaçao as well (Gerard van Buurt, unpubl. observations). If the presence of juveniles indicates local reproduction, this is a source of conservation concern because, similar to the invasive brown treesnake (*Boiga irregularis*; Rodda et al., 1999. Problem snake management: the habu and the brown treesnake. Cornell University Press, Ithaca, 534 pp.), *E. g. guttata* has a generalized vertebrate diet. What effect the presence of introduced Indian mongooses in St. Thomas (Horst et al. 2001. In Woods and Sergile [eds.], Biogeography of the West Indies: patterns and perspectives, pp. 409-424. CRC Press, Boca Raton, Florida) might have on the future and impact of the species remains to be seen.

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Program Book and Abstracts

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JOINT MEETING OF ICHTHYOLOGISTS AND HERPETOLOGISTS

July 3–8, 2002

PERRY, GAD
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Do *Anolis* lizards change their foraging behavior as environmental conditions change?

Foraging theory includes the assumption that foraging behavior is highly labile. It therefore predicts that animals will modify their allocation of effort in accordance with conditions such as food availability and presence of predators. In contrast, some recent work shows that foraging behaviors are conservative, and closely related species share similar time allocation patterns. I tested this by comparing foraging behavior of congeners from highly different environments. I studied *Anolis carolinensis* in Texas and two introduced populations, Hawaii and the Commonwealth of the Northern Mariana Islands. *Anolis cristatellus* was studied in the British Virgin Islands and in an introduced population in Costa Rica. In the British Virgin Islands I compared populations on wet and dry islands and on the same island between years with greatly variable rainfall. All populations of both species showed the highly sedentary foraging behaviors typical for the genus. Moreover, differences between populations and within populations between years were very small. This supports a view of foraging behaviors that are phylogenetically conservative, rather than highly plastic. (Session 20, Sunday, June 27, Penn Stater, Room E, 8:30)

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Intra-island altitudinal difference in reptilian water loss rates on Guana Island, British Virgin Islands

Many locations in the British Virgin Islands are strikingly xeric. In such environments, conserving water can become an important consideration, especially for small animals inhabiting exposed habitats. We have previously demonstrated the existence of inter-island differences in evaporative water loss in *Anolis cristatellus* from the BVI, and shown that skin resistance to water loss is positively correlated with the aridity of their habitats. We report the findings of work comparing water loss rates of altitudinal populations of three species (*Alsophis portoricensis, Anolis cristatellus,* and *Sphaerodactylus macrolepis*) on Guana Island (approximately 300 ha; maximum elevation: 250 m). We hypothesized that sea-level populations, being exposed to warmer and drier conditions, would show reduced water loss rates. However, we predicted that *Sphaerodactylus*, which inhabits a relatively protected leaf litter habitat, would not show a difference on so small an island. Our findings partially supported our predictions. Water loss in *Alsophis* was not correlated with altitude, perhaps because Guana is too small for relatively large and active animals to show populational differences. In contrast, both *Anolis* and *Sphaerodactylus* had significantly higher water loss rates at higher elevations. Whether genetic differences or phenotypicplasticity is responsible for these differences remains unknown. (59: 7July; Pershing S (AM); Amphibian & Reptile Physiology)

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Locomotor performance and home range size in free-ranging male *Anolis cristatellus*

In the highly territorial lizard *Anolis cristatellus*, male locomotor performance is correlated with both social dominanc in the laboratory and display frequency in nature. Here, we test the hypothesis that male locomotor performance in th laboratory is correlated with home range size under natural conditions. We collected 39 adult males and immediatel measured their endurance using a treadmill. Males were then individually marked and released at the site of captur For the next three weeks, we attempted to re-sight each lizard at least once a day. For the 23 individuals sighted multi ple times (mean = 21), we used the minimum convex polygon method to calculate home range size. Male endurance an home range size were positively and significantly correlated. Thus, high endurance in *Anolis cristatellus* is correlated nc only with the ability to win fights under laboratory conditions, but also with obtaining and maintaining large home range in nature. Our findings demonstrate the usefulness of laboratory measures of locomotion as indicators of realized per formance in the field. Because larger home ranges allow access to more females, we speculate that males with high enduranc also enjoy higher fitness. (58: 4 July; Pershing N (PM); Reptile Behavior)

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Research Highlights
Range, Wildlife, and Fisheries Management
2002

Texas Tech U., Lubbock, TX

The Importance of Locomotor Physiology for Crested Anole Social Status

Gad Perry and Kate LeVering

The crested anole is a common lizard found throughout the Puerto Rico Bank. Both sexes, but especially the males, are highly territorial. A male typically defends an area encompassing several trees and the ground underneath them. Several females will use the same area for feeding. Reproductive opportunities for the male are presumably determined by the number of females it is associated with: the larger the territory, the more females are found in it. Yet surprisingly little is known about the proximal mechanisms that determine social dominance.

Together with a number of collaborators, we have been trying to address this gap, working on Guana Island, British Virgin Islands. Most recently, we tested two hypotheses in this system. Our first hypothesis was that male social dominance is determined, in part, by locomotor abilities. We found that winners of staged fights had greater endurance than did losers, but that sprint speed did not differ between the two groups.

Studies of locomotor performance are typically conducted under laboratory conditions, and the results are assumed to be relevant to behavior in nature. However, this crucial assumption has rarely been tested. Our second hypothesis, therefore, was that the locomotor abilities we measured in the laboratory are correlated with behavior in the field. We found that assertion displays in the field are related to both locomotor performance and laboratory-assessed social dominance. Even more telling, home range size in this species is significantly correlated with endurance. Thus, laboratory tests of locomotor performance and social dominance provide a reliable indicator of field performance in this species.

Editors
Gene R. Wilde and Loren M. Smith

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AMPHISBAENA FENESTRATA (Virgin Islands Amphisbaena). **PREDATION**. Relatively little is known about the biology of many fossorial reptiles and amphibians. For example, almost nothing is known about the predators of any species of *Amphisbaena*. Here we report, for the first time, two cases of predation on *A. fenestrata* observed on Guana Island, British Virgin Islands. In both cases, predation was by the locally abundant colubrid snake *Alsophis portoricensis*.

On October 7 2001 at 1000h (air temperature = 27.2 °C), we captured a male *Alsophis portoricensis* (520 mm SVL, 285 mm TL, mass 52.3 g). It was encountered at an elevation of 160 m, near a forest trail, on a substrate of dry leaves and small pebbles. The snake was placed in a cloth bag and approximately 30 min later regurgitated a freshly eaten adult *A. fenestrata* (210 mm SVL, 15 mm TL). The specimen was in very good condition and was deposited at the Yale Peabody Museum (accession number YPM 12060).

A second predation event was recorded on videotape by Troy Peliwan on October 20 2001. Around 18:00h, he encountered an *Alsophis portoricensis* attempting to capture and subdue an adult *Amphisbaena fenestrata*. The snake was first observed on a concrete floor. When disturbed, it moved into the nearby bushes, dragging the *Amphisbaena* with it. Mastication continued until the snake disappeared, with the prey still in its mouth, approximately 10 min later. Both predator and prey were identified from the videotape by Gad Perry.

Alsophis portoricensis is known to primarily prey on lizards, though other small vertebrates are also commonly taken (Schwartz and Henderson 1991. Amphibians and Reptiles of the West Indies: Descriptions, Distributions, and Natural History. Univ. of Florida Press, Gainesville, Florida. 720 pp). However, this is the first record of amphisbaenians in its diet.

We thank J. Lazell and R. Henderson for discussions of these events and the staff of Guana Island for technical assistance. Financial support was provided by The Conservation Agency through a grant from the Falconwood Foundation.

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CYCLURA PINGUIS (Stout Iguana, Anegada Rock Iguana). **JUVENILE PREDATION**. The Stout Iguana was restored to Guana Island, British Virgin Islands, in 1986. Its population has since expanded considerably (Lazell 2002. Ecol. Restor. 20:179-185). Sightings have become more common as the numbers of juvenile iguanas increased. Over the last few years, we have regularly observed juvenile iguanas in early October. However, little is known about the ecology of this critically endangered species under natural conditions. Here we describe three predation events on juvenile *C. pinguis* which we observed on Guana Island. We believe these are the first recorded cases of natural predation on this species, which also suffers from predation by cats (Mitchell 2000. Pp. 22-27 *In* Reading and Miller [eds.], Endangered animals: a reference guide to conflicting issues, Greenwood Press, Westport, Connecticut).

Two observations involved the locally abundant colubrid snake *Alsophis portoricensis*. The first occurred at about 15:30 hr on 12 October 2001. We were told an adult snake was seen attempting to swallow a juvenile iguana and had the head of the lizard in its mouth. The snake was gone when we arrived and the iguana was dead. It was preserved, tagged, and catalogued (JL F-4890), but remains in the British Virgin Islands because of CITES regulations. We made the second observation on 9 October 2002. At approximately 18:40 hr, the snake was seen wrapped around the midsection of the lizard, which had already been envenomated but was still struggling. We took both pictures and video footage of the ingestion process, which was completed at approximately 20:40. The snake was subsequently caught and measured. Snout-vent length was 68 cm and tail length was 35 cm. *Alsophis portoricensis* primarily preys on lizards (Henderson and Sajdak 1996. *In:* R. Powell and R. W. Henderson [eds.], Contributions to West Indian herpetology: a tribute to Albert Schwartz, pp. 327-338. SSAR, Ithaca, 457 pp). However, these are the first records of iguanas in its diet.

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A third predation event occurred around 15:30 hr on 8 October 2002. A female kestrel (*Falco sparverius*), also locally abundant on Guana, was observed feeding on a freshly killed juvenile iguana which it had carried up to a tree perch. We observed the process of feeding, which began at the head of the lizard, for approximately 15 minutes, taking pictures and videotaping the event. At the end of this period, the bird flew off with the partially consumed lizard in its talons.

We thank C. Matthias, S. Slater, and R. Snelling for helping us locate these events, the staff of Guana Island for technical assistance, and H. and G. Jarecki for access to Guana Island. Financial support was provided by The Conservation Agency through a grant from the Falconwood Foundation.

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CYCLURA PINGUIS (Stout Iguana, Anegada Rock Iguana). **JUVENILE AGONISTIC BEHAVIORS**. Following its restoration in 1986, the Stout Iguana is flourishing on Guana Island, British Virgin Islands (Lazell 2002. Ecol. Restor. 20:179-185). Juvenile iguanas are now frequently encountered in early October, but their behavior in nature remains unstudied. As part of a census effort, the marking of iguanas has afforded us the opportunity to follow animals and individually identify them. Here we provide preliminary observations on the agonistic behaviors of three individuals, observed on multiple occasions during October 2002, in juvenile *C. pinguis*.

We used white water-based latex paint to individually mark all iguanas encountered. The paint is squirted on the lizard from a distance, using a syringe. Lizards show no adverse effects from the marking, and continue normal activities. Juveniles were repeatedly sighted in the same localities. One of these individuals was seen displaying aggressive behaviors towards two other juveniles who arrived in the same area during our study. Agonistic behaviors were varied. Head bobs and push ups were the most common elements, typically followed by chasing and biting. During one lengthier interaction, which lasted over 10 min, we also observed full apposition and lateral compression. Although several interactions, over a period of three days, occurred in one case, both opponents left the area soon after these interactions. *C. pinguis* adults are known to avoid each others' center of activity (Mitchell 1999. Pp. 45-70 *In* Alberts [ed.], West Indian Iguanas: status survey and conservation action plan. IUCN/SSC West Indian Iguana Specialist Group. IUCN, Gland, Switzerland and Cambridge, UK) and display aggression towards both adults and juveniles that approach them (N. Mitchell, unpublished observations). Our observations suggest that juveniles of this species begin establishing territories early in life, and that aggressive encounters are important in determining the boundaries of these early territories. We thank the staff of Guana Island for technical assistance, and H. and G. Jarecki for access to Guana Island.

Perry

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Anegada iguana programme inches on

• Several citizens protest slow progress

BY PETE TATTERSALL

A National Parks Trust programme designed to protect the indigenous Anegada Rock Iguana is drawing small pockets of fire from several local residents.

Apparently the iguanas were having a difficult time maturing to full growth in the wild, due to predators and a sometimes-insufficient food source.

"The project was devised to provide a safe haven, a stop-gap measure, to ensure that they had a fighting chance. Especially that they could be in a protected environment, where you will lessen the chances of predation, both natural and man-made, for example snakes and cats," said Joseph Abbott Smith, director of the BVI National Parks Trust.

Started in '97

The Anegada Iguana Rehabilitation Programme was hatched in 1997 and, according to some sources, was originally designed to last three years.

"The programme was initiated as a result of predation of stray cats. The stray, wild cats were eating the juveniles…so therefore we have an aging adult population with little juvenile recruitment in to the older age classes," the director said.

However, three years have come and gone, and no fully matured iguanas have yet been released back into the wild.

The concerned residents worry that, by being confined to cages, the iguanas are failing to reach their full growth, and provide too inviting a target for snakes.

Snake food?

"There will be a small portion of those that will be lost to snakes, naturally," acknowledged Mr. Smith.

"We don't deny …that there are instances where snakes have gotten into the cages, and which we've had to remove. So that has taken place. We certainly attempt to minimize the number of incidents that do occur, but it's inevitable," said the parks director.

"But certainly we view the overarching need for such a facility overrides these quirks, because the alternative is to not have a protective measure," he added.

Expert guidance

The facility was designed with guidance and technical support from the International Union for the Conservation of Nature, a species survival commission, according to Mr. Smith.

"There is a standing iguana specialist group, of which we are a member. So the design of cages, and especially the mechanisms by which we track progress, are following guidelines developed in cooperation with the group. For example, the design of the facility, mesh sizes, and so forth," he said.

Flooding?

A concern raised by Sue Wheatley, an owner and manager of the Anegada Reef Hotel, was that the cages were not being properly overseen after heavy rains.

"The people from the programme should be here more frequently to monitor the progress of these iguanas. At times there's been a lot of floodwater in the cages, and a lot of the young iguanas were clinging to the sides of the cages and had to go through the water to get to the food supply…the cages should be made to drain more easily," said Ms. Wheatley, who said she called the park service over the Christmas holidays to report flooding in the cages.

Constant monitoring

Two caretakers on Anegada regularly visit the iguana cages, according to Mr. Smith.

Much monitoring takes place daily, he maintains, "so although a visitor may go to the facility, and in their eyes it may seem as though nothing is happening, like I said, there is quite a lot that is taking place on site," he said.

"We do strive to ensure that, as need arises, measures are employed to isolate, perhaps weaker animals, that may be facing fierce competition for food within the cage," added Mr. Smith.

Roam free?

Programme managers are still trying to determine when to release the iguanas back into the wild.

"One of the things that we've done over the years is to compare, for instance, the wild population of animals versus those that are in captivity, in terms of their rates [of growth] and so on." Those rates of growth are monitored monthly, and results reported to the group, "and we do receive feedback," Mr. Smith said.

After observing the programme for some time, Ms. Wheatley has a different position.

"I believe they're not growing at the rate they should be growing. They apparently would have grown more out of captivity than in captivity," she contends.

Barren ground

Another concern is whether there will be enough natural vegetation to sustain the iguanas once they are released. Between people clearing land for development, and goats and cattle grazing on the same food sources, Ms. Wheatley fears there will be nothing left to sustain the iguanas once they are set free.

Anegada ... programme..., con't:

"I really feel these iguanas should probably be shipped to Guana Island," she said.

"I would say a few have died in captivity. And that's a situation we do not like to see happen because they are indeed rare animals. But certainly we ensure that we employ whatever measures are at our disposal to minimize that," he said.

Once released, the Parks Trust will track the iguana's progress using passive integrated transponders, which identify each animal and sends out beacon locator signals, added Mr. Abbot.

Stout Iguanas: Historical Perspectives and Status Report

John Binns
International Reptile Conservation Foundation

Anegada

R.H. Schomburgk first noted the presence of the *Cyclura pinguis* (Stout or Anegada Iguana) on Anegada in 1832, but literature documenting the status of this species has been sparse. However, each progressive publication has described or implied an ever-increasing concern for its survival. Accounts from the 1940s and 1950s are essentially non-existent. By the early 1960s, large-scale development was planned for Anegada. Although these plans were never fully realized, the initial groundwork destroyed the traditional stone paddocks used to corral livestock, unleashing goats, sheep, cattle, and burros to roam and propagate freely. Excessive grazing has since reduced the natural plant community to secondary, largely toxic vegetation. Today, almost all free-ranging cattle and burros are emaciated and only goats are thriving.

In 1968, W. Michael Carey conducted a field study on the ethoecology of the Stout Iguana and, in his classic 1975 paper, stated: "whatever the methods, steps must be taken now to ensure the continued existence of *C. pinguis* on Anegada." This statement was based in large part on his observations of competition for available food between Stout Iguanas and livestock and of predation on iguanas by domestic mammals.

Following Carey, James Lazell worked with Stout Iguanas in 1980 and 1982–1986 and Numi Mitchell worked with them in 1987–1996. Glenn Gerber, then with the University of Tennessee and presently with the Zoological Society of San Diego, began working on the species in 1998 under auspices of the IUCN/SSC Iguana Specialist Group (now funded by the International Iguana Foundation) and the British Virgin Islands National Parks Trust (BVINPT).

James Lazell first observed Stout Iguanas on Anegada in 1980 while employed by The Department of Natural Resources and the Environment (DNRE), Government of the British Virgin Islands. Expecting to find large densities at Citron Bush, the site of Carey's 1968 study, he instead found that iguanas had completely disappeared from the area in the intervening 11 years. Lazell subsequently found the highest remaining concentration of iguanas at Bones Bight, which today remains one of the core areas for the species.

Carey's warning was reiterated by others, but efforts to fund the removal of livestock and feral predators remain mostly unsuccessful, despite some recent activity. In 1997, concrete efforts to secure the species' future materialized in the form of the Anegada Iguana Head-starting Facility. In October 1997, at the request of BVINPT, West Indian Iguana Specialist Group (WIISG) members Rick Hudson (Fort Worth Zoo), Jeff Lemm (San Diego Zoo, CRES), and Rondel Smith (BVINPT) constructed a small facility to house three juvenile Stout Iguanas found floating in Manhead Pond. The facility provides a safe haven for collected hatchlings until they are large enough to reduce the threat of feral predators A year later, a grant from the UK Foreign Commonwealth Office to the BVINPT and WIISG T-shirt and poster sales funded construction of the main complex by Rick Hudson and Jeff Lemm, joined this time by Mike Fouraker and Glenn Gerber. In August 2001, the International Reptile Conservation Foundation (IRCF) and the BVINPT funded an upgrade to the facilities to increase captive capacity. Team members for this project were John and Sandy Binns (IRCF), Alberto Alvarez (DNCR), Juliann Sweet, Joel Friesch (IRCF), and Rondel Smith and Lee Vanterpool (BVINPT).

To date, none of these head-started captives have been released into the wild, but plans call for a limited release on Anegada this year, coupled with the relocation of a few captives to a neighboring island. In conjunction with these plans, a population assessment for the Stout Iguana is planned during July 2003 to update the previously published estimate of fewer than 200 remaining in existence.

Controlling livestock or feral predators on Anegada is nearly impossible due to the island's remote location and the tens of thousands of dollars that would be required. So, in 1980, in light of the obviously rapid and apparently unchecked decline of the iguana population in the previous decade, Lazell and his colleagues believed that the species was headed for extinction — unless something was done immediately. Because a solution on Anegada was not feasible and Anegada was the only place where the species still existed, the obvious recourse was to establish a second population — but where and by what means?

Guana

Essentially all possible relocation sites in the British Virgin Islands were equally infested with feral predators and goats. However, in 1932, Chapman Grant had noted the presence of iguanas on Guana Island and had identified the species as *Iguana iguana* (Common or Green Iguana), but the presence of that species was never confirmed and none has been seen since. Sometime in the mid-1930s, Louis Bigelow, then owner of Guana Island, had extirpated goats and had banned woodcutting for making charcoal. This had left only a couple of domesticated burros and free-ranging sheep on the island. The latter are far less destructive than goats.

In 1974, Henry and Gloria Jarecki purchased Guana Island. Access to this small island (300 ha) is limited, although it lies only a few kilometers from Tortola. The exclusive Guana Island Club had been constructed in a location designed to minimize impact on the natural habitat, attributable to the foresight of Louis Bigelow, who chose the construction site of the main clubhouse in the 1930s. Hiking trails around the island also were conceived to protect and minimize destruction of the lush vegetation.

In 1980, Lazell initially approached Mary Randall, then Guana Island Club Manager, to determine if the owners would allow relocation of Stout Iguanas. Randall was very enthusiastic about the concept, but two years would pass before Lazell would meet the owners and take the next step.

In the interim, he continued working on a plan that would establish a second population of Stout Iguanas while promoting other conservation and restoration goals in the British Virgin Islands. An idea for an exchange of species came with the realization that the vast salt ponds of Anegada, which had supported large colonies of Greater Flamingos (*Phoenicopterus ruber)* in the 19th century, could be restored if funds could be found. The beauty of this plan was mutual benefit to all parties involved: the British Virgin Islands and the residents of Anegada would benefit from the reintroduction of flamingos and, at the same time, the second population would provide some assurance of the long-term survival of Stout Iguanas.

Lazell first discussed the plan with several Anegada residents. One of them was the late Clement Faulkner, who maintained a Stout Iguana feeding station adjacent to his home in Bones Bight.

The plan was next presented to Robert Creque (DNRE), Lazell's boss at that time. Everyone agreed that the idea made eminently good sense.

In March 1982, Lazell finally discussed the possibility of relocating iguanas with the Jareckis, who were initially apprehensive. Would Stout Iguanas damage the island they had worked so hard to protect? Would they bite staff or visitors or destroy ornamental plants on the hotel grounds? These questions would take some time to answer. However, that meeting was instrumental in developing the long-term relationship between the Jareckis and The Conservation Agency (Lazell) that continues today.

During the remainder of March and April 1982, Lazell surveyed the island with the help of Lianna, Divonne, and Tom Jarecki (nieces and son of Henry and Gloria) and the late author, Gerald Durrell, who happened to be vacationing there.

Lazell visited Guana regularly over the next several years, conducting fieldwork with the aid of the managers, Mary Randall and her successor John Damron. Lazell also continued to build a portfolio of published papers and testimonials noting the disastrous effects of feral competitors and predators on Stout Iguanas and their habitat. Major contributors were the late Dr. William MacLean (University of the Virgin Islands), Walter Phillips of Water Island, USVI, Dr. Robert Chipley, and Nick Clarke, and Rob Norton, former Directors of the National Parks Trust, BVI.

In 1984, the Jareckis agreed to rid their island of sheep, provide a sanctuary for Stout Iguanas, and fund the relocation of flamingos. Their decision certainly was influenced by Lazell's efforts, but they also were drawn into wildlife conservation through the interest their sons and nieces had shown. Today, Eugene Jarecki remains interested in conservation, Tom Jarecki works for the Environmental Defense Fund, and Lianna Jarecki is teaching biology at H.L. Stoutt Community College on Tortola, BVI and finishing her Ph.D. with a thesis on salt pond ecology.

In July 1984, Lazell and four colleagues set off to Anegada in search of the first Stout Iguana to be relocated to Guana Island. Lazell eventually captured a large, healthy, gravid female (SVL 46 cm) that was taken to Guana, where she was released on 29 July 1984. The other seven iguanas that comprised the founding stock (sex, SVL, and release date) were: male (41 cm; 19 July

1985), female (44 cm; 19 July 1986), female (22.4 cm, 27 July 1986), two females (33.5 and 43 cm, latter gravid) and two males (50.4 and 50.9 cm; 31 July 1986). Guana now had the foundation for a second population, but years would pass before the success of the relocation could be evaluated.

Lazell next set out to complete the species exchange plan. The Bermuda Aquarium, Museum, and Zoo (BAMZ) had both captive-bred and wild-stock flamingos and agreed to donate a number sufficient for establishing a population. Numi Mitchell (TCA) arranged the international transfer of the birds (BVI Agriculture and Fisheries Permit, veterinary certification with respect to the birds' health, especially Newcastle's Disease). Numi, Glenn Mitchell (TCA), and James Conyers (BAMZ) transported the birds by jet from Bermuda to Tortola and then by boat to Anegada. The flamingos initially were released into a net holding pen at the salt ponds, allowing them to recuperate and adjust to their new environment. On 7 March 1992, in a ceremony at the north end of the salt ponds, the Governor, the National Parks Trust, and the Anegada community celebrated the arrival of the first 18 birds. By 2002, the flock had multiplied to approximately 80 resident birds (Guana also supports 4–6 pinioned flamingos in a small salt pond, but they do not reproduce because the population density is too low).

Necker

Necker Island, like Guana, is privately owned and exclusive, with a single luxurious resort, the Balinese Great House, situated on the highest point and overlooking the coral reef-studded waters of the Caribbean. The island supports dense tropical vegetation, composed of both native and non-native plants and enhanced by irrigation. The other half of the island is more typical of the region, with rocky terrain and small clusters of hardy trees, low shrubs, and dense stands of cacti. Designated a bird sanctuary, Necker is home to pelicans, doves, and hummingbirds.

In 1994, Richard Branson, owner of Necker Island (30 ha), expressed an interest in establishing a third population of Stout Iguanas. Because the iguanas on Guana had enhanced the natural setting of the island and were well received by visitors, Branson was eager to expand the conservation effort. Lazell had worked previously on Necker and knew the island to be free of feral livestock and rats.

In October 1995, four hatchlings were taken to Necker and head-started for a year before being released. During that time, one female escaped, but was seen later and appeared to be gravid. In 2000, Lazell reported seeing the first hatchling and subsequent reports from the island indicated that Stout Iguana hatchlings were abundant. Although the population is still in its infancy, during the October 2002 population assessment conducted on Necker, founding stock, young adults, and hatchlings were recorded.

Today

Long after these second and third populations were established, their existence is not commonly acknowledged, little pertinent information is available, and some controversy remains regarding the circumstances under which they were established. In 2002, I was invited to participate in an assessment of the Guana and Necker populations. That survey, directed by Lazell and Mitchell, was conducted during "Scientists Month" from 4–29 October (each year, Guana hosts a large contingent of scientists who conduct research on the island).

After 14 hours of travel and delays, Guana was like a little piece of paradise. At the dock, my gear was loaded into the Club's pickup and we proceeded up the steep, twisting road to the clubhouse. The Club overlooks the dense tropical vegetation of the island's southern end, the salt pond — home to the six flamingos, and the white beach of a little cove that merges imperceptibly with the crystalline waters of the Caribbean.

When I arrived at the patio, which overlooks the equally picturesque northern end of the island, it was alive with more scientific dialog than I could begin to imagine — scientists, some 20 of them, at lunch. After brief introductions, focus quickly returned to the population survey that was already in progress.

That same afternoon, we were issued several 2-oz syringe barrels loaded with white latex paint and began a survey of the Club's wooded perimeter and nearby support structures. Many Stout Iguanas, including the founders, live in close proximity to the Club. The weather was cloudy and damp from the morning's rain, which kept iguanas from venturing far to bask or forage.

The first sighting was somewhat unusual. We came upon four workmen digging a ditch next to a small structure while talking loudly to be heard over the radio playing in the background. Above them on a rock ledge, a large iguana lay casually, as if supervising their work. We marked the animal with paint, which did not appear to disturb it, and it remained nearby, seemingly unaffected by the intrusion. The remainder of the day included marking or sightings of younger adults and juveniles, but the weather was clearly hampering our efforts. The founding iguanas and other older adults were nowhere to be found.

The next day, Mitchell and I explored the area west of the main facility, accessed from the "Iguana Trail," while another team surveyed the southern area. The weather had improved, but remained partly cloudy and cool compared to typical conditions. Our first marking was a subadult on a steep wooded slope not 50 m from the trail's entry point. Like our first iguana on the previous afternoon, he was rather nonchalant about our presence.

That afternoon, we focused our attention on the northern section of the island where iguanas were not known to occur. Tail-drags are common on trails in the area south of North Beach, but they abruptly disappear to the north of a line roughly parallel with Crab Cove. The trail eventually splits into two routes, and Mitchell and I separated to cover more ground. About halfway between Crab Cove and Chicken Rock Steps, I observed one large, unmarked adult, who, unlike others we had observed, responded to the intrusion by quickly thundering off into a cactus thicket. We saw no other iguanas or tail-drags, but did see some scat.

The survey continued and the weather improved each day, as did the frequency of iguana sightings. In addition to the population size estimate (see "Assessment" on p. ??), we recorded three incidents of predation on juvenile Stout Iguanas, two by Racers (*Alsophis portoricensis)* and the other by a female Kestrel (*Falco sparverius*).

Early on the morning of 14 October, ten of us left Guana by boat for Necker Island to assess the third population of Stout Iguanas, only seven years after the initial four hatchlings were released. The survey was limited to two days, and the team members quickly dispersed upon arrival.

Mitchell and I began our survey at a location near the main facilities where iguanas are fed twice a day. The ground and trails showed many signs of tail-drags clearly produced by individuals of vastly different sizes. We saw several iguanas in the thick shrubs around this area. From there, I worked the very dry northern section of the island and saw only one drag and one scat. Mitchell sighted a few animals as she worked an area near where the iguanas are fed.

Others on the survey team successfully marked several individuals and recorded sightings of hatchlings along the pathways around the maintenance and support facilities. Two Racers (*Alsophis portoricensis*) also were observed in the same area.

The next day, starting where the iguanas are offered food, we saw two of the founding iguanas. A conservative estimate placed these animals at about 47 cm SVL and well over 5 kg. Both appeared in excellent health, alert, and with coloration of rich brown above blending into turquoise flanks. We spent our remaining time around the nursery and beach facilities and saw several iguanas, including a subadult and hatchlings. As on Guana, the Necker iguanas appeared to concentrate near the developed areas.

In stark contrast to the boisterous excitement that characterized the boat ride to Necker, we quietly sought a comfortable spot for the return trip. Although tired from the day's hard work in blazing sun, we had time to reflect on events that had led us to this one point in time and space.

The absence of committed, long-term funding continues to impede efforts to secure the species' survival on Anegada. Compounding loss of habitat is ongoing development. Consequently, Stout Iguanas are fighting for survival, suffering simultaneously from habitat degradation and predation on juveniles. Some fear that the upcoming assessment will determine that the Anegada population has declined to critically low numbers and may be functionally extinct in the wild. However, I believe we all shared a warm feeling knowing that the outlook for Stout Iguanas had improved considerably through the efforts of a few very special people.

Acknowledgements

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Guana and Necker Island Population Assessment Results 2002

Gad Perry and Numi Mitchell
The Conservation Agency

Only rarely is a population so thoroughly known that every member is individually recognized and a full census possible. Because of this, a variety of statistical methods, some of them extremely sophisticated, are normally employed to estimate population size. As with all statistical methods, population estimates have limitations. The amount of available data is one crucial factor: the more, the better. In addition, certain assumptions, some of them unique to one set of estimators or another, apply.

Unfortunately, studies on critically endangered species tend to run afoul of one or both issues, making reliable population estimates difficult. This is the case with Stout Iguanas. Not only are the populations small, they are unreliable subjects (a captured adult iguana may retreat into its burrow for up to three weeks in response to the stress), hard to spot in the field (the terrain is rough and the animal is cryptically colored), and often not accessible (work on Guana can normally be conducted only during the month of October). These limitations render any estimate of population size less reliable than one would like, and therefore much less satisfying to a wildlife manager. Nonetheless, work with endangered species requires that their populations be estimated, so that one can determine if the population is stable, growing, or — in a worst-case scenario — declining. A preliminary estimate, known to be imperfect, is better than none, as long as the limitations of the estimate are kept firmly in mind when management decisions are being made.

Several attempts to monitor the Guana iguana population were made over the years. Combined with the evidently growing numbers ~~of hatchlings~~ every year, they suggested that the population was doing well and growing at a steady pace. In October 2002, a more concerted effort was made by marking ~~several~~ individuals with water-based, white, exterior latex paint (which quickly dries waterproof) squirted from a two-ounce (60 cc) syringe barrel. Marking began on 4 October and continued until 13 October, Twenty-three individuals were marked, but on most days some sighted iguanas escaped unmarked. Beginning on 15 October, we did six "round-up" counts of marked and unmarked individuals, finishing on 29 October. These provided six population estimates, based on the Petersen Index (Ricker 1975): 69, 115, 138, 138, 138, and 207. The numbers are relatively close to one another, suggesting that they probably represent a fairly robust estimate. A calculated mean (134) is probably not too far from the real value. A calculate~~s~~d standard deviation (45 in this case) allows us to say that we are 95% confident that the true population size is between 44 and 224: two standard deviations from the mean in each direction. Unfortunately, this method does not meet all the assumptions of the test, which renders the numbers uncertain.

A second method for calculating population sizes was proposed by Z.E. Schnabel in 1938. Using this method, we can add to the six Petersen Index tallies the data from 4–13 October. This method generates remarkably similar numbers, estimating the population size at 95 individuals and the 95 % confidence interval at 58–185. Once again, not all assumptions are met, but the fact that two very different methods with different assumptions lead to similar estimates gives us more confidence that the population size really is about 100 individuals.

We arrived on Necker Island on the afternoon of 14 October 2002 and quickly marked five Stout Iguanas. The next day before our departure, we saw six iguanas only one of which was marked. The implication is that one-sixth of the population was marked; so five times six is 30. No statistics can be done on a single estimate, but it conforms remarkably well with the opinion of resident naturalist and caretaker, Brian Andrews, who believes that about 20 individuals are present, not counting the current year's hatchlings.

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To: Iguana Specialist Group principals Dr. Allison Alberts and Rick Hudson: 2 Dec. 2002.

Dear Allison and Rick:

Rumor Central tells me TCA figures in the proposed recovery plan for C. pinguis That is certainly appropriate and, I believe, necessary. However, if we are included we must be privy to the plan. I formally request a copy.

Our oft-repeated offer of individuals for stocking -- on Anegada or almost any other island -- still stands, and may prove critical to realistic, long-term recovery.

Please send me a copy of the proposed plan.

Sincerely,

James Lazell, Ph.D.
P.O. Box 86
Lane, OK 74555

- -

Dear Skip,

The recovery plan document is still very much in draft form - once it is approved by NPT, I'd be happy to send a copy your way. My understanding is that the plan proposes that avenues of communication be encouraged between TCA and NPT such that the Guana/Necker populations can recognized an important element in the overall conservation strategy for the species. I hope to have something to send you soon!

Hope all's well with you,

Allison

12/2/2002

7 May 2003: I have received nothing yet.

Skip.

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Wenhua Lu

From: "Miguel A. Garcia"
To: <hq@theconservationagency.org>
Sent: Wednesday, December 18, 2002 7:57 AM
Subject: pinguis in Puerto Rico

Hi Skip:

Thanks for the reprints. We have been working quietly and had evaluated several islands around Puerto Rico for reintroducing C. pinguis. There are many good options, but to start, Caja de Muertos (202 ha) seems to be the best option.

1. It is protected (natural reserve)
2. Belongs to the Commonwealth of Puerto Rico
3. Adequate size
4. No cats
5. No green Iguanas (at least none have been observed lately)
6. Good habitat-Subtropical Dry Forest
7. Facilities to conduct the monitoring after the release.

At this point BVI National PArk Trust is reluctant to allow "the transfer" of some pinguis outside the BVI. My best understanding is that we need "their authorization" for the CITES permit, since they represent the BVI goverment on this matter.

ISG has been very diplomatic about this initiative, although EVERYONE is convinced that is the obvious next step to recover this species. Anyway is a sensitive topic because BVINPT is a active member of ISG. As you know, I also work for the goverment and I will no receive " a green light" without BVI approval. In summary, moving pinguis within BVI is one thing, and moving pinguis outside BVI is a Totally Different Scenario.

However, bringing pinguis to PR is unavoidable, it will happens sooner or later. The situation of this species in Anegada push harder everyday the initiation of the reintroduction. I live thinking the way to accelerate or potentially circumvent the obstacles to accomplish this important goal.

Regards,
Miguel

From: "Josh Donlan" <cjd34@cornell.edu>
To: "James Lazell" <hq@theconservationagency.org>
Cc: '"Bernie Tershy'" <tershy@islandconservation.org>; "Harry W. Greene"
Sent: Sunday, October 06, 2002 5:12 PM
Subject: ecological/evolutionary analogs

Dr. Lazell,

It was exciting to see you recent article about restoring communities with ecological/evolutionary analogs on the British Virgin Islands. Our organization, the Island Conservation & Ecology Group (http://www.islandconservation.org) has also been heavily influenced by Ian Atkinson's thinking over the past few years. Over the past 5 years, we have removed 29 introduced mammal populations from 23 islands in Northwest Mexico - and now have been thinking of taking the next step in preserving ecological and evolutionary processes by reintroducing congeners of extinct rodents to these islands.

It is exciting to see these ideas finally moving out of pubs and coffee shops and into the literature. I had a few questions for you.
1. With the whistling frogs and the reintroduction onto Little Thatch Island, was there evidence that E. schwartzi was once present on the island, or was there just evidence there was a species of Eleutherodactlyus?
2. On the islands where you have done these conspecific reintroductions (frogs, tortoises, iguanas, pigeons, flamingoes), are these islands now free of introduced predators and if not, are eradication programs underway?

Congratulations on your work and please keep me informed on your progress. I would also be interested in hearing of any response you have received concerning your recent article in Ecological Restoration.

Bests,
josh donlan

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Pp. 86-103 *in* Studies in Trinidad and Tobago Ornithology Honouring Richard ffrench (F. E. Hayes and S. A. Temple, eds.). Dept. Life Sci., Univ. West Indies, St. Augustine, Occ. Pap. 11, 2002.

GROUND-BASED NEARCTIC-NEOTROPIC LANDBIRD MIGRATION DURING AUTUMN IN THE EASTERN CARIBBEAN

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ABSTRACT.–We examined ground-based Nearctic-Neotropic landbird migration during autumn at coastal sites on two islands about 775 km apart in the eastern Caribbean, where autumn migration had not been previously studied using mist-nets. We sampled migrants using mist-nets at Harrison Point (HP), Barbados, for 42 days in 1997 and 31 days in 1998-1999, and at Guana Island (GI), British Virgin Islands, for 52 days during 1995-1999. We also obtained information on landbird migration from sight observations. We recorded 28 species of Nearctic-Neotropic landbird migrants at HP and 23 species at GI, for a total of 36 species. The volume of migration was low at both sites. The Blackpoll Warbler (*Dendroica striata*) was the most abundant migrant (98 captures, 206 observations at HP; 132 captures, 263 observations at GI). The Yellow-billed Cuckoo (*Coccyzus americanus*) was the second most abundant migrant at HP (six captures, 101 observations), but was rare at GI (seven observations). The Red-eyed Vireo (*Vireo o. olivaceus*), previously considered a vagrant or scarce transient in the eastern Caribbean, was the third most abundant nocturnal migrant at HP (12 captures, 8 observations). At HP and GI, respectively, 23% and 33% of captured Blackpoll Warblers were after hatching year birds, compared to 8% and 14% for other Nearctic-Neotropic migrants. At both sites we recorded many scarce transients or apparent vagrants, some verified or seen for the first time in the eastern Caribbean. All species recorded except Northern Rough-winged Swallow (*Stelgidopteryx serripennis*) at HP and Nashville Warbler (*Vermivora ruficapilla*) at GI, have been recorded at least once during winter in South America; however, more species wintering primarily within the West Indies occurred at GI. Autumn migration of Nearctic-Neotropic landbirds is a regular phenomenon to the eastern Caribbean for a few relatively abundant species moving to their winter range in South America, and also includes a large variety of scarce species. Other than Blackpoll Warblers, which migrate during autumn over the western North Atlantic Ocean through the West Indies to South America, the other Nearctic-Neotropic landbird migrants probably departed from southeastern North America for a shorter over-water crossing through the Greater Antilles and over the Caribbean Sea.

RESUMEN.–Se estudió la migración por tierra del neártico al neotrópico de aves terestres durante el otoño en sitios costeros de dos islas separadas aproximadamente 775 km la una de la otra en el este del Caribe, donde no se ha estudiado previamente la migración de otoño usando redes de neblina. Se muestrearon migratorios usando redes de neblina en Harrison Point (HP), Barbados, por 42 días en 1997 y 31 días en 1998-1999, y en Isla Guana (IG), Islas Vírgenes de Inglaterra, por 52 días durante 1995-1999. También se obtuvo información sobre la migración de aves terrestres por observaciones visuales. Se registraron 28 especies de aves migratorias terrestres neártico-neotrópico en HP y 23 especies en IG, para un total de 36 especies. El volumen de migración fue bajo en ambos sitios. La Reinita Rayada (*Dendroica striata*) fue el migratorio más abundante (98 capturas, 206 observaciones en HP; 132 capturas, 263 observaciones en IG). El Cuclillo Pico Amarillo (*Coccyzus americanus*) fue el segundo migratorio más abundante en HP (seis capturas, 101 observaciones), pero fue raro en IG (siete observaciones). El Julián Chiví Ojirrojo (*Vireo o. olivaceus*), previamente considerado vagante o escaso, fue el tercer migratorio nocturno más abundante en HP (12 capturas, 8 observaciones). En HP y GI, respectivamente, 23% y 33% de las capturas de Reinita Rayada fueron de aves de más de un año de edad, comparados con 8% y 14% de otros migratorios neártico-neotrópico. En ambos sitios se registraron muchos transeuntes escasos o vagantes aparentes, algunos documentados u observados por primera vez en el este del Caribe. Todas las especies registradas, salvo la Golondrina Ala de Sierra (*Stelgidopteryx serripennis*) en HP y la Reinita de Nashville (*Vermivora ruficapilla*) en IG, han sido registradas por lo menos una vez durante el invierno del norte en Sudamérica; sin embargo, en IG se registraron más especies que invernan principalmente dentro de las Indias Occidentales. La migración de otoño neártico-neotropico de las aves terrestres es un fenómino regular en el este del Caribe para las especies relativamente abundantes que migran hacia su área de invernada en Sudamérica, y también incluye una amplia variedad de especies escasas. Ademas de las Reinitas Rayadas, que migran durante el otoño sobre el Noroeste Atlántico por las Indias Occidentales hasta Sudamérica, las otras especies migratorias terrestres neártico-neotrópico probablemente parten del sudeste de Norteamérica realizando un cruce más corto sobre el Mar del Caribe por las Antillas Mayores.

KEY WORDS.–abundance, age, autumn migration, Barbados, Caribbean Sea, *Coccyzus americanus*, *Dendroica striata*, landbirds, migratory routes, Nearctic-Neotropic migrants, vagrants, *Vireo o. olivaceus*, Virgin Islands

Radar-based observations from Puerto Rico and several locations in the Lesser Antilles (Antigua, Barbados), aided by visual confirmation of species identification, documented that large numbers of small landbirds, including Blackpoll Warblers (*Dendroica striata*), fly over these regions during autumn migration (Hilditch et al. 1973, Williams et al. 1974, 1977a,b, 1978, Richardson 1976, 1980, Williams and Williams 1978a,b, Larkin et al. 1979, Williams 1985, Nisbet et al. 1995), although the density of landbirds east of Puerto Rico is much less (Richardson 1976). Sight observation data obtained over many years from Antigua and Barbados, where observer effort has been relatively high for the Lesser Antilles (Holland and Williams 1978; Hutt et al. in prep.), have documented a relatively large number of species and generally low numbers of individuals of Nearctic-Neotropic migrants during autumn, with a broad peak of occurrence in October and early November. Norton (1981), Norton et al. (1989), Keith (1997), Steadman et al. (1997) and Feldmann et al. (1999) cited few observations of Nearctic-Neotropic landbirds during autumn migration in the British Virgin Islands, St. Lucia, St. Kitts, and Guadeloupe and Martinique. Although the Virgin Islands (at the eastern end of the Greater Antilles) has a fair number of overwintering Nearctic-Neotropic landbirds compared to the Lesser Antilles (Robertson 1962, Pashley 1988, Wunderle and Waide 1993), the general scarcity of overwintering Nearctic-Neotropic landbirds in the eastern Caribbean, especially in the southern Lesser Antilles (Terborgh and Faaborg 1980, Wunderle and Waide 1993, Keith 1997), has reinforced the perception that grounded migrants during autumn are sporadic and scarce here. The low number of grounded Nearctic-Neotropic landbird migrants east of Puerto Rico is not concordant with the large volume documented by radar data.

Nearctic-Neotropic landbird migration has not been investigated using mist-nets in the eastern Caribbean, except documentation of new and rare species of Nearctic-Neotropic landbird migrants during autumn 1997 at Barbados (McNair et al. 1999). Previous studies using mist-nets to sample populations of Nearctic-Neotropic landbirds in the West Indies have concentrated on wintering birds (Wunderle and Waide 1993, Wallace et al. 1996, Wallace et al. 1999, and references cited therein). We operated mist-net stations during autumn along the coast of two island sites about 775 km apart in the eastern Caribbean, at Harrison Point (hereafter HP), Barbados, and Guana Island (hereafter GI), British Virgin Islands. Our sampling periods were primarily restricted to October to coincide with the Blackpoll Warbler migration (see Nisbet 1970, Pashley and Hamilton 1990, Nisbet et al. 1995).

The primary purpose of our combined efforts was to obtain samples of patterns of Nearctic-Neotropic landbird migration in the eastern Caribbean. We use this information to address which of two migratory routes these species take during autumn to reach the eastern Caribbean. Birds may fly from northeastern North America over the western North Atlantic Ocean through the West Indies to South America (Blackpoll Warbler: Nisbet 1970, Hilditch et al. 1973, Williams et al. 1974, 1977b, 1978, Richardson 1976, 1980, Williams and Williams 1978a, Larkin et al. 1979, Williams 1985, McNair and Post 1993, Nisbet et al. 1995) or may depart from southeastern North America for a shorter over-water crossing through the Greater Antilles and over the Caribbean Sea (Richardson 1976, 1980; also see route number three in Rappole et al. 1979).

STUDY AREAS AND METHODS

Study areas.–Harrison Point (13°19'N, 59° 39'W) is located at the northwest tip of Barbados on a raised coral limestone terrace about 30 m above sea level. The mean annual rainfall is 110-125 cm; surface water is absent. The vegetative cover is highly disturbed coastal scrub, thickets and woodlots, which now surround an abandoned sugar cane plantation house. Naturalised species are numerous, especially quick stick (*Gliricidia sepium*), casuarina (*Casuarina equisetifolia*), clammy cherry (*Cordia obliqua*) and Pride of India (*Tamarindus indica*), although the native whitewood (*Tabebuia pallida*) is one of three dominant trees. Other native trees or shrubs which are numerous include bread-and-cheese (*Pithecellobium unguis-cati*), dog wood (*Capparis flexuosa*), sage (*Lantana* spp.), black sage (*Cordia curassavica*) and coffee fence (*Clerodendrum aculeatum*). HP is about 16 ha, excluding adjacent sugar cane fields.

Guana Island (18°30'N, 64°30'W), 340 ha, is located in the British Virgin Islands just northeast of Tortola Island. The British Virgin Islands are about 130 km north-northwest of Anguilla, the northernmost large island of the Lesser Antilles. The mean annual rainfall is 102 cm. Freshwater on GI is scarce and restricted to a small seasonal seep (other than pools associated with a hotel). A large salt pond is present. The vegetative cover is primarily open xerophytic forest with more than 40 native tree species, plus artificially maintained grassy fields and some ornamental vegetation around the only hotel. The forest is recovering from overgrazing by sheep that ended about 10 yr ago. Native trees and shrubs include the frequent dominant tabebuia (*T. heterophylla*), gumbo-limbo (*Bursera simaruba*), loblolly (*Pisonia subcordata*), frangipani (*Plumeria alba*), buttonwood (*Conocarpus erectus*), acacia (*Acacia muricata*) and sea grape (*Coccoloba uvifera*; Lazell 1996). Naturalised species, which are not an important component of the vegetation, include coconut (*Cocos nucifera*), royal poinciana (*Delonix regia*) and tamarind (*Tamarinda indica*).

Sampling methods.–In 1997, McNair, Massiah and Frost monitored 16 30-mm mist-nets at HP from 29 September to 9 November (42 days) for a total of 5,909 net hours. Nets were usually operated from sunrise to sunset, although occasionally closed 1-2 hours before sunset. We temporarily closed the nets for a few hours on some days because of inclement weather, but did not miss a single day of sampling. We placed half of the mist-nets in fairly open forest (mean score of 60% for canopy density; James and Shugart 1970) dominated by quick stick. The other eight nets were placed in fairly closed mixed forest (mean score of 75% for canopy density) where whitewood was usually the dominant tree, along with a variety of naturalised and native species. Casuarinas emerged above the canopy in mixed habitat in more than half of the net lanes, to 13.3-17 m. Otherwise, the mean heights of the vegetation in the 'whitewood' net lanes was still higher than in the 'quick stick' lanes (7.5-9.5 m vs. 5.5-6.0 m). In 1998-1999, Massiah and Frost monitored 8-12 mist-nets and operated nets on an intermittent basis from 26 September to 8 November (31 days) for a total of 1,333 net hours. We usually opened the nets in the morning; the nets were always open at midday (4-8 hours post-sunrise), but rarely later. We also used sight observation data obtained during autumn migration from 1993-1999 (excluding 1997, 52 days) to augment our results from mist-netting.

Sibley and associates operated 2-12 30/36 mm mist-nets at GI during October for 5 yr (1995-1999; 52 days) for a total of 1,869 net hours. The length of our visits each year varied from 1-3 weeks. Unlike HP, where mist-net operations were standardised, we frequently moved nets at GI in attempts to increase capture rates of Nearctic-Neotropic migrants and closed or failed to open nets during unproductive periods. We placed the nets at many locations (ridges, along trails) in the open forest where mean height of the vegetation ranged from 5-7 m, and across hedgerows with nets extended to the fields, roads or margin of the salt pond at one or both ends. We often operated the nets throughout daytime, but favoured morning hours. We also used sight observation data obtained during autumn migration from 1994-1999 (58 days) to augment our results from mist-netting.

Data collection and analyses.–For all birds captured in mist-nets, we recorded date of capture, age (AHY = adult; HY = immature) and sex, flattened wing length (mm; at HP) or wing chord (mm; at GI), mass (nearest 0.1 or 0.25 g, but nearest 0.5 g for Yellow-billed Cuckoo [*Coccyzus americanus*]), and fat class (HP: 0-5, Foster and Cannell 1990; GI: 0-3, Manomet Bird Observatory [a trace of fat was scored as 0.5]). Birds were aged and sexed when possible by skull ossification and plumage characters following Pyle et al. (1987, 1997). A small proportion (<5%) of HY Blackpoll Warblers from mid-October onward had fully ossified skulls, so these individuals were aged solely by plumage characters including the non-singular use of pointedness of the rectrices.

We assessed the abundance of birds at each site by calculating the number of daily captures and estimated sight observations for each species and summed these totals for each category over the year or years. Observations of banded birds were excluded from the sight observation totals. Sight observations may include duplicate data, so we estimated these numbers conservatively for the most numerous species. We assessed the frequency of birds at each site by calculating the number of days each species was recorded, based on both captured birds and sight observations.

We calculated migratory volume at both sites using capture rates from mist-net sampling only, although we recognise that we did not use standardised procedures at GI. Yellow-billed Cuckoos were excluded from this analysis because they were not adequately sampled by the small mesh sizes that we used. Indigo Buntings (*Passerina cyanea*) at HP were also excluded from this analysis because we captured these birds 5-7 days after their arrival by moving one mist-net to a favoured location and beating the birds in (McNair et al. 1999).

We assessed the seasonal distribution of Yellow-billed Cuckoo at HP in 1997 by combining the number of daily captures and estimated sight observations to obtain a daily estimated total and then calculated the number of birds for 5-day periods. Using the same method, we added this information to results from sight observations only from 1993-1996 and 1998-1999, but adjusted for the number of days each period was sampled since this was unequal. Our unit of measure is bird-day (for each 5-day period), as used by bird observatories in Britain. We also assessed the seasonal distribution of Blackpoll Warbler, but this information will be presented elsewhere (McNair et al. in prep.).

We used chi-square analysis to compare differences in the diurnal timing of migration for captured birds at HP in 1997 after adjusting the expected frequencies for minor differences in netting effort among the three time periods used. We also performed Chi-square analysis for sight observations, with $\alpha = 0.05$.

We obtained information on estimated mean fat-free masses, adjusted for age, sex, and wing length category when possible (although information on wing length category is rarely available) for nocturnal Nearctic-Neotropic migrants from Connell et al. (1960), Odum *in* Dunning (1993) [which supercedes Odum *in* Nisbet et al. (1963) for Blackpoll Warbler], Rogers and Odum (1964, 1966) and Child (1969). Estimated mean fat-free masses used are: Yellow-billed Cuckoo, 46.8 g; Red-eyed Vireo (*Vireo o. olivaceus*), 14.59 g; Gray-cheeked Thrush (*Catharus m. minimus*), 25.2 g; Swainson's Thrush (*C. ustulatus*), 24.18 g; Northern Parula (*Parula americana*, 5.93 g; Chestnut-sided Warbler (*D. pensylvanica*), 8.03 g; Magnolia Warbler (*D. magnolia*), 6.92 g; Black-throated Blue Warbler (*D. caerulescens*), 7.64 g; Blackpoll Warbler, 10.34 g; American Redstart (*Setophaga ruticilla*), 6.49 g; Ovenbird (*Seiurus aurocapillus*), 15.52 g; Northern Waterthrush (*S. noveboracensis*), 13.68 g; Kentucky Warbler (*Oporornis formosus*), 11.36 g; Scarlet Tanager (*Piranga olivacea*), 24.13 g; and Indigo Bunting, 12.34 g. Using these values, we calculated the mean percentage above fat-free mass for each of these species that we captured at either site. We compared these calculated values at our two sites to the mean percentage above fat-free mass of trans-Gulf migrants during spring (published mass data are not available for arrival of trans-Gulf migrants during autumn in the Yucatan peninsula; see Winker 1995a) that were captured at East Ship Island, a barrier island 14 km off the Mississippi coast, following a long (approximately 1050 km) over-water flight (Kuenzi et al. 1991); we also obtained information on the mean mass value of Gray-cheeked Thrushes that were not recaptured at a coastal woodland chenier in Cameron Parish, Louisiana; Yong and Moore 1997). We used the same fat-free values as above in our calculations of the mean percentage above fat-free mass for these trans-Gulf migrants except for Chestnut-sided Warbler (8.01 g), Scarlet Tanager (24.5 g), and Indigo Bunting (11.97 g for females, 12.69 g for males).

We estimated the rate of mass loss (g/hr) as a function of mass for each species from the empirically-derived formula for small passerines (8-32 g) during nocturnal flight (Hussell and Lambert 1980), which estimates that mean mass loss is 0.91% of body mass/hr. This formula is $L_W = 0.0533\ W^{0.40}$, where L = mass loss (g/hr) and W = mass. We assumed that mass loss only represents loss of metabolized adipose fat. We also used this formula for our only medium-sized non-passerine (Yellow-billed Cuckoo). We used measured, not derived values of mean mass loss for four species (Swainson's Thrush, Red-eyed Vireo, American Redstart, and Ovenbird) in Hussell and Lambert (1980). We used the empirically derived value of mass loss (0.144 g/hr) for Blackpoll Warbler, despite the perception that Blackpolls may have lower flight metabolism costs than other passerines (Hussell and Lambert 1980), as well as the estimated values of 0.107 g/hr and 0.07 g/hr (for birds of low mass; less than 13.2 g) in Nisbet et al. (1963) since all three values are of similar magnitude (not 0.062 g/hr which pertains to captured [resting] birds not undergoing migratory flight *contra* Hunt and Eliason [1999]). Then using mean fat loads for each species, we converted rates of mass loss to the estimated number of hours each species could fly before reaching their fat-free mass and converted this value to the estimated distance each species could fly, using an average air speed of 38.5 km/hr for small passerines over the Lesser Antilles under conditions of no wind (Nisbet et al. 1963, Williams et al. 1977b, 1978, Williams and Williams 1978a, Williams 1985, Pennycuick 1989).

RESULTS

Species composition and abundance.–We captured or observed 22 species of nocturnal Nearctic-Neotropic landbird migrants at HP during 1993-1999 (Tables 1 and 2), plus six species of diurnal migrants (Chimney Swift [*Chaetura pelagica*], hirundinids and Bobolinks [*Dolichonyx oryzivorus*]). At GI, we captured or observed 20 species of nocturnal landbird migrants during 1994-1999 (Table 1), plus three species of diurnal migrants (hirundinids and Bobolinks). At both sites combined, we recorded a total of 36 species.

The Blackpoll Warbler was the most abundant

TABLE 1. Number of birds captured in mist-nets and estimated number of birds observed, number of days recorded and range of dates for each species of Nearctic-Neotropic landbird migrant at Harrison Point, Barbados, from 29 September to 9 November 1997 (42 days), and at Guana Island, British Virgin Islands, in October 1995-1999 (52 days).

	Harrison Point, Barbados				Guana Island, British Virgin Islands			
Species[a]	Number captured	Number observed	Number of days	Range of dates	Number captured	Number observed	Number of days	Range of dates
Nocturnal Migrants								
Coccyzus americanus	6	45	30	2 Oct-8 Nov	–	7	5	14-25 Oct
Contopus virens / sordidulus	–	1	1	19 Oct	–	–	–	–
Vireo flavifrons	–	–	–	–	–	1	1	12 Oct
Vireo o. olivaceus	10	5	12	5-23 Oct	6	1	6	14-21 Oct
Catharus m. minimus	1	–	1	12 Oct	–	–	–	–
Catharus ustulatus	1	–	1	19 Oct	–	–	–	–
Vermivora chrysoptera	–	1	1	1 Nov	1	1	2	14-18 Oct
Vermivora ruficapilla	–	–	–	–	–	1	1	13 Oct
Parula americana	–	1	1	22 Oct	2	1	3	19-28 Oct
Dendroica petechia	1	–	1	9 Nov	–	–	–	–
Dendroica pensylvanica	1	–	1	8 Nov	–	2	2	18-26 Oct
Dendroica magnolia	–	–	–	–	1	–	1	20 Oct
Dendroica tigrina	–	–	–	–	1	2	7	16-22 Oct
Dendroica caerulescens	–	–	–	–	2	–	2	4-22 Oct
Dendroica discolor	–	–	–	–	–	10	4	4-14 Oct
Dendroica striata	75	98	25	1 Oct-9 Nov	132	263	49	3-30 Oct
Mniotilta varia	–	–	–	–	5	7	9	6-28 Oct
Setophaga ruticilla	2	–	2	13-15 Oct	1	–	1	26 Oct
Seiurus aurocapillus	–	–	–	–	3	1	4	21-28 Oct
Seiurus noveboracensis	–	–	–	–	5	13	16	5-29 Oct
Oporornis formosus	2	–	2	2-4 Oct	1	–	1	20 Oct
Oporornis agilis	1	–	1	1 Nov	–	–	–	–
Piranga olivacea	1	–	1	4 Nov	–	–	–	–
Pheucticus ludovicianus	1	3	4	22 Oct-1 Nov	1	3	3	19-22 Oct
Guiraca caerulea	–	1	1	8 Nov	–	2	2	10-12 Oct
Passerina cyanea	9	1	9	1-9 Nov	1	–	1	22 Oct
Diurnal Migrants								
Tachycineta bicolor	–	–	–	–	–	1	1	21 Oct
Stelgidopteryx serripennis	–	1	1	6 Oct	–	–	–	–
Riparia riparia	–	17	4	2-13 Oct	–	–	–	–
Petrochelidon pyrrhonota	–	5	2	8-12 Oct	–	–	–	–
Hirundo rustica	–	47	9	2-16 Oct	–	7	2	21-25 Oct
Dolichonyx oryzivorus	–	154	26	29 Sep-29 Oct	–	5	2	12-22 Oct

[a] Species names not mentioned in text include: Yellow-throated Vireo (*Vireo flavifrons*), Tree Swallow (*Tachycineta bicolor*), Bank Swallow (*Riparia riparia*), Cliff Swallow (*Petrochelidon pyrrhonota*), Yellow Warbler (*Dendroica petechia: aestiva* group), Prairie Warbler (*Dendroica discolor*), Black-and-white Warbler (*Mniotilta varia*), Rose-breasted Grosbeak (*Pheucticus ludovicianus*), and Blue Grosbeak (*Guiraca caerulea*).

migrant at both sites (Tables 1 and 2). Excluding Yellow-billed Cuckoos, Indigo Buntings, and diurnal migrants at HP, Blackpolls accounted for 78% of all captured birds and 89% of all observed birds in 1997. Results at HP in other years since 1995 were similar except that the number of captured birds in 1998-1999 was lower. Excluding Yellow-billed Cuckoos and diurnal migrants at GI, 81% of all captured birds from 1995-1999 and 85% of all observed birds from 1994-1999 were Blackpoll Warblers. The Yel-

TABLE 2. Estimated number of observations, number of days observed, and range of dates for each species of Nearctic-Neotropic landbird migrant at Harrison Point, Barbados, from autumn 1993-1996 and 1998-1999 (52 days). The number of birds captured in mist-nets during non-standardized operations in 1998-1999 (31 days) is also given.

	Observations			Captures		
Species[a]	Number observed	Number of days	Range of dates	Number captured	Number of days	Range of dates
Nocturnal Migrants						
Coccyzus americanus	56	27	29 Sep-13 Nov	–	–	–
Vireo o. olivaceus	3	3	6-23 Oct	2	2	27 Sep-6 Nov
Parula americana	1	1	22 Oct	–	–	–
Dendroica petechia	3	3	11-18 Oct	–	–	–
Dendroica striata	131	40	26 Sep-8 Nov	–	–	–
Mniotilta varia	1	1	7 Oct	–	–	–
Setophaga ruticilla	5	4	24 Sep-7 Nov	–	–	–
Protonotaria citrea	1	1	6 Oct	–	–	–
Seiurus noveboracensis	2	2	17 Oct-6 Nov	–	–	–
Oporornis agilis	–	–	–	1	1	6 Nov
Wilsonia canadensis	–	–	–	1	1	31 Oct
Piranga rubra / olivacea	1	1	20 Sept	–	–	–
Icterus galbula	–	–	–	1	1	25 Oct
Diurnal Migrants[b]						
Chaetura pelagica	3	2	30-31 Oct	–	–	–
Riparia riparia	17	2	23 Oct-6 Nov	–	–	–
Petrochelidon pyrrhonota	7	2	3 Oct-6 Nov	–	–	–
Hirundo rustica	18	2	23 Oct-6 Nov	–	–	–
Dolichonyx oryzivorus	65	5	2-24 Oct	–	–	–

[a] species names not mentioned in text or at bottom of Table 1 include: Canada Warbler (*Wilsonia canadensis*), Summer Tanager (*Piranga rubra*), and Baltimore Oriole (*Icterus galbula*)

[b] the data for all four diurnal migrants are incomplete

low-billed Cuckoo was the second most numerous nocturnal migrant at HP, where its frequency of occurrence was similar to Blackpoll Warbler, but Yellow-billed Cuckoo was rare at GI. Red-eyed Vireo was the third most numerous nocturnal migrant at HP in 1997 (10% of all captured birds excluding Yellow-billed Cuckoos and Indigo Buntings) and it also occurred (six captured birds, one seen) at GI. Other nocturnal migrants we captured or observed at both sites included a large number of scarce transients or apparent vagrants. Among diurnal migrants, only Barn Swallows and Bobolinks occurred at both sites; Bobolinks were relatively abundant and frequent migrants at HP in 1997 (Table 1), mainly in adjacent sugarcane fields.

Migratory volume as measured by mist-net captures was low at HP. Capture rates in 1997 for all nocturnal Nearctic-Neotropic migrants, excluding Yellow-billed Cuckoos and Indigo Buntings, were 16.7 birds/1000 net hours (from 1 October, the first day we captured a Nearctic-Neotropic migrant), including 13 birds/1000 net hours for Blackpoll Warblers only. The capture rate in 1998-1999 combined was 3.8 birds/1000 net hours. Migratory volume at GI as measured by non-standardised mist-net efforts was higher although still low. The capture rate from 1995-1999 combined was 85.6 birds/1000 net hours, including 69.6 birds/1000 net hours for Blackpoll Warblers only. Excluding 1998 data, capture rates declined to 48 birds/1000 net hours and 33.5 birds/1000 net hours for all birds and Blackpoll Warblers only, respectively.

Recaptures.–At HP, the only recaptured birds were two Red-eyed Vireos (of ten banded; 20%) in 1997, both 2 days after the original capture date. At GI, the only recaptured birds were three Blackpoll

TABLE 3. The seasonal distribution of Yellow-billed Cuckoos during autumn migration at Harrison Point, Barbados, based on the daily estimated total of birds per day for 5-day periods from 1993-1999. Numbers in 1997 are based on both captured and observed birds, totals in other years on birds seen only (see text).

Five-day period	No. of days	No. of birds	No. of birds/day
21-25 Sep	2	0	0
26-30 Sep	6	4	0.7
1-5 Oct	10	13	1.3
6-10 Oct	9	7	0.8
11-15 Oct	8	12	1.5
16-20 Oct	15	1	1.2
21-25 Oct	15	25	1.7
26-30 Oct	11	8	0.7
31 Oct - 4 Nov	9	9	1.0
5-9 Nov	8	10	1.2
10-14 Nov	1	1	1.0
TOTALS	94	107	1.1

Warblers, two individuals 2 days later, the other bird 9 days later.

Age classes.–At HP in 1997, 17 (23%) Blackpoll Warblers were AHY birds. Only three of 36 (8%) other Nearctic migrants we captured at HP were AHY birds, including one of ten (10%) Red-eyed Vireos, a Gray-cheeked Thrush and a Swainson's Thrush. All remaining individuals of the other nine species we captured at HP were HY birds. At GI, 39 of 118 (33%) Blackpoll Warblers were AHY birds (excluding 14 birds of unknown age). Of all individuals of the other 13 species we captured at GI, three of 22 (14%) were AHY birds (excluding eight birds of unknown age).

Seasonal timing of occurrence.–The low number of birds and restricted sampling period at GI did not permit further analyses for most species except to present the range of dates of occurrence (Tables 1 and 2). At HP, mid- to late-October was the peak of migration for Blackpoll Warblers and Yellow-billed Cuckoos (Table 3); detailed analyses of Blackpoll Warbler will be presented elsewhere (McNair et al. in prep.). Blackpolls were scarce after October although Yellow-billed Cuckoos occurred regularly in early November. Among diurnal migrants, the number of hirundinids and Bobolinks peaked in early to mid-October; Bobolinks were absent after late October although hirundinids continued into early November.

Daily timing of occurrence.–Excluding Blackpoll Warblers (McNair et al. in prep.) and Indigo Buntings, more Nearctic-Neotropic migrants (n = 18) were captured at HP during midday (4-8 hours after sunrise) than earlier in the morning (n = 5) or later in the afternoon (n = 4; $\chi^2 = 9.31$, $P < 0.01$).

Mass and fat class.–Most individuals of most species had low mass and little visible fat (Tables 4-6), although variability characterised the samples. The mean mass of unsexed Blackpoll Warblers at HP in 1997 was 12.0 g, 15.8% above their mean fat-free mass. The mean mass of Blackpoll Warblers at GI was also low (11.2 g), 8.3% above their mean fat-free mass. The mean mass of unsexed Red-eyed Vireos was 18.2 g at HP, 24.7% above their fat-free mass, and 15.6 g at GI, 6.9% above their fat-free mass. The mean fat class of the Red-eyed Vireo was double that of Blackpoll Warbler at HP and similar at GI. The two Red-eyed Vireos recaptured at HP lost mass (0.15 g to 0.45 g/day). The single Blackpoll Warbler at GI that was re-measured maintained its mass.

Fat-load as a percentage of mean fat-free mass of 15 selected nocturnal Nearctic-Neotropic migrants captured in mist-nets at both HP and GI during autumn migration averaged approximately 15-20%, higher than nine of the same species captured during spring migration on East Ship Island, Mississippi, following a long over-water flight across the Gulf of Mexico (Table 5). Along the northern Gulf coast these birds averaged approximately 7% fat-load as a percentage of fat-free mass.

Flight range estimates.–Ignoring differences among 'fallout' birds and other Blackpoll Warblers at HP (McNair et al. in prep.), Blackpolls had estimated flight ranges of about 435-895 km at HP and 235-475 km at GI. Red-eyed Vireos had an estimated flight range of 1015 km at HP and 285 km at GI. Excluding Scarlet Tanager at HP, which was below its mean fat-free mass, the flight range estimates for the other nocturnal Nearctic-Neotropic migrants at HP and GI were similar, with a mean for all species combined of approximately 600 km (range: HP, 350-

TABLE 4. Mass and fat class for 13 species of nocturnal Nearctic-Neotropic landbird migrants captured in mist-nets at Harrison Point, Barbados, from 29 September to 9 November 1997 and in 1998[a], and mass and fat class for 14 species captured at Guana Island, British Virgin Islands, from 1995-1998[a].

	Harrison Point, Barbados		Guana Island, British Virgin Islands	
	Mass (g)	Fat class	Mass (g)	Fat class
Species[b]	Mean±SD(range)	Mean±SD(range)	Mean±SD(range)	Mean±SD(range)
Coccyzus americanus	51.9±7.4(44.3-61.3)	0	–	–
Vireo o. olivaceus	18.2±1.3(16.5-20.9)	1.5±0.9(0-3)	15.6±0.8(14.1-16.5)	0.4±0.4(0-1)
Catharus m. minimus	27.2	0	–	–
Catharus ustulatus	30.5	1	–	–
Vermivora chrysoptera	–	–	7.6	0
Parula americana	–	–	8.15±0.6	0.5[c]
Dendroica petechia	8.9	0	–	–
Dendroica pensylvanica	9.5	1	–	–
Dendroica magnolia	–	–	7.9	0.5
Dendroica tigrina	–	–	9	na[d]
Dendroica caerulescens	–	–	8.5±1.7(7.3-9.7)	0.25±0.35(0-0.5)
Dendroica striata[e]	11.97±1.2(8.9-15.2)	0.7±0.8(0-3)	11.2±1.2(9-14.7)	0.5±0.5(0-2)
Mniotilta varia	–	–	10.4±1.1(9-12)	0.4±0.4(0-1)
Setophaga ruticilla	9.1±0.1(9-9.2)	1±1.4(0-2)	7.8	0.5
Seiurus aurocapillus	–	–	19±2.6(16-23)	0
Seiurus noveboracensis	–	–	16.9±1.4(16-19.3)	0
Oporornis formosus	12.7[f]±1.1(11.9-13.5)	0	14.1	0
Oporornis agilis	12.9	0	–	–
Piranga olivacea	22.8	0	–	–
Pheucticus ludovicianus	37.4	0	30.2	1
Passerina cyanea[g]	14.3±0.5(13.6-14.9)	0.4±0.5(0-1)	16.5	2

[a] no Nearctic-Neotropic landbird migrants were captured at HP or GI in 1999

[b] sample sizes given in Table 1

[c] data missing for one observation

[d] not available

[e] combines data from 'fallout' and other birds (McNair et al., in prep.)

[f] includes mass data from one bird killed in the net (McNair et al. 1999)

[g] all birds were captured 5-7 days after they arrived at HP (McNair et al. 1999)

1050 km; GI, 265-975 km; Table 6).

DISCUSSION

We have provided the first quantitative data using mist-net captures of ground-based Nearctic-Neotropic landbird migrants during autumn migration in the eastern Caribbean. Our results document that autumn Nearctic-Neotropic landbird migration is a regular phenomenon over the eastern Caribbean for a few relatively abundant species moving to their winter range in South America, and also includes a large variety of scarce species as would be predicted by the renowned vagrancy of long-distance migrants (Grinnell 1922). The use of mist-nets substantially increased our ability to detect migrants at HP and GI, especially secretive species such as *Catharus* thrushes and *Oporornis* warblers that occupy dense habitats. The timing of our sampling periods (primarily October) in the eastern Caribbean coincided with the migration of Nearctic-Neotropic landbirds (Richardson 1976, 1980; Holland and Williams 1978; Williams and Williams 1978a; Bond 1985; Bosque and Lentino 1987, Williams 1985; Raffaele 1989; Pashley and Hamilton 1990; Hutt et al., in prep.). Continued and more extended observer effort would augment and enhance our knowledge of ground-based Nearctic-Neotropic landbird migration during autumn in this region. Nonetheless, we have shown that migration as

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TABLE 5. Fat-load as a percentage of mean fat-free mass of 15 selected nocturnal Nearctic-Neotropic landbird migrants captured in mist-nets during autumn migration in the eastern Caribbean at Harrison Point (HP), Barbados, and Guana Island (GI), British Virgin Islands[a] compared to nine of the same species captured during spring migration on East Ship Island (ESI), Mississippi[b], following a long over-water flight across the Gulf of Mexico. Fat-free masses were obtained from published weights (see text).

Species	HP	GI	ESI
Coccyzus americanus	10.9	–	-0.8
Vireo o. olivaceus	24.7	6.9	2.8-6.9
Catharus m. minimus	7.9	–	–
Catharus ustulatus	26.1	–	0.5-9.6
Parula americana	–	37.4	14.7-23.1
Dendroica pensylvanica	18.3	–	11.1
Dendroica magnolia	–	14.2	2.6-9.8
Dendroica caerulescens	–	11.3	–
Dendroica striata	15.8	8.3	–
Setophaga ruticilla	40.2	20.2	4.8-10.9
Seiurus aurocapillus	–	22.4	–
Seiurus noveboracensis	–	23.5	–
Oporornis formosus	11.8	24.1	–
Piranga olivacea	-5.5	–	-2.4-8.2
Passerina cyanea	15.9	33.7	0.3-11.9

[a] sample sizes given in Table 1

[b] sample sizes given in Kuenzi et al. (1991) and Yong and Moore (1997); mass data for *Catharus m. minimus* was obtained from Cameron Parish, Louisiana

determined through sampling of grounded landbirds is more pronounced than heretofore appreciated although migratory volume is generally low. The higher volume at GI can only be attributed to our non-standardised mist-netting protocol, plus proximity to larger numbers of wintering Nearctic-Neotropic migrants in the Greater Antilles.

We discovered that Red-eyed Vireo, previously thought to be a vagrant or scarce transient in the eastern Caribbean, was relatively numerous at HP. Red-eyed Vireos also occurred at GI, where previous surveys in the British Virgin Islands did not cover migration during September or October (Norton et al. 1989). Our results indicate the autumn migration route of Red-eyed Vireo in the West Indies occurs much farther east than depicted in Winker (1995b), but is consistent with their winter range in South America (Paynter 1995). The conundrums about earlier evaluations of its status in the eastern Caribbean are presented and discussed in Keith (1997) and McNair et al. (1999).

We verified or observed some other species for the first time in the eastern Caribbean (see McNair et al. 1999, Sibley and Arendt in prep.). Local environmental conditions such as the absence of surface water and appropriate habitat at HP undoubtedly accounted for the scarcity of Prothonotary Warblers (*Protonotaria citrea*) and Northern Waterthrushes (*Seiurus noveboracensis*), two of the few Parulidae that overwinter regularly in Barbados (principally in mangrove forest at Graeme Hall Swamp; cf., Wunderle and Waide 1993, Wallace et al. 1996).

The most abundant species we recorded in the eastern Caribbean winter primarily in South America (Barn Swallow [*Hirundo rustica*]) or winter exclusively or almost exclusively in South America (Blackpoll Warbler, Yellow-billed Cuckoo, Red-eyed Vireo and Bobolink; Paynter 1995, American Ornithologists' Union 1998). All species that occurred at HP, except Northern Rough-winged Swallow (*Stelgidopteryx serripennis*), and all species at GI except Nashville Warbler (*Vermivora ruficapilla*), have been recorded at least once during winter in South America (Paynter 1995), although records of several species (e.g., Golden-winged Warbler [*V. chrysoptera*], Kentucky Warbler and Indigo Bunting] have been restricted to northwestern South America (Paynter 1995). Northern Rough-winged Swallow has been observed in the Netherlands Antilles (Voous 1983) and Nashville Warbler has been observed as far south as western Panama (Ridgely and Gwynne 1989, American Ornithologists' Union. 1998). The species composition of Nearctic-Neotropic migrants among HP and GI was fairly similar, although proportionally more species that primarily winter within the West Indies occurred at GI (also see Robertson 1962, Holland and Williams 1978, Pashley 1988, Wunderle and Waide 1993). This pattern is consistent with its location at the eastern end of the Greater Antilles, where most Nearctic-Neotropic landbird migrants in the West Indies overwinter (Wunderle and Waide 1993, Wallace et al. 1996, Wallace et al. 1999). All

TABLE 6. Estimates of rate of mass loss (g/hr) as a function of mass, mean fat load (g), time of flight (hr) given mean fat load and rate of mass loss, and distance (km) flown based on time of flight with a mean air speed of 38.5 km/hr under conditions of no wind for 15 selected nocturnal Nearctic-Neotropic landbirds at Barbados and the British Virgin Islands during autumn migration (see text).

	Harrison Point, Barbados				Guana Island, British Virgin Islands			
Species	Mass loss (g/hr)	Fat load (g)	Time of flight (hr)	Distance flown (km)	Mass loss (g/hr)	Fat load (g)	Time of flight (hr)	Distance flown (km)
Coccyzus americanus	0.26	5.1	19.7	760	–	–	–	–
Vireo o. olivaceus	0.34	3.61	26.3	1015	0.14	1.01	7.4	285
Catharus m. minimus	0.20	2	10	385	–	–	–	–
Catharus ustulatus	0.23	6.32	27.2	1050	–	–	–	–
Parula americana	–	–	–	–	0.12	2.22	18.1	695
Dendroica pensylvanica	0.13	1.65	12.6	485	–	–	–	–
Dendroica magnolia	–	–	–	–	0.12	0.98	8	310
Dendroica caerulescens	–	–	–	–	0.16	0.86	6.9	265
Dendroica striata	0.14- 0.07[a]	1.63	11.3- 23.3[b]	435- 895[c]	0.14 0.07[a]	0.86	6.1- 12.3[b]	235- 475[c]
Setophaga ruticilla	0.13	2.61	19.5	750	0.13	1.31	9.8	375
Seiurus aurocapillus	–	–	–	–	0.20	3.48	17.8	685
Seiurus noveboracensis	–	–	–	–	0.17	3.22	19.5	750
Oporornis formosus	0.15	1.34	9.1	350	0.15	2.74	17.8	685
Piranga olivacea	0.19	-1.33	0	0	–	–	–	–
Passerina cyanea	0.15	1.96	12.7	490	0.16	4.16	25.4	975

[a] range of rate of mass loss
[b] range of time of flight
[c] range of distance flown

Nearctic-Neotropic migrants at both sites were of species that breed in eastern North America, which suggests that the wood-pewee at Barbados (McNair et al. 1999) was an Eastern Wood-Pewee (*Contopus virens*), not Western Wood-Pewee (*C. sordidulus*), although both species winter in South America (Paynter 1995).

Richardson (1976, 1980), Williams et al. (1977a) and Williams and Williams (1978a) stressed that Nearctic-Neotropic landbirds take two routes during autumn migration to reach the eastern Caribbean: the long overwater 'Atlantic' route across the western North Atlantic Ocean from northeast-ern North America (e.g., Blackpoll Warbler), or the 'Greater Antillean' route down the Atlantic slope of southeastern North America through the Florida peninsula and thence southeastward through the Greater Antilles. Later, Williams (1985) ascribed Nearctic-Neotropic migration along the 'Greater Antillean' route to the 'Atlantic' route instead, although he did not dispute two routes for the two groups of birds in Richardson (1976, 1980). His conclusion assumed that migrants take a constant compass heading (mean of around 152 degrees) from departure areas in northeastern North America, from Virginia to Nova Scotia (Stoddard et al. 1983, Williams 1985). Williams (1991) and Williams and Webb (1996) further modified their hypothesis that the uniform orientation of Nearctic-Neotropic landbirds resulted in a broad front migration during autumn over the western North Atlantic Ocean to the West Indies rather than the use of a more exclusive, narrower 'Atlantic' route, with the extent of transoceanic crossing dependent upon how far north the migrant breeds (Williams, pers. comm.). Williams (pers. comm.) stated that the orientation (heading of 152 degrees) of migrants from Miami, Florida (Williams et al. 1977a), was consistent with broad front migration over the western North Atlantic Ocean from departure areas he sampled farther north.

In southern Florida, where Blackpoll Warblers are scarce during autumn (McNair and Post 1993), Williams et al. (1977a) documented that nocturnal movements of migrant landbirds continue southeastward along a single compass heading toward the nearest coast of Cuba, not farther east; headwinds are avoided by flying at high altitudes. However, Richardson (1976) documented directed movements of landbirds along the 'Greater Antillean' route to the east/south-southeast from and to Puerto Rico (from Hispaniola). These movements would require reorientation (change of headings from a constant compass direction) of birds once they reached land over Cuba, after flying over water, assuming birds arriving in Hispaniola or Puerto Rico did not depart from areas farther north in southeastern North America. We doubt that the constant compass mechanism postulated by Williams is valid once migrants reach Cuba, their first main goal along the 'Greater Antillean' route; they probably reorient both to the west-southwest (toward Yucatan) and the east-southeast (toward Hispaniola). Although most birds taking this route winter in the Greater Antilles (excluding species flying to South America, e.g., Yellow-billed Cuckoo), some species also winter in the eastern Caribbean.

Furthermore, we cannot reconcile our results with the transoceanic route or its recent broad-front modification as proposed by Williams, other than for Blackpoll Warbler. The combination of a large variety yet low numbers of nocturnal migrants, the proportionally low numbers of all species (excluding Yellow-billed Cuckoo at Barbados) compared to Blackpoll Warbler (including other species that are numerous in northern or northeastern North America during the breeding season or autumn migration), and the predominance of immatures of other Nearctic-Neotropic migrants compared to a higher proportion of adults for Blackpoll Warbler (Nisbet et al. 1963, Ralph 1981), suggest that these Nearctic-Neotropic species other than Blackpoll Warbler probably migrated along the fringe of the 'Greater Antillean' route to reach the eastern Caribbean, including the southern Lesser Antilles (Richardson 1976). If other Nearctic-Neotropic landbirds are migrating over the western North Atlantic Ocean, very few individuals of any of these species must use this route to reach the eastern Caribbean. In contrast, despite their generally low numbers on the ground, we believe that Blackpoll Warblers in the eastern Caribbean are flying along their main transoceanic route, not along the margin of either route. Our evidence supporting the 'Atlantic' route for Blackpoll Warbler is indirect (Nisbet et al. 1995) although still consistent with Nisbet et al. (1995), who predicted that few Blackpolls are grounded in the West Indies as they are taking a long over-water flight en route to South America. Murray (1989) implied that the number of grounded Blackpolls would be much higher in the West Indies since he states they are 'fairly common' there during a shorter over-water flight.

Other nocturnal Nearctic-Neotropic migrants (and Blackpoll Warblers; McNair et al. in prep.) that we captured at HP (and GI; F. Sibley, pers. obs.) arrived throughout the day, which is consistent with birds undergoing long-distance migration over a large water barrier on either route. While nocturnal movements are much heavier than diurnal movements along the 'Greater Antillean' route (where birds occur in much higher densities than along the 'Atlantic' route), the number of birds moving during the daytime are nonetheless substantial (Richardson 1976). Richardson (1976) used the term 'island-hopping' to describe the nocturnal and diurnal movements of landbirds along the 'Greater Antillean' route. He did not specify whether birds landed on one island before departing for the next one or whether birds continued to fly over islands sequentially. The timing of departure of nocturnal passerines during autumn migration in the West Indies is more protracted than in more northerly latitudes (Richardson 1976, Williams et al. 1978), and may continue as long as 6 hr after sunset.

Despite later departure times for many birds, they evidently are not 'island-hopping' (Richardson 1976, Keith 1997) short distances on the 'Greater Antillean' route. 'Island-hopping' to Barbados, lying east of the Lesser Antillean arc, would also be maladaptive. Outside Cuba (and possibly Hispaniola), our Nearctic-Neotropic migrants had enough time and fat to arrive at their destination before dawn or within 2-3 hr after dawn if they are only 'island-hopping' short distances (Gauthreaux 1978, Bingman 1980, Wiedner et al. 1992). Most of our Nearctic-Neotropic migrants, although of low mass, were not emaciated, unlike many trans-Gulf landbirds during spring migration (Kuenzi et al. 1991). Although our sample sizes of other Nearctic-Neotropic migrants were low, the modest amount of fat above fat-free mass of many captured birds at landfall on two small islands in the eastern Caribbean may be 'insurance' when flying over a large ecological barrier (long over-water distances). Most birds had sufficient fat for continued flight, especially at Barbados where many migrants could have covered the distance of approximately 450 km to South America. The high mass of Red-eyed Vireos compared to other species at Barbados is difficult to explain; these birds could have reached South America easily, even allowing for a reservoir of unused fat as 'insurance'. Birds at GI would require longer times to refuel for the longer crossing to South America (approximately 880 km), if this is their destination. Alternatively, non-emaciated birds may have landed at both islands during daytime because conditions are more favorable for migration at night (Biebach 1992). Regardless, most of our other Nearctic-Neotropic migrants have probably flown appreciable distances between departure areas along the 'Greater Antillean' route and arrival at GI and Barbados, regular migrants and vagrants alike.

Rather than take the 'Greater Antillean' route, Rappole et al. (1979) suggested that some migrants departing from southern Florida during autumn may fly southwest to Yucatan and Central America. Although Williams et al. (1977a) failed to detect strong southwest flights, recent studies using WSR-88D radar have confirmed that landbird migrants may depart southwest from southern Florida during autumn, although the flights are fewer and of lesser magnitude than north of Tampa (K. P. Able, pers. comm.). Nearctic-Neotropic migrants that predominantly winter in this region are widely dispersed during autumn migration in the Florida peninsula (Robertson and Woolfenden 1992), although several of these species are generally scarce on the southeastern Atlantic coastal plain in autumn (e.g., Golden-winged Warbler, which has nonetheless increased recently in the West Indies [Gochfeld 1974, Raffaele 1989, this study]). Some of the scarcer species we captured or observed in the eastern Caribbean winter primarily in Middle America and may have been wind-drifted vagrants displaced eastward. However, wind-drifted vagrancy to the eastern Caribbean from regions along the Gulf of Mexico west of the Florida peninsula is unlikely, since none of the preferred flight directions of trans-Gulf migrants are to the southeast during autumn when northerly winds are infrequent and usually from the northeast (Able 1972).

The relative abundance and frequency of occurrence of Yellow-billed Cuckoo, Red-eyed Vireo and Bobolink at Barbados suggest these three species may be candidates for the long overwater route across the western North Atlantic Ocean to South America. However, no compelling evidence exists which supports this possibility. Unlike Blackpoll Warblers, surveys of these species' distributions during autumn indicate that they initiate migration from southeastern North America, Yellow-billed Cuckoos and Red-eyed Vireos as both trans-Gulf migrants and down the Florida peninsula and Bobolinks from the Atlantic slope only (Chapman 1890; Bent 1940, 1958; Hamilton 1962, Taylor and Anderson 1973, Crawford 1980, 1981, Taylor and Kershner 1986, Robertson and Woolfenden 1992, Stevenson and Anderson 1994, Winker 1995b, Remsen et al. 1996, Woodrey and Moore 1997). Aboard ships in the western North Atlantic Ocean, only one Bobolink was captured and no others were reported seen (McClintock et al. 1978), where the status of Nearctic-Neotropic landbird migrants other than Blackpoll Warbler is consistent with wind-drifted vagrancy (Murray 1989). Williams et al. (1977b) suggested that Yellow-billed Cuckoos crossed the western North Atlantic Ocean and saw cuckoos greater than 320 km from the coast, but otherwise cited no specific reports. Furthermore, its status as an uncommon autumn migrant in the northern Bahamas (parallel to the southern Florida coast where it is numerous) compared to its greater abundance in the southern Bahamas (and Greater Antilles) farther south (Raffaele et al. 1998) is also inconsistent with passage of Yellow-billed Cuckoos over the western North Atlantic ocean. Red-eyed Vireos have not been captured or seen at all. The status of these three species during autumn migration in the eastern Caribbean is consistent with their status elsewhere in the West Indies.

Hilditch et al. (1973) and Williams and Williams (1978a) stressed that few of the many birds which fly over the West Indies are grounded, in part because birds can frequently detour around approaching storms. This assessment agrees with our observations of the frequent absence of 'fallouts' during autumn migration even when storms occur. In addition, the occurrence of birds in waves separated by several days with little or no migration (Williams et al. 1977b, 1978; Williams 1985) would also contribute toward the absence of 'fallouts' during storms. Nonetheless, documented 'fallouts' of nocturnal Nearctic-Neotropic landbirds during autumn migration have occurred in the West Indies, including the eastern Caribbean. Most 'fallouts' have been primarily limited to two species. 'Fallouts' of Blackpoll Warblers are documented elsewhere (McNair et al., in prep.), but have occurred throughout the northern, eastern, and southern Caribbean during autumn, e.g., in the Bahamas (Kale et al. 1969). Yellow-billed Cuckoos are rare to locally common breeders in the Greater Antilles (Kepler and Kepler 1978, Raffaele et al. 1998) and at two sites in the Lesser Antilles, St. Kitts and St. Martin (Steadman et al. 1997, Feldmann et al. 1999), but their breeding status should not unduly affect assessment of their status during autumn migration, which occurs primarily from late September to November (not 'very few' birds in November and not 'uncommon to rare' in the Lesser Antilles *contra* Raffaele et al. 1998).

Most 'fallouts' (arbitrarily defined as ≥ 10 birds/day) of the Yellow-billed Cuckoo have occurred in the southern Caribbean, at the Netherlands Antilles, Barbados and Tobago, near northern South America (Voous 1983, ffrench 1993, Hutt et al. in prep.). Bonhote (1903) collected 12 Yellow-billed Cuckoos on 15 October 1901 at Bird Rock off Crooked Island in the Bahamas and Robertson (1970) stated Yellow-billed Cuckoos in association with other Greater Antillean migrants were numerous on 14 October 1969 at a lighthouse at Cayo Caiman off Caibarien near the coast of Cuba, but both locations in the Straits of Florida would be consistent with migration down the Florida peninsula. Raffaele (1989) and Raffaele et al. (1998) stated that sometimes very large concentrations of Yellow-billed Cuckoos pass through the largest islands of the Greater Antilles during October, but cited no numbers. 'Fallouts' of Yellow-billed Cuckoos may have been overlooked in the northern and eastern Caribbean, but their primary restriction despite their visibility (large size) to the southern portion of the Caribbean Sea is consistent with an over-water crossing of the Caribbean Sea (fat birds have been collected during September and October in the Dominican Republic and Puerto Rico; Schwartz and Klinikowski 1965), not over the western North Atlantic Ocean. Their rarity at GI despite suitable habitat (also generally rare during autumn at St. Croix, American Virgin Islands, where F. W. Sladen [pers. comm.] had 34 birds on 19 days over 10 yr [1980-1989]) is also inconsistent with migration over the western North Atlantic Ocean. Documented 'fallouts' of Yellow-billed Cuckoos have also occurred independently of 'fallouts' of Blackpoll Warblers, e.g., Kale et al. (1969), Meier et al. (1989), this study. Except for several thrushes and some parulids (Kale et al. 1969, Robertson 1970), no other species have been documented to have occurred in substantial numbers during 'fallouts' of either Yellow-billed Cuckoos or Blackpoll Warblers in the West Indies, although this is certainly possible for species [e.g., Red-eyed Vireo, Connecticut Warbler (*O. agilis*)] that arrive at northern South America after an over-water crossing of the Caribbean Sea during autumn migration. We believe the scarcity of conspicuous 'fallouts' of species other than Blackpoll Warbler in the northern Caribbean strengthens our argument that we have not overlooked other possible candidate species for an over-water crossing of the western North Atlantic Ocean.

In addition, low numbers, predominance of immatures of birds captured or salvaged aboard ships, generally low masses and low fat classes, and improbable destinations based on the winter range and known migratory routes of most Nearctic-Neotropic migrants other than Blackpoll Warblers seen south of Bermuda (only two species listed by McClintock et al. [1978] winter in South America) do not support the long over-water route across the western North Atlantic Ocean during autumn (Ralph 1981, Murray 1989; *contra* McClintock et al. 1978, Williams and Williams 1978b, Williams 1985 [although Williams' two publications included a retraction for species that do not winter in the Neotropics]). The occurrence of these species over the western North Atlantic Ocean is consistent with wind drift from the North American mainland.

Recently, Morris et al. (1996) nominated Tennessee Warbler (*V. peregrina*) as another potential trans-oceanic migrant over the western North Atlantic. However, this species is a trans-Alleghanian migrant in continental North America (e.g., one of the two most abundant parulids during autumn migration at high elevations of the Southern Appalachian Mountains; McNair, unpubl.) that moves to the northern Gulf coast and onward to the winter range from southern Mexico to northwest South America (Paynter 1995). Furthermore, the Tennessee Warbler is found only in the northern and western Caribbean on the eastern fringe of its autumn migration route and is generally rare to uncommon here (Gochfeld 1974, Raffaele et al. 1998). Uncritical evaluation of the autumn migration route of Tennessee Warbler has not contributed to the legitimate debate about transoceanic migration of Blackpoll Warblers and other Nearctic-Neotropic landbirds from northeastern North America to the West Indies and South America (see Nisbet et al. 1995). Excluding Blackpoll Warbler, an unknown proportion of a few species (e.g., Cape May Warbler [*D. tigrina*], Connecticut Warbler and Northern Waterthrush) may migrate during autumn over the western North Atlantic Ocean after departing from north of southeastern North America, but this has not yet been convincingly documented.

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Letters to the Editor

Letters (~300 words) discuss material published in *Science* in the previous 6 months or issues of general interest. They can be submitted by e-mail (science_letters@aaas.org), the Web (www.letter2science.org), or regular mail (1200 New York Ave., NW, Washington, DC 20005, USA). Letters are not acknowledged upon receipt, nor are authors generally consulted before publication. Whether published in full or in part, letters are subject to editing for clarity and space.

Migratory Birds and the Spread of West Nile

WE READ WITH SUBSTANTIAL APPREHENSION the News Focus article on the spread of West Nile Virus (WNV) across the United States and its concomitant decimation of bird populations ("West Nile's surprisingly swift continental sweep," M. Enserink, 20 Sept., p. 1988; and sidebar "Bird advocates fear that West Nile virus could silence the spring," D. Malakoff, p. 1989). Many of the survivors among these populations are very likely to spread WNV throughout the Neotropics in this northern winter, if they have not already done so during the last several winters. It is particularly ominous that our observations of scores of species of small northern migrants (e.g., warblers and thrushes) this January in the Area de Conservacion Guanacaste in northwestern Costa Rica (*1*) suggest that there is a precipitous decline in their abundance compared with previous years. Parallel observations from other neotropical continental areas would be opportune, as well as from the Caribbean, as mentioned in the sidebar by Malakoff. This apparent decline in Costa Rica could well be due to fewer migrants arriving, virus-based death in transit or on the wintering grounds, or even disproportionally harsh predation by resident predators accustomed to preying on abundant migrants. Our ongoing inventory of the internal parasites of these migrants and their sympatric residents (*2*) hopefully will indicate whether WNV has arrived as we expect and is spreading [however, there are no recorded cases of

The yellow-rumped warbler (bottom) and the Kentucky warbler (top) are two of the numerous North American bird species known to have tested positive for West Nile virus.

CREDITS: C. S. ROBBINS/PWRC/USGS; (INSET) D. A. [illegible]

(5608)

U.S. DEPARTMENT OF THE INTERIOR
MARCH 3, 1849

U.S. GEOLOGICAL SURVEY
BIOLOGICAL RESOURCES DIVISION

Texas Cooperative Fish and Wildlife Research Unit
TEXAS TECH UNIVERSITY
Lubbock, TX 79409-2120
Phone: 806/742-2851 FAX: 806/742-2946

11 March 2003

Dr. Skip Lazell
P.O. Box 86
Lane, OK 74555

Dear Dr. Lazell:

Thank you for taking the time to discuss the possibility of conducting research and monitoring of avian species on Guana Island. Since my brief period working with Red-tailed Hawks in the Luquillo Forest of Puerto Rico, I have been seeking an opportunity to engage in more complex, longer-term research in the Caribbean. Thus, I would welcome the opportunity to join the group of biologists conducting studies on Guana Island, and would appreciate you considering this as an application to join the group.

Following our conversation, I spoke with Fred Sibley to discuss the ornithological work he conducted over the last several years on Guana. Fred was very forthcoming and encouraging, discussing many of the logistical aspects of mist netting on the island. I now have a better understanding of the species typically banded, the annual variability in the number of individuals netted, and some of the research possibilities. I would be happy to continue, or collaborate with another researcher in continuing, the mist netting and banding operations on Guana. I believe the mist netting and banding operations could easily mesh with a personal research program.

I would need to gain a sense of familiarity with the ecology and logistical aspects of the island before I could fully develop a topic of personal research. However, following my discussions with Fred and Gad Perry, it appears there may be many possible avenues of research. One that comes immediately to mind is involves the kestrel population on the island. It would be quite interesting to examine predation on other island species (perhaps in collaboration with Gad Perry) or genetic relationships among kestrels on Guana, the local islands, and also the North American continent, which really starts getting at island biogeography and dispersal issues.

Another research question involving avifauna on Guana Island is the spread of West Nile Virus (WNV). This virus be devastating to some species (e.g., corvids, raptors) but seems to be of lesser impact on others (e.g., some passerines). Given the small size of Guana Island, WNV could have dramatic impacts if established there. There are also increasing concerns regarding the possibility of neotropical migrants serving as reservoirs for WNV and spreading it to geographically isolated areas, such as the islands of the Caribbean. I have previous experience conducting studies on avian diseases and parasites, and have the skills necessary for hematological sampling of mist-netted passerines. I would welcome the opportunity to pursue this line of research on Guana Island, and believe funding sources could be found to support such efforts.

My current position is acting unit leader and research wildlife biologist with the USGS Texas Cooperative Fish & Wildlife Research Unit, and assistant professor in the Department of Range, Wildlife and Fisheries Management at Texas Tech University. I hold a master-banding permit and have experience mist-netting avian species in prairie and desert grasslands, Sonoran desert, and desert riparian corridors. Currently I am directing graduate student research on grassland passerine use of native and introduced grasses in Conservation Reserve Program lands, breeding season ecology of Cassin's Sparrows, survival and behavior of Blue Jays, resource partitioning of grassland raptors, and avian and mammal associations with prairie dog colonies.

I have discussed the possibility of conducting research on Guana Island with my regional supervisor. He understands the amount of time that would be required in the field each October and has given me full support in this endeavor. I am enthusiastic at the prospect of joining the research activities on Guana Island and hope you consider me favorably for the opportunity. Please feel free to contact me if you have any questions regarding my qualifications and interests.

Sincerely,

Clint W. Boal
Assistant Unit Leader: TXCFWRU
Assistant Professor: Texas Tech University

Clint W. Boal

U.S.G.S.- B.R.D., Texas Cooperative Fish and Wildlife Research Unit
Texas Tech University, Lubbock, TX 79409-2120
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EDUCATION

Ph.D.	Wildlife Ecology, Renewable Natural Resources minor, University of Arizona, Tucson, August 1997.
M.S.	Wildlife Ecology, University of Arizona, August 1993.
B.S.	Wildlife and Fisheries Science, University of Arizona, May 1991.

PROFESSIONAL EXPERIENCE

2000-present	Assistant Unit Leader and Research Wildlife Biologist, USGS-BRD Texas Cooperative Fish & Wildlife Research Unit, Texas Tech University, Lubbock, TX.
1998-2000	Doctoral Research Fellow, USGS-BRD Minnesota Cooperative Fish & Wildlife Research Unit, Univ. Minnesota, St. Paul, MN.
1998	Biological Consultant, International Institute for Tropical Forestry, USDA-Forest Service, Palmer, Puerto Rico.
1993-1997	Graduate Research Associate, Univ. Arizona, Tucson, AZ.
1990-1992	Graduate Research Assistant, Univ. of Arizona, Tucson, AZ.

ACADEMIC APPOINTMENT AND TEACHING

2000-present	Research Assistant Professor, Department of Range, Wildlife and Fisheries Management, Texas Tech University, Lubbock, TX.
1998-present	Adjunct Assistant Professor, School of Renewable Natural Resources, Univ. Arizona, Tucson, AZ.

PROFESSIONAL ACTIVITIES

- Symposium Committee Chair, International Symposium on the Ecology and Management of Northern Goshawks scheduled for September 2003.
- Associate Editor, Journal of Wildlife Management June 2002 - present
- New faculty position development and search committee, Dept. Range, Wildlife and Fisheries Management, Texas Tech University. July 2001 – April 2002
- Texes Tech University Animal Care and Use Committee. Nov. 2001 - present
- Elected Board Member, Urban Wildlife Working Group, The Wildlife Society. Sept. 2001 – present
- Associate Editor, Journal of Raptor Research. June 2001 - present
- Referee for: *Auk* (1), *Condor* (2), *Forest Science* (1), *J. Field Ornithology* (2), *J. Raptor Research* (7), *J. Wildlife Diseases* (2), *J. Wildlife Management* (2), *Northeastern Naturalist* (2), *Wildlife Society Bulletin* (1), *Wilson Bulletin* (4). 1996-present.
- Member, Texas Partners in Flight Working Group. April 2001

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- Committee Chair, Fran and Frederick Hamerstrom Award, Raptor Research Foundation. Nov. 2000 – present. Committee member 1998-2000.
- Moderator: Habitat Studies. 4th International Symposium on Urban Wildlife Conservation, Tucson, AZ, 1999
- Tucson Audubon Society Avian Electrocution Review Committee, Tucson, AZ. 1996-97
- Tucson Audubon Society Wildlife Feeding Committee, Tucson, AZ. 1996-97
- Moderator: Bird Ecology and Management Session. 29th Annual Meeting of the Arizona-New Mexico Chapters of The Wildlife Society, Sierra Vista, AZ. 1996.
- Moderator: Raptor Ecology Session. Joint Annual Meeting of the American Ornithologist Union and the Raptor Research Foundation, Boise, ID. 1996
- Reviewer for the book: *Raptors of Arizona*. 1998. R. Glinski, ed. University of Arizona Press, Tucson, AZ. 1996.
- Reviewer for the book: *Desert hawking, with a little help from my friends*. Harry McElroy, Private Publ., Wilcox, AZ. 1995
- Poster Session Chair: Annual Raptor Research Foundation Meeting, Flagstaff, AZ. 1994

PAPERS PUBLISHED

- Boal, C.W. 2001. Nonrandom mating and productivity of adult and subadult Cooper's hawks. *Condor* 103:381-385.
- Boal, C.W. 2001. Agonistic behavior of Cooper's hawks. *Journal of Raptor Research* 35:253-256.
- Boal, C.W., and B.D. Bibles. 2001. Responsiveness of elf owls to conspecific and great horned owl vocalizations. *Journal of Field Ornithology* 72:66-71.
- Boal, C.W., and R. W. Mannan. 2000. Cooper's hawks in urban and exurban areas: a reply. *Journal of Wildlife Managment* 64:601-604.
- Boal, C.W., and R.L. Spaulding. 2000. Helping at a Cooper's hawk nest. *Wilson Bulletin* 112:275-277.
- Mannan, R.W., and C.W. Boal. 2000. Home range characteristics and habitat selection of male Cooper's hawks in an urban environment. *Wilson Bulletin* 112:21-27.
- Mannan, R.W., C.W. Boal, W.J. Burroughs, J.W. Dawson, T.S. Estabrook, and W.S. Richardson. 2000. Nest sites of five raptor species along an urban gradient. Pages 447-453 *in* R.D. Chancellor and B.-U. Meyburg [eds.] . Raptors at risk; proceedings of the V World Conference on Birds of Prey and Owls. Midrand, Johannesburg, South Africa, 4-11 August 1998. Hancock House; WWGBP, Blaine, Washington; Berlin, Germany.
- Boal, C.W., and R.W. Mannan. 1999. Comparative breeding ecology of Cooper's hawks in urban and exurban environments. *Journal of Wildlife Management* 63:77-84.
- Boal, C.W., K.S. Hudelson, R.W. Mannan, and T.S. Estabrook. 1998. Hematology and hematozoa of adult and nestling Cooper's hawks in Arizona. *Journal of Raptor Research* 32:281-285.

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- Boal, C.W., and R.W. Mannan. 1998. Nest-site selection of Cooper's hawks in an urban environment. *Journal of Wildlife Management* 62:864-871.
- Boal, C.W., R.W. Mannan, and K.S. Hudelson. 1998. Trichomoniasis in Cooper's hawks from Arizona. *Journal of Wildlife Diseases* 34:590-593.
- Boal, C.W., B.D. Bibles, and R.W. Mannan. 1997. Nest defense and mobbing behavior of elf owls. *Journal of Raptor Research* 31:286-287.
- Boal, C.W., and R.W. Mannan. 1996. Prey sizes of male and female northern goshawks. *The Southwestern Naturalist* 41:355-358.
- Boal, C.W. 1994. A photographic and behavioral guide to aging nestling northern goshawks (*Accipiter gentilis*). *Studies in Avian Biology* 16:32-40.
- Boal, C.W. and J.E. Bacorn. 1994. Siblicide and cannibalism at northern goshawk nests. *Auk* 111:748-750.
- Boal, C.W., E.L. Bibles, and R.E. Brown. 1994. Unusual parental behavior by male northern goshawks. *Journal of Raptor Research* 28:120-121.
- Boal, C.W. and R.W. Mannan. 1994. Northern goshawk diets in ponderosa pine forests on the Kaibab Plateau. *Studies in Avian Biology* 16:97-102.

PAPERS SUBMITTED

- Boal, C.W., T.S. Estabrook, and A.E. Duerr. Productivity and breeding habitat of loggerhead shrikes in an urban environment. Accepted *Southwestern Naturalist*
- Boal, C.W., D.E. Andersen, and P.L. Kennedy. Home range and residency status of northern goshawks breeding in Minnesota. In revision *Condor*
- Boal, C.W., H.A. Snyder, B.D. Bibles, and T.S. Estabrook. Temporal and spatial stability of red-tailed hawks in the Luquillo Experimental Forest, Puerto Rico. Submitted to *Journal of Raptor Research*

FINAL REPORTS

- Boal, C.W., D.E. Andersen, and P.L. Kennedy. 2001. Home range and habitat use of northern goshawks (*Accipiter gentilis*) in Minnesota.
- Boal, C.W. 2001. Strategies for monitoring common black-hawk (*Buteogallus anthracinus*) populations in North America. USGS- NARMS
- Nishida, C., S. DeStefano, and C. Boal. 2001. Status of Swainson's hawks in southeastern Arizona. Final Report Arizona Game and Fish Department Heritage Grant Project I98013.
- Boal, C.W. 1996. Bird inventory. Pages 47-52 *in* L.K. Harris, ed., Wildlife inventory of the Saguaro National Park expansion area. Final Report, Saguaro National Park, Tucson, Arizona.
- Boal, C.W., and R.W. Mannan. 1996. Conservation assessment for the common black-hawk (*Buteogallus anthracinus*). Final Report, USDA Forest Service, Tonto National Forest, Contract No. 43-8180-5-0271.
- Boal, C.W and R.W. Mannan. 1995. Bird inventory. Pages 80-92 *in* L.K. Harris, and C.R. Schwalbe, eds., Wildlife inventory of the Rincon Valley. Final Report Heritage Project U93007, Arizona Game and Fish Department, Phoenix, Arizona.

PRESENTATIONS

- Merriman, J., P. Zwank, C.W. Boal, T.A. Bashore. Assessing raptor-aircraft strike risk associated with prairie dog colonies. 68th Annual North American Wildlife and Natural Resources Conference, Winston-Salem, NC. March 2003.
- Thompson, T.R., C.W. Boal, and D.R. Lucia. Effectiveness of native seeding of CRP in providing summer habitat for grassland passerines. Texas Chapter of The Wildlife Society 38th Annual Meeting, Waco, TX. Feb. 2003.
- Pruett, A., C.W. Boal, M.Wallace, P. Robertson and J. Ray. Black-tailed prairie dogs and small mammal diversity in the southern high plains of Texas. Texas Chapter of The Wildlife Society 38th Annual Meeting, Waco, TX. Feb. 2003.
- Merriman, J., P. Zwank, C.W. Boal, T.A. Bashore. Spatial distribution of raptors in relation to prairie dog colonies. Texas Chapter of The Wildlife Society 38th Annual Meeting, Waco, TX. Feb. 2003.
- Smithers, B.L., C.W. Boal, and D.E. Andersen. Assessment of northern goshawk food habits using time-lapse video monitoring systems. Texas Chapter of The Wildlife Society 38th Annual Meeting, Waco, TX. Feb. 2003.
- Mannan, R.W., and C.W. Boal. Recruitment in a population of urban-nesting Cooper's hawks. 36th Joint Annual Conference of the New Mexico/Arizona Chapters of The Wildlife Society and the American Fisheries Society, Arizona and New Mexico Chapter, Gallup, NM. Feb. 2003
- Boal, C.W., and R.W. Mannan. Birds of Prey in urban landscapes. Defenders of Wildlife's Carnivores 2002: a conference on carnivore biology and conservation. Monterey, CA. Nov. 2002.
- Thompson, T.R., C.W. Boal, and D.R. Lucia. Effectiveness of native seeding of CRP in providing summer habitat for grassland passerines. The Wildlife Society 9th Annual Conference, Bismarck, ND. Sept. 2002.
- Nishida, C., S. DeStefano, C. Boal and R. Hobbs. Productivity and nest site selection of Swainson's hawks in southeastern Arizona. 3rd North American Ornithological Conference, New Orleans, LA. Sept. 2002.
- Andersen, D.E., C.W. Boal, and P.L. Kennedy. Home range and habitat use of northern goshawks (*Accipiter gentilis*) in Minnesota. Forest Systems of the Upper Midwest: Research Review. Cloquet Forestry Center, University of Minnesota, U.S. Forest Service, and Minnesota Forest Resources Council, Cloquet, MN. Jan. 2002
- Boal, C.W. Distribution and productivity of ferruginous hawks and Swainson's hawks in Dallam County, Texas. Texas Chapter of The Wildlife Society 37th Annual Meeting, Corpus Christi, TX. March 2002
- Boal, C.W., and R. Lee. Ecology and management of urban birds of prey. Texas Recreation Areas and Parks Annual Workshop, Lubbock, TX. Nov. 2001
- Boal, C.W. (presented by Jeff Smith in abstentia). 2001. Strategies for monitoring common black-hawk (*Buteogallus anthracinus*) populations in North America. Annual meeting of the Raptor Research Foundation, Winnipeg, Manitoba. Oct. 2001
- Boal, C.W., D.E. Andersen, and P.L. Kennedy. Breeding season foraging habitat of male northern goshawks in Minnesota. The Wildlife Society 8th Annual Conference, Reno, NV. Sept. 2001
- Boal, C.W. Ecology of northern goshawks in Minnesota. Llano Estacado Audubon Society, Lubbock, TX. April 2001

- Boal, C.W. Hierarchical assessment of northern goshawk foraging habitat in Minnesota. Seminar, Department of Range, Wildlife and Fisheries Management, Texas Tech University. Feb. 2001
- Boal, C.W. Hierarchical assessment of northern goshawk foraging habitat in Minnesota. Seminar, Department of Range, Wildlife and Fisheries Management, Texas Tech University. Feb. 2001
- Boal, C.W., D.E. Andersen, and P.L. Kennedy. Habitat use of northern goshawks in Minnesota. Annual meeting of the Raptor Research Foundation, Jonesboro, AR. Nov. 2000
- Boal, C.W. Ecology of northern goshawks in Minnesota. Keynote address, Headwaters Audubon Society, Bemidji, MN. May 2000. *Invited.*
- Boal, C.W., T.S. Estabrook, and A.E. Duerr. Breeding habitat and productivity of loggerhead shrikes in an urban interface. 4th International Symposium on Urban Wildlife Conservation, Tucson, AZ. April 1998.
- Boal, C.W. The status of northern goshawks in Minnesota. Annual meeting of the Minnesota Ornithologists Union, St. Paul, Minnesota. Dec. 1998. *Invited.*
- Boal, C.W. The urban environment as an ecological trap for Cooper's hawks. Dept. of Fisheries and Wildlife, University of Minnesota. Oct. 1998. *Invited.*
- Boal, C.W., and R.W. Mannan. Comparative ecology of Cooper's hawks in urban and exurban environments. Annual Raptor Research Foundation Meeting, Ogden, UT. Nov. 1998.
- Mannan, R.W., C.W. Boal, W.J. Burroughs, J.W. Dawson, T.S. Estabrook, and W.S. Richardson. Nest sites of five raptor species along an urban gradient. Fifth World Congress on Birds of Prey and Owls, Midrand, Republic of South Africa. 1998.
- Boal, C.W., and R.W. Mannan. Nest-site selection by Cooper's hawks in an urban landscape. Joint meeting of the 114th Annual Meeting of the American Ornithologist Union and the Annual Meeting of the Raptor Research Foundation, Boise, ID. Aug. 1996.
- Boal, C.W., and R.W. Mannan. Reproduction and mortality rates of urban nesting Cooper's hawks. 66th Annual Meeting of the Cooper Ornithological Society, San Diego, CA. April 1996.
- Boal, C.W. Hard-wired, soft-wired or hay-wired: Cooper's hawks in Tucson. 1996. School of Renewable Natural Resources, University of Arizona, Tucson. *Invited.*
- Boal, C.W., and R.W. Mannan. The urban landscape as an ecological trap for Cooper's hawks. 1995. The Wildlife Society Second Annual Meeting, Portland, OR. Sept. 1995.
- Boal, C.W., and R.W. Mannan. Intersexual prey partitioning in northern goshawks. Annual Raptor Research Foundation Meeting, Flagstaff, Arizona. Nov. 1994.
- Boal, C.W., and R.W. Mannan. Northern goshawk diets in ponderosa pine forests on the Kaibab plateau. 63rd Annual Meeting of the Cooper Ornithological Society, Sacramento, CA. April 1993.
- Boal, C.W., and R.W. Mannan. Northern goshawk diets in ponderosa pine forests on the Kaibab plateau. Annual Raptor Research Foundation Meeting, Bellevue, WA. Nov. 1992.

PROPOSALS

Submitted & Funded

- Habitat and prey partitioning by sympatric ferruginous hawks and Swainson's hawks. 2003. U.S.D.A. Forest Service. $3,000
- Resource partitioning and overlap of a raptor assemblage associated with prairie dog colonies. 2002. Texas Parks and Wildlife. $72,839
- 2002. Breeding season prey use of northern goshawks in Minnesota. Minnesota Forest Industries. $10,000 (Co-authored with D.E. Andersen)
- 2001. Playa lakes as habitat reserves for black-tailed prairie dogs. 2001. Texas Parks and Wildlife Department. $117,000
- 2001. Playa lakes as habitat reserves for black-tailed prairie dogs. 2001. USGS-BRD Cooperative Unit System. $19,845
- 2001. Effectiveness of the conservation reserve program native species seeding requirements in providing summer and winter habitat for grassland birds. 2001. USGS-BRD Cooperative Unit System. $22,150
- 2001. Inventory of northern goshawks (*Accipiter gentilis*) on the Superior National Forest. $19,931 (Co-authored with D.E. Andersen)
- 2001. Breeding season prey use of northern goshawks in Minnesota. U.S. Forest Service ($14,000) (Co-authored with D.E. Andersen)
- 2001. Effectiveness of the Conservation Reserve Program (CRP) native species seeding requirements in providing summer and winter habitat for grassland birds. Texas Parks and Wildlife ($42,104) <u>and</u> USGS-Biological Resources Division ($22,150). $64,254
- 2000. Home range and habitat use of male northern goshawks in north-central Minnesota. Grants received from the Chippewa National Forest, Leech Lake Band of Ojibwa Minnesota Department of Natural Resources, NCASI, Potlatch Corporation, The Raptor Center, Superior National Forest, U.S. Fish and Wildlife Service totaling $86,000 (Co-authored with D.E. Andersen and P.L. Kennedy)
- 1999. Home range and habitat use of male northern goshawks in north-central Minnesota. Grants received from the Chippewa National Forest, Leech Lake Band of Ojibwa Minnesota Department of Natural Resources, NCASI, Potlatch Corporation, The Raptor Center, Superior National Forest, U.S. Fish and Wildlife Service totaling $81,600 (1999) (Co-authored with D.E. Andersen and P.L. Kennedy)
- 1998. Status of Swainson's hawks in Arizona. Arizona Game and Fish Department. $82,028. (Co-authored with S. DeStefano)
- 1997. Breeding habitat of urban nesting loggerhead shrikes. T&E Inc., Research Grant Program. $2,100.
- 1995. Temporal changes in behavior and habitat use of urban nesting Cooper's hawks. Arizona Game and Fish Department. $13,670. (Co-authored with R.W. Mannan)
- 1995. Development of a conservation assessment for common black-hawks. Tonto National Forest, U.S. Forest Service. $5,000. (Co-authored with R.W. Mannan)
- 1994. Nest-site selection of Cooper's hawks in urban environments and the effects of trichomoniasis on reproductive success. Arizona Game and Fish Department. $66,352. (Co-authored with R.W. Mannan)

Submitted & Pending

- Comparative home range sizes and foraging habitat use of sympatric ferruginous hawks and Swainson's hawks. Texas Parks and Wildlife Conservation Action Program. $43,244
- Experimental assessment of the influence of radio telemetry on predation and survival of birds. Texas Parks and Wildlife. $50,228

GRADUATE EDUCATION

Graduate Committee Chair:

- Nishida, Catherine. MS (Univ. Arizona). *Distribution and status of Swainson's hawks in Arizona.* Completed 12-01
- Smithers, Brett. MS. *Breeding season prey use of northern goshawks in Minnesota.* In progress – anticipated completion 5-03.
- Pruett, Alison. MS. *Playa lakes as habitat reserves for black-tailed prairie dogs.* In progress – anticipated completion 5-04.
- Thompson, Thomas. MS. *Effectiveness of the conservation reserve program native species seeding requirements in providing summer and winter habitat for grassland birds.* In progress - anticipated completion 5-03.
- Merriman, Joel. MS. *Raptor association with black-tailed prairie dog colonies on Canon Air Force Base: implication for bird strikes.* In progress - anticipated completion 8-03.
- Giovanni, Matthew. MS. *Resource partitioning between sympatric grassland raptors.* In progress – anticipated completion 5-05.

Graduate committee member:

- Barnett, Terri. 11/01. *Rio Grande wild turkey nesting ecology in Kansas and the Rolling Plains of Texas.*
- Teaschner, Andrew. 8/02. *Influence of residency status on burrowing owl productivity and habitat use.*

Saving species with a song

By Cynthia Berger, Globe Correspondent, 10/29/2002

Male songbirds fight to defend their breeding-season territories - but not necessarily with beaks and claws. Often, their duels are duets, with song lyrics that seem obvious: "Stay off my turf!"

Forget the obvious. Last month, at the annual meeting of the American Ornithologists' Union in New Orleans, University of Illinois graduate students Scott Schlossberg and Michael Ward announced they had coaxed black-capped vireos - a critically endangered species - to nest in protected habitats by attracting them with the songs of other vireos.

The technique, Schlossberg said, was simple: "We digitized vireo sounds, put them on CDs, and played them on discount-store boom boxes." The results were stunning. In the first year, the team attracted 73 birds to five new locations on Fort Hood in Texas. "We would have been pleased to get five birds," Schlossberg said.

This achievement not only turns scientific convention on its head, it's great news for the vireos, with a US breeding population of fewer than 2,000 birds in Texas and Oklahoma.

Though scientists have been studying bird communication for decades, they have by no means translated the entire avian lexicon. Schlossberg conceded that a male vireo ought to interpret male songs as a signal to avoid the neighborhood - and not just for fear of a fight. "The more neighbors you have," he said, "the more time you spend defending your territory. And the greater the chance that a neighboring male will sneak a copulation with your mate."

Still, Schlossberg and Ward were intrigued by an obscure research report with "marginally significant" evidence that male songbirds are attracted by other males' songs. The students also knew that recorded sounds - together with lifelike decoys - are often used to lure threatened seabirds to new or favorable habitat. The technique even has a name: social attraction.

But seabirds and songbirds have different nesting habits. While songbirds defend spacious territories, seabirds gather in crowded colonies, often on islands. The raucous sounds of a colony probably send a reassuring message: "No predators are near."

Are vireo sounds somehow reassuring to other vireos? Steve Kress, the National Audubon Society biologist who pioneered social attraction, said perhaps. "Maybe you have to think of songbird territories in a different way," he said, noting that vireos nest in patches of scrub-oak that are like islands in a sea of grass. "The presence of one or two calling males may tell other vireos the patch is good habitat."

Other songbirds could also benefit from the technique of social attraction, said Arch McCallum of Applied Bioacoustics in Eugene, Ore. "For example, the Oregon State Park system is restoring native Willamette Valley oak savannah," he said. "They want to bring back birds that used to be there, like the vesper sparrow and western meadowlark. But there's no plan to attract the birds. This methodology looks very promising."

Scientists used social attraction in another innovative way this summer - to benefit not birds but fish. The species of concern were coho salmon, chinook salmon, and steelheads - all endangered species. As the juvenile fish made their run down the Columbia River to the sea, they had to swim past Rice Island, with a nesting colony of nearly 20,000 Caspian terns. The birds were scarfing fish down like cocktail peanuts.

To protect the fish, biologists decided to relocate the birds downstream, to East Sand Island. "Closer to the sea, there's more mixing of ocean and freshwater," said Oregon State University's Dan Roby. "So, the birds have other prey - marine fish like anchovies, herrings, and sardines."

Relocation involved several steps. Biologists planted wheat and set up plastic fences on Rice Island, making it less attractive to terns, which like open space. Down river on East Sand Island, the Army Corps of Engineers created a tern-friendly, bare-sand habitat. Finally, Roby and colleagues set out tern decoys, hooked a CD player to patio speakers, and punched play. "It was remarkable how quickly the birds were attracted," Roby said. The new digs must be satisfactory because the relocated colony has grown by nearly 10 percent. Meanwhile, the percentage of salmon in the birds' diet has dropped significantly.

Clearly, recorded sounds can attract birds to new habitats. But they may help threatened birds in another way - by triggering the internal changes that make reproduction possible.

Evidence is derived from recent research on flamingos. Some of these flamboyant wading birds, declared extinct in the British Virgin Islands around 1950, have since been flown back to tiny Guana Island in the Caribbean from the Bermuda Zoo. So far, however, Guana's small flock has failed to breed.

"Historically, flamingos occur in very large flocks," said Caitlin O'Connell-Rodwell, a research affiliate at Stanford University's Center for Conservation Biology. "Before courtship and breeding, they engage in an elaborate group display for a whole month." Studies of captive-bred ring doves show that when females hear singing males, their ovarian follicles undergo pre-breeding changes. Perhaps, O'Connell-Rodwell reasoned, female flamingos need to hear the sounds of a large, noisy flock.

She arranged for 10 flamingo decoys in lifelike poses to join the live birds, and serenaded the group with the sounds of a displaying flock. "By the end of the month, we saw a significant difference in behavior," she said. Some flamingos even went through the motions of nest building.

This experiment took place in summer, however; not optimal for flamingo breeding. "But we were really encouraged," said O'Connell-Rodwell, who will present her results next month at the annual meeting of the Waterbird Society. She plans to repeat the experiment next year, during the spring breeding season.

Though social attraction has been an effective conservation tool for many species, it arrives too late for others. "Think about passenger pigeons," Roby said. "Once, they bred in huge colonies. At a certain point during their decline, lots of birds were left - but there weren't enough to form the really big colonies needed for reproduction.

"Maybe if biologists back then had this technique, they could have kept passenger pigeons in the game."

This story ran on page D1 of the Boston Globe on 10/29/2002.

FIELD CONSERVATION FUNDS
APPLICATION INSTRUCTIONS

PROJECT TITLE:

Strategies for facilitating the reproductive success of the reintroduced population of Caribbean flamingos *(Phoenicopterus ruber ruber)* on Guana and Anegada Islands, BVI

Location of Project: Guana Island Marine Sanctuary/Anegada Island, British Virgin Islands

Neotropic/Africa/Asia Fund
(circle one)

Primary Investigator: Caitlin O'Connell-Rodwell, Ph. D.

PROJECT INFORMATION:

Date Project Was/Will Be Started __7/2001 (Mo/Year) Anticipated Completion Date ___9/2003_____ (Mo/Year)

Duration of Support Requested In This Proposal: _3/03______ (Mo/Year) to __9/03______ (Mo/Year) (Max 12 Mos)

Amount Requested In This Proposal: $ __6,860____________ US

Funds Previously Received From Lincoln Park Zoo Field Conservation Funds $__0________US

Is this Pre-Proposal a part or phase of a larger ongoing program? YES / NO

PRIMARY INVESTIGATOR:

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CO-INVESTIGATORS: (List All)	**TITLE/INSTITUTION**
Nora Rojek, M. S.	California Department of Fish and Game
Timothy Rodwell, Ph. D.	Stanford University School of Medicine
Lianna Jarecki, Ph. D.	H. Lavity Stoutt Community College, BVI
Esther George	BVI National Parks Trust

PROJECT DESCRIPTION

Project Title: Strategies for facilitating the reproductive success of the reintroduced population of Caribbean flamingos *(Phoenicopterus ruber ruber)* on Guana and Anegada Islands, BVI

A Feasibility Study by Caitlin O'Connell-Rodwell, Ph.D. [1], Nora Rojek, M. S.[2], Timothy Rodwell, Ph.D.[3], Esther Georges[4], Lianna Jarecki, Ph.D.[5]

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Primary Investigator: Caitlin O'Connell-Rodwell, Ph. D.

Background:
The success of restoration programs for colonially breeding birds depends on several factors, including food abundance, predation pressure, and reproductive success that in some species is dependent on social stimulation and a threshold population size. Caribbean flamingos *(Phoenicopterus ruber ruber)* were reintroduced to two British Virgin Islands in 1992, Anegada and Guana Islands. Although both populations appear to not be limited by food supply or excessive predation, only the Anegada population has successfully bred and has grown from 18 to 63 individuals. Group displays and reproductive behaviors were artificially induced in the Guana Island population in July, 2001, using social attraction techniques. Decoys, breeding calls and artificial nests and eggs were nsed to artificially simulate a breeding colony to induce reproductive behaviors in the four males and two females. Behaviors were monitored prior to and after the introduction of the stimuli and analyzed to determine differences in behaviors. There was a significantly greater presence of reproductive behaviors after the introduction of the artificial stimuli ($p < .0001$) (O'Connell-Rodwell et al., submitted). We suggest that social attraction techniques may be a useful tool to stimulate breeding in captive and wild small populations of flamingos.

Specific Aims:
Group display and nesting behaviors were successfully induced during the month of July, 2001on Guana Island while March-April is the season where the initiation of group displays, nest building and ultimately breeding occurs naturally on the neighboring Anegada Island.

Specific Aim 1: Determine whether the social attraction techniques that were used to induce group displays and nesting behaviors in the reintroduced population of 6 Caribbean flamingos on Guana Island, BVI, would induce successful mating attempts when administered in the appropriate season (March-April).

Very little systematic data has been collected on the reproductive success of the Anegada population of flamingos. For example, the sex ratio is not known, nor is it known how many of the females reproduce each year and what their individual reproductive success rates are. These data would allow us to calculate a population viability analysis (PVA), a powerful yet simple predictive model to project the long-term population viability of this population. If viable in the long term, it may be possible use this population as a source for other local reintroductions and as a model for other flamingo reintroduction and captive breeding programs.

PROJECT DESCRIPTION/BUDGET

Specific Aim 2: Introduce an improved monitoring system for the successfully breeding Anegada population of Caribbean flamingos.

Methods:

Specific Aim 1: The Head-Flagging call, a call associated with Head-Flagging, the first display in a series of group displays, will be broadcast from 4-7 pm during the months of March-April, 2003 on Guana Island, BVI. 7 decoys in Head-Flagging postures and 3 in incubation postures positioned on nests with eggs will also be placed on the bank of the salt pond. Behaviors will be monitored during the peak group display hours of 4-7 pm. Behaviors from a control period prior to the introduction of the social attraction tools will be compared to behaviors exhibited after the introduction of the artificial stimuli to determine if there is an increase in group displays, nest building and breeding attempts. The population will be monitored through August to determine if any breeding attempts were successful at producing viable eggs.

Specific Aim 2: We will work with the local British Virgin Islands National Parks Trust staff (Raymond Walker, Nancy Woodfield and Esther Georges) to initiate the collection of data on annual nesting attempts, egg laying, hatching success and chick survival as well as data on individual reproductive success on Anegada Island. The data collection sheets will be developed by Caitlin O'Connell-Rodwell and Nora Rojek. Raymond Walker of NPT and a college student from Lavity Community College will be trained on data collaction techniques during the month of March, 2002. Demography data will then be collected on the Anegada population between April and July, 2002.

If successful, this project will continue over the next few years in collaboration with the BVI National Parks Trust's conservation monitoring program in conjunction with Lianna Jarecki and her students at H. L. Stoutt Community College.

Budget:

The budget requested from Lincoln Park Zoo for this project is $6,860, with a matching grant from the Falconwood Corporation to support accommodation and food while residing on Guana Island during March 2002. The field conservation funds will be used for travel costs of the three investigators from California to the BVI and for expenses to reside on Anegada while training local staff and students in techniques to monitor flamingos on Anegada Island. All of the necessary field equipment has been sponsored through other grants from the National Geographic Society and the U.S. Fish and Wildlife Service.

Airfare CA-BVI x 3 @1,250 = $3,750
flight Beef Isl-Anegada $150 x 4 = $600
Hotel on Anegada $100 x 2 x 3 nights= $600
Per diem on Anegada $40 x 4 x 4 days= $640
Transporation on Anegada $25 x 4 days= $100
Video tape @ $5.50 x 10 = $55
Audio tape @ $6.50 x 5 = $32.50
35 mm film @7.50+developing x 10 = $75
Pentax 7 x 25 binoculars= $120

References:

O'Connell-Rodwell, C. E., Rojek, N., Rodwell, T. C. & Shannon, P. (submitted). Artificially induced group display and nesting behaviors in the reintroduced population of Caribbean flamingos *(Phoenicopterus ruber ruber)* on Guana Island, BVI. *Bird Conserv. Internatl.*

O'Connell-Rodwell, C. E., Rojek, N., Rodwell, T. C. & Shannon, P. Social attraction techniques induce group displays and nesting behavior in Caribbean flamingos on Guana Island, BVI. Meeting of the Annual Waterbird Society, November 9, 2002.

December 20, 2002

Lincoln Park Zoo Field Conservation Funds
Department of Conservation and Science
Lincoln Park Zoo
2001 North Clark Street
Chicago, IL 60614

Dear Sir/Madam:

I strongly support the research proposed by Dr. Caitlin O'Connell-Rodwell entitled, "Strategies for facilitating the reproductive success of the reintroduced population of Caribbean flamingos *(Phoenicopterus ruber ruber)* on Guana and Anegada Islands BVI". I am thrilled that Dr. O'Connell-Rodwell and her colleagues are taking on this study. They had excellent results in their initial efforts (submitted to *Bird Conservation International*) and as head of The Conservation Agency, and as the person who initially reintroduced these birds to the British Virgin Islands, I am confident that their efforts will make a difference for the future viability of this very small population of Caribbean flamingos.

In addition, any scientific exchange made with the BVI National Parks Trust will bolster their efforts at managing the small but growing population of flamingos on Anegada. The Parks Trust researchers have been very enthusiastic about the possibility of collaborating with O'Connell-Rodwell and her colleagues and I encourage you to help foster this relationship, as it promises to greatly enhance the conservation monitoring programs the Parks Trust have in place in the BVI.

Sincerely,

James Lazell, Ph. D.

ELIZABETH RIGHTER
ARCHAEOLOGICAL CONSULTANT
104 26TH ST. NW
BRADENTON, FLORIDA 34205
March 9, 2003

Dr. Skip Lazell
870 Pebble Creek Rd.
Lane, Oklahoma 74555

Dear Skip:

Here, at last is my proposal for archaeology at the Guana Island site in October of 2003. None of this is cast in stone, but it is what I think would be the best approach. If you need to change the schedule etc., let me know. I do know that Mr. Pederson is the most qualified to do the work and he can only come on the dates that I mentioned in the proposal or maybe a little later. I do need Monique to do the organizing and sorting too; so unless there are more accommodations available, this schedule is the most economical and I hope will work best. . My other assistant is great too but he has to come all the way from Oregon and is more expensive.

I hope you and Wenhua are well. I will send this by email and by regular mail.

Best wishes,

Elizabeth Righter

Let me know if you remember if I left any supplies there--I think I left some screens etc. Also let me know your reaction to the proposal and what if any changes we might need to make.

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ELIZABETH RIGHTER
ARCHAEOLOGICAL CONSULTANT
104 26TH ST. NW
BRADENTON, FLORIDA 34205
March 7, 2003

TECHNICAL PROPOSAL AND COST ESTIMATE

Elizabeth Righter, Archaeological Consultant, is pleased to submit a technical proposal and cost estimate for limited data recovery to take place at the Guana Island prehistoric site in October of 2003. The goal of the research is threefold: 1) To attempt to locate evidence of the settlement plan, i.e. to expose house remains, refuse areas and other features to reveal the village plan and structure; 2) to recover faunal and floral material representative of the natural history of Guana Island, and 3) to increase our growing data base to learn more about the natural habitats and prehistoric human occupants of the island.

Previous investigations by Righter and her associates at the Guana Island prehistoric site have revealed the presence of a prehistoric settlement on the flat grassy ground on the shore adjacent to the beach used by the resort. From this area a ceramic vessel and several faunal samples were collected. In the past, numerous ceramic sherds also have been collected from the garden area at one end of the settlement. It is likely that this area was a midden or disposal area for the settlement; however, this remains to be proven.

Prehistoric Caribbean island village plan and structure have been the subjects of recent archaeological investigations on other Caribbean islands. A few village plans have been exposed by machine scraping of large areas at such sites as Tanki Flip, Aruba (Bartone & Versteeg, 1997), Golden Rock, St. Eustatius (Versteeg & Schinkel, 1992), Maisabel, Puerto Rico (Siegel, 1989; 1992; 1996), and Tutu, St.Thomas (Righter, 2002). These investigations have yielded village configurations that were oval or horse-shoe shaped during the early or Saladoid occupation and oval or circular during later (Ostionoid) phases of occupation. In the Saladoid period (ca. 500 B.C.- A.D. 700), the habitation area ringed a central open space, that also frequently served as a burial precinct; and midden or waste deposits were located behind the structures. Midden areas either formed a continuous ring at the rear of the residential area, or were discontinuous, forming discrete disposal areas related to specific domestic structures. During the later Ostionoid period (ca. A.D. 700-1492), the village plan known from non-shoreline sites was oval or circular with a central plaza. From investigation at sites in Puerto Rico, which was closely related to the Virgin Islands at this time, it appears that diversity in settlement pattern and village type increased during the Ostionoid period, and villages ranged from small hamlets of one or two houses, to complex villages with one or more stone-lined ball and/or dance courts. Worship of zemis (spiritual gods represented in stone, wood, ceramic, cloth and other materials) becomes highly formalized and, according to the historical chronicles, society was stratified into three classes.

None of the archeologically investigated sites in the Virgin Islands and Puerto Rico, however, is directly on the shore line and there is some question as to whether or not shoreline sites might have been linear in configuration. Archaeological investigations on Guana Island offer an excellent opportunity to investigate and address this question. If it is possible to determine the configuration of the shoreline settlement at Guana Island, a significant contribution would be made to the theoretical model for understanding Caribbean island village plans, and important new information would be added to the existing data base.

A related issue is the time of settlement of the Guana Island site. A very early radiocarbon date obtained from a test pit near the existing fresh water pond on Guana Island suggests possible Archaic occupation in this area. However, ceramic styles and other radiocarbon dates indicate settlement of the flat area by the beach after the Saladoid period and by about A.D. 1100. If this date can be supported with additional Carbon-14 dates from carefully collected carbon samples, another important issue in Caribbean island archaeology can be addressed. Many Caribbean archeologists hypothesize a population increase at the same time that site diversity apparently occurs during the early Ostionoid period. This issue, however, is under debate. Questions of expansion into a wide variety of ecological zones, a possible intrusion from new people from South America and population increase vs. break up of large villages into many smaller settlements are still unanswered. The socio-political mechanisms for changes also are unknown. Evidence from other smaller offshore Virgin Islands indicates initial settlement of these smaller islands after the Saladoid period,. Additional carefully collected dates from Guana Island would possibly strengthen the argument supporting a period of expansion and new settlement during the beginning of the Ostionoid period. In any case, the Guana Island site is strategically placed to contribute to our understanding of cultural changes during the post-Saladoid period.

Faunal samples collected during an initial survey and limited excavations at Guana Island were sent for analysis to the University of Massachusetts in Boston, under the care of Michael Gibbons. A formal report of this analysis has not been received, however it has been reported verbally by Skip Lazell that bones of now extinct monk seal were found, as well as iguana bone. If indeed monk seal bones were present in the faunal material recovered from the prehistoric waste deposits at Guana Island, this raises several issues. Monk seal remains have been recovered from other sites in the Caribbean islands, such as the Golden Rock site in St. Eustatius (van der Klift, 1992) and the Tutu site in St. Thomas (Righter, 2002). At Tutu, a single tooth was found and it had been fashioned into a pendant. Monk seal remains have been reported from other Caribbean island sites also (verbal communication, Elizabeth Wing), but the exact nature of the bones is unknown. At the documented sites mentioned above, monk seal remains have been limited to teeth and mandibles. This raises the question of whether monk seals actually lived in the waters around the specific islands or whether their mandibles and teeth were traded in order to produce body ornaments. If additional monk seal remains can be recovered from the Guana Island prehistoric site, their presence and natures may indicate whether or not, in the prehistoric past, there were monk seal habitats around Guana Island. Such information would contribute significantly to our understanding of the natural history of the island.

Similarly, the recovery of iguana bones and remains of other animals will indicate the species present at different past periods of human occupation of the island. Human refuse middens are capsules of natural history that permit recreation of past environment and ecological conditions on the island. Additionally carefully collected radiocarbon dates will indicate the time periods when certain species were present. In addition to faunal material, floral remains also reveal a great deal about the natural history of the island. During the proposed archaeological investigations on Guana Island in 2003, samples will be collected for flotation and recovery of charred plant remains. It is likely that pollen will be poorly preserved in the shoreline environment, however, soil samples also will be collected for pollen and phytolithic analysis.

Many other research issues may be addressed at the Guana Island prehistoric site. Samples collected during 2003, as well as accumulated materials from previous investigations, may be used in the future to address such questions as the relationship between health and diet, changes in dietary patterns; adaptations and changing adaptations to the natural environment, size and social makeup of the community, mechanisms of cultural and socio-political change as expressed in village structure, evidence for ancestor worship and other forms of spiritual beliefs, the relationship between cultural and social change and changes in ceramic styles, and many more. The Guana Island prehistoric site has great potential for contributing important new information to a growing understanding of prehistoric human lifeways and adaptations in the Caribbean islands. A small prehistoric site, on an offshore island such as Guana Island, may provide laboratory-like conditions in which certain mechanisms of change are more apparent and readily studied than at larger sites. In this respect, if undisturbed areas are present, the Guana Island prehistoric site may be one of exceptional archaeological value.

PROPOSED WORK PLAN

TASK 1:

Task 1 will consist of review of reports of previous work on Guana Island in order to compile existing data and select areas for research during the 2003 field season. To accomplish the first goal of the research, it is likely that a large expanse of the site (several contiguous units) will be exposed to locate house posts, possible burials, fire pits and hearths and other features. Every effort will be made to identify and map features as they are exposed; however, past experience has indicated that normally, it is necessary to investigate and record each feature to determine its true nature. If many features are exposed, locations of all exposed features and stains will be mapped but it is probable that there will not be time to complete careful investigation of all features during one season. If such occurs, the excavation units will be carefully backfilled, protecting exposed features, and left for further investigation during the next research season.

During excavation of the contiguous units, it will be determined whether or not surface layers are disturbed. Disturbed overburden will be removed as bulk soils and screened through 1/4-inch screen. All artifacts and a representative number of ecofacts will be collected and retained in labeled field bags. Once undisturbed strata are reached, exposed features will be systematically investigated. Human burials, however, will be left in place. It is likely that not all exposed features can be investigated during the 2003 season. However, should there be few features and should it be possible to conduct deep excavations, stratigraphic layers will be systematically removed by archaeologists using hand-held trowels. Each layer will be carefully removed and samples will be collected from good contexts. Locations of sample collection areas will be plotted on maps of the excavation area and each sample will be separately bagged and labeled. Each stratigraphic layer that is removed will be mapped and photographed. When the excavation reaches subsoil beneath the occupation layers, the excavation unit walls will be profiled and photographed. Location of the excavation unit or units will be mapped on a site map prepared using a hand-held GPS system.

It is anticipated that setting up the excavation areas will require the work of two persons for two days. Preparing a site map with GPS, setting up a flotation device, and initiating excavation of contiguous units will require the work of two or three persons for between 6 and 8 days.

TASKS II and III::

It would be ideal to locate areas of undisturbed midden where excavation may take place to recover faunal and floral remains, as well as artifacts and other material germane to understanding the natural history and prehistoric human occupation of Guana Island. It is believed that the present garden area formerly was a midden disposal area and careful inspection and testing of this area might yield undisturbed midden for data recovery. Once one or more midden areas have been located, limited excavations will take place in the manner described above. During excavation of these midden units, faunal, charred plant, pollen and phytolithic samples will be recovered from each stratum. For collection of faunal material, at least 15 liters of soil from each stratum will be sieved through 1/16th inch screen. Charred plant remains will be recovered from a flotation device, and for pollen and phytolithic analysis, 15 liters of soil will be collected from each stratum. Collection and analysis of such samples constitutes responsible archaeology, and justifies excavation of undisturbed and un-threatened resources that otherwise might be left in place until a future time when more sophisticated equipment is available. On offshore islands, such as Guana Island, obtaining and transporting necessary equipment will always be a problem; and because of this, work must proceed slowly and carefully. By conducting limited archaeological excavation in undisturbed midden areas, it is anticipated that it will be possible to collect a representative faunal sample, as well as plant remains which will allow reconstruction of the natural history of the island during its prehistoric human occupation.

SCHEDULING, ACCOMMODATION REQUIREMENTS AND PROJECTED COSTS

Archaeological investigations on Guana Island are projected to take place between about October 14 and 31, 2003. It is planned that Elizabeth Righter will fly to St. Thomas to pick up equipment and meet with Ellen MacClean who will accompany her to Beef Island where it is anticipated they will be picked up and taken to Guana Island. Ms. MacClean will assist Ms. Righter in preparing for the field investigations and in locating and setting up excavation areas. Ms. Righter and Ms. MacClean will can share a bedroom for accommodation but require separate beds.

It is expected that Mr. Robert Pederson, Ms. Righter's assistant , will be able to arrive on or about October 17 and remain until October 26. He will bring additional equipment, construct a flotation device, conduct GPS mapping and assist with excavation of selected units. If necessary, Ms. Righter and Mr. Pederson also can share one room for accommodation.

Following Mr. Pederson's departure, Ms. Monique Purguy is expected to arrive on October 27 and will remain until October 31, 2003. Ms. Purguy was laboratory manager for the Tutu archaeological excavagtions in St. Thomas and is highly qualified to oversee all necessary laboratory tasks. Ms. Purguy is prepared to assist with sorting, cleaning and labeling the collected materials and preparing samples for analysis. She and Ms. Righter can share one room with two separate beds for accommodation.

PROJECTED COSTS

Careful data recovery requires adequate field and mapping equipment, as well as storage facilities. Analysis of recovered materials by experts in various fields is also necessary. Such requirements incur some costs; however, these can be reduced by cooperative efforts among scientists working at Guana Island. It is anticipated that storage space and some equipment also will be available on Guana Island.

Ms. Righter and her assistants will volunteer their expertise and time at no cost. They will, however, require, room and board and transportation. Costs of most supplies will be borne by Ms. Righter.

Known costs:

1. Round trip airfare for Ms. Righter from Tampa, Florida to St. Thomas. And round trip transportation costs from St. Thomas to Beef Island, Tortola, where it is anticipated that she will be transported to and from Guana island.

2. Round trip transportation costs for Ms. MacClean from St. Thomas to Beef Island, where she also will be transported to and from Guana Island.

3. Round trip transportation for Mr. Pederson from Tampa, Florida to Beef Island, Tortola and round trip transportation to Guana Island. If time allows, it may be possible for Mr. Pederson to drive to Miami to obtain a reduced airfare.

4. Round trip transportation for Ms. Purguy from St. Thomas to Beef Island and transportation to and from Guana Island.

Note: It is not yet known whether Ms. Righter and her assistants from St. Thomas will travel by air to Beef Island, or by ferry to Tortola and taxi to Beef Island.

5. Costs of radiocarbon and other analyses. These can be expensive and it may be possible to apply for a small grant to assist with them Mr. Skip Lazell also has indicated that he and others can assist with faunal analysis. It may also be possible to obtain contributed radiocarbon dating from a laboratory known to Guana Island scientists interested in the results of the excavations. Charred plant, pollen and phytolithic analysis are specialized subjects that are only conducted by a handful of qualified experts in the United States. If the results are promising and of interest to other scientists, it may be possible to obtain some assistance at no or very little cost; or it may be that samples will have to be stored until adequate funding is available for some of the analyses.

LITERATURE CITED

Bartone, R, & A. Versteeg. 1997. The Tanki Flip features and structures. In: A. Vertseeg & S. Rostain (eds), The Archaeology of Aruba and the Tanki Flip Site. Aruba and Amsterdam Publication of the Archaeological Museum Aruba 8, Publications of the Foundation for Scientific Research in the Caribbean Region 141.

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Versteeg A.H. & K. Schinkel (eds). 1992. The archaeology of St. Eustatius: the Golden Rock site. Publication of the St. Eustatius Historical Foundation No. 2: Amsterdam Foundation for Scientific Research in the Caribbean Region.

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From: "Perry, Gad" <gad.perry@ttu.edu>
To: <guana@candwbvi.net>
Cc: <wenhua@etal.uri.edu>
Sent: Wednesday, November 06, 2002 8:07
Attach: Scientists of Guana.doc
Subject: what the scientists do

Dear Roger:

Following our discussion the night before we all (finally) left you in peace, Skip and I put together a short piece that explains, in plain English, what it is the scientists do on Guana. It is attached, in Word format. You're welcome to hand it out to guests, or just use the information as you see fit. We hope that this starts to fill the need you identified. More will follow as we get to it, hopefully soon. If additional questions emerge, please let us know and we'll work on more info-bites. Unless you'd like it in electronic form, the rainfall information I promised will be coming by snail-mail, as I think it'll look better in color. Is the BVI address the best one to send it to, or would you rather it was sent elsewhere? I don't know if you still use a USVI forwarding service.

While I'm on-line, this is a great opportunity to say "Thank you" on behalf of Kate and Susan and myself. We had a very productive month, and greatly appreciate your personal contributions to this success, as well as those of the entire Guana Island staff.

Hoping to see you next October,

Gad

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Gad Perry, Assistant Professor
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****

The Scientists on Guana Island

Twice a year, in the summer and in the fall, Guana Island empties of our usual guests. In their stead, we are invaded by scientists, who spend anything from a few days to both months conducting research on the island. Two of the most frequent questions we are asked are: Who are these people? And why are they here?

Who are these people?

The scientists who come to Guana Island arrive from all over the world. A partial list includes Australia, Austria, Bermuda, Canada, China, Croatia, Dominica, England, Finland, Israel… and, of course, the United States and the British Virgin Islands. They represent all racial groups, and have ranged in age from twelve to over 70. Many are affiliated with research universities, but others are based at other institutions, such as public museums and government agencies. Many are professors, but others are teachers, students, retirees…. On land and in the ocean, they study plants, mushrooms, and animals ranging from the smallest insect to birds and mammals. What unites this diverse group and brings it here year after year is a burning interest in the unique environment that is Guana Island.

Why are they here?

The owners of Guana Island believe that good stewardship requires a deep understanding of the biology and history of the land. The Caribbean Basin, with its multitude of small islands, holds some of the most unique and endangered floras and faunas in the world. So much so, in fact, that it was recently recognized as one of the top 10 "hotspots" for biodiversity in the world! In the Book of Life, the British Virgin Islands offer an especially thick chapter. Unfortunately, surprisingly little is known about these unique ecosystems and organisms, and about the problems that increasingly confront them. We know the chapter is there, but we cannot yet decipher the language it is written in. What is worse, extinction keeps ripping pages out of our book before we have even had a chance to look at them, let alone understand them! The research conducted by the Guana Island scientists is an attempt to translate this monumental work, little by little, into a language we can understand. Each project focuses on a tiny aspect, trying to translate a single line, or even just a few words. By itself, the result may appear to make very little sense. But the number of random-seeming snippets keeps growing. As more and more of them are put together, paragraphs are starting to emerge. Although we are still far from being able to read the whole chapter, our research is increasingly allowing us to make more educated guesses about what the whole work holds. And, as the researchers reveal more about Guana and nearby islands, we also have a better understanding of how to protect this unique environment for ourselves, and for future generations.

What use is this work?

Like their colleagues worldwide, the researchers who come to Guana Island are primarily focused on basic research – work that often does not produce an immediate benefit, because the snippet of information is too small and isolated to fit into the bigger picture yet. For example, it turns out that the sphere-toed geckos are so abundant on Guana that, despite the fact that each weighs less than a peanut does, there is more weight of geckos per unit area here than of elephants in Africa! Results of such work are published in scholarly journals and help scientists from all over the world in better understanding how our global ecosystem works.

One never knows when a piece of basic research will become useful. For example, a large part of the effort has been to document what species are found on Guana and in the BVI. Ongoing work on the beetle fauna, which until recently was of interest only to a few specialists, allowed the Guana Island scientists to be the first to identify in the BVI the cause of the alarming century plant mortality – a beetle – and alert BVI authorities. The Guana scientists have since begun work to determine how this non-native beetle arrived in the BVI, in the hope of learning how to fight it, and how to prevent the next invasive species from coming in and attacking some other native organisms.

The science conducted on Guana has also had some very applied facets. Scientists whose specialty is archeology are the ones who excavated the ruins on the island and made the sites and the information accessible to tourists. Biological information is continuously used in making decisions about how to minimize run-off from Guana Island and its impacts on the marine environment, and how to best develop Norman Island in a responsible way. Our biologists have even used the private jet of Guana's owner to gather data on temperature in various "stowaway" spots on aircraft. These data are now being used both to prevent the unwanted arrival of invasive species and to help treat human stowaway in aircraft.

Most visibly, it is the scientists who have spearheaded the return to Guana of species that used to be found here, but have become extinct over the years as a result of human activities. With the enthusiastic support of the owners of Guana Island, this work has already resulted in the successful return of magnificent creatures such as the iguana and the flamingo. We are still assessing the success of other attempts, such as the return of the white-crowned pigeon. And planning continues on how to return other native species, such as the whistling duck and the local parrot, to Guana Island.

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ORIGINAL RESEARCH

Wheel-Well and Cargo Compartment Temperatures of Large Aircraft in Flight: Implications for Stowaways

GAD PERRY

PERRY G. *Wheel-well temperatures of large aircraft in flight: implications for stowaways.* Aviat Space Environ Med 2002; 00: 000–00.

Background: Desperate people sometimes risk journeys as stowaways in aircraft wheel-wells. Some of them survive, despite the risks of being crushed by retracting landing gear, falling when the gear deploys for landing, or experiencing severe hypoxia and hypobaria in-flight. This study evaluates the level of hypothermia to which stowaways in aircraft may be exposed. ***Methods:*** Miniature dataloggers were used to record in-flight temperatures in aircraft wheel-wells and cargo compartments. Temperatures were measured for front and side wheel-wells (FW and SW, respectively) on 36 flights by C-130 aircraft (mean duration 3.3 h, mean cruise altitude 5588 m (18,333 ft)) and 11 flights by C-141 aircraft (6.7 h and 10,744 m (35,250 ft)). ***Results:*** Mean minimum temperatures for the C-130 remained above freezing and averaged 5.1°C for FW and 11.9°C for SW. The higher, longer C-141 flights produced temperatures below freezing with mean minimum temperatures of −18.0°C for FW and −12.4°C for SW. In general, temperatures in wheel-wells remained AQ: 1 about 20°C above outside air temperature (OAT) at all altitudes. This elevation reflects the fact that wheel-wells are closed spaces within the aircraft body, in addition to which they contain sources of heat such as hydraulic lines and electrical equipment. A search of the medical literature and lay press produced information on 46 incidents of people found in wheel-wells after landing where there was no evidence of trauma. The 15 survivors had stowed away on relatively short flights (mean = 4.8 h, maximum = 10 h) compared with fatalities (mean = 7.5 h, range = 3–12 h). ***Conclusions:*** Temperatures in wheel-wells during short flights may sustain life. Long flights add severe hypothermia to acute hypoxia and hypobaria as potentially fatal environmental factors faced by wheel-well stowaways.

Keywords: temperature, wheel-well, cargo compartment, hypothermia.

THE VOLUME OF AIR traffic has increased tremendously in the past few decades. For desperate people, this creates a temptation to stow away in commercial or military aircraft in the hopes of improving their lot in life. The exact number of stowaways is hard to assess. However, popular articles periodically recount the stories of stowaways in wheel-wells and cargo compartments. It appears there are multiple cases every year.

Cabin environments in modern aircraft are maintained within a narrow comfort zone. Cargo holds are also heated and pressurized to provide a relatively benign environment, although control is less precise than for cabins. Unfortunately, stowaways frequently sequester themselves inside wheel-wells, which are not so hospitable (1,7). Risks occur at several stages: stowaways may be crushed as the landing gear retracts following takeoff; they are exposed to acute hypoxia during flight; and they may fall from great height as the gear deploys for landing (6). Exposure to hypobaria in-flight may also produce life-threatening decompression sickness (4,7). For stowaways who survive those threats, the cold temperatures at high altitudes add the risks of frostbite and potentially fatal systemic hypothermia (1,2,5,7).

Unfortunately, data on conditions inside wheel-wells in flight have not been available. For example, when Veronneau et al. (7) reviewed the cases of ten wheel-well stowaways from the period 1947–1993, they were forced to estimate cold exposure from outside air temperature (OAT) for flight altitude. They recorded a survivor of several hours at 11,887 m (39,000 ft) when OAT was about −60°C (7) and speculated that extreme cold and hypoxia induced a "hibernative state." However, the actual temperature in the wheel-well may not have been so low; wheel-wells in modern aircraft contain multiple sources of heat such as hydraulic lines and electrical equipment. When the doors close behind the retracted gear, the wheel-well becomes a compartment within the aircraft body with limited air flow and one or more heat sources that may produce a stable temperature that is well above OAT.

This study was designed to collect data on actual wheel-well temperatures of large jet aircraft in flight and is presented here to assist medical personnel with treatment of survivors and investigation of fatalities. However, these data were collected in a different context. The brown treesnake (*Boiga irregularis*) is an invasive species accidentally introduced to Guam at the end of World War II and responsible for extensive ecological and economic damage, as well as occasional human envenomation (3). The snake is an excellent disperser, stowing away in ships and aircraft, including wheel-

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From the USGS Brown Tree Snake Project, Dededo, Guam.

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wells and cargo compartments. As with human stowaways, some snakes die in transit, whereas others arrive alive (3). Animal stowaways face the same risks as their human counterparts, and the current study was initiated to assess the likelihood of live snake arrival at destinations served from Guam.

METHODS

Miniature dataloggers (Hobo loggers, Onset Computer Corporation, Pocasset, MA) were used to collect data on temperatures in wheel-wells and cargo compartments of a variety of aircraft. The dataloggers were equipped with internal thermistors, measuring temperature with an accuracy of ±0.7°C; sampling intervals were $<$ 5 min. Dataloggers were tested prior to use and at regular intervals during the study. Installation of loggers in wheel-wells was conducted by military and airline ground crews, with permissions from the relevant authorities. For each aircraft, one datalogger was positioned inside the front wheel-well and one at a side wheel-well near the auxiliary power unit. Data were collected for entire flight paths (source to destination). The type of aircraft was recorded, and information on flight parameters was obtained from notes provided by the pilots. In cargo compartments, loggers were primarily installed in cargo prior to regular commercial flights.
AQ: 2 Aircraft type, flight duration, maximum cruise altitude, and minimum OAT were recorded. Partial correlation analysis, performed using SPSS for Windows 9.0, was used to separate the effects of flight parameters on measured temperatures.

RESULTS

The 47 data sets for wheel-well temperatures were obtained from military aircraft (C-130, n = 36, and C-141, n = 11). Each set comprised data for wheel-wells at the front (FW) and the left side (SW). After a small uptick at take-off, temperature plummeted at a rate exceeding 0.5°C · min^{-1}. Cooling then slowed and stabilized at less than 0.04°C · min^{-1} (**Fig. 1** A, B). The two F1 types of aircraft flew different profiles. Compared with the C-130, the C-141 flew missions that were longer (mean duration 6.7 h vs. 3.3 h) and higher (mean 10,744 m vs. 5588 m (32,250 ft vs.18,333 ft)). The differences were highly significant (duration: t = 7.60, df = 45, p < 0.001; altitude: t = 17.55, df = 43, p < 0.001). Mean minimum temperatures for the C-130 were FW = 5.1 ± 4.4°C (range = −6.3 to 12.9°C) and SW = 11.9 ± 6.2°C (range = −2.9 to 23.2°C). Corresponding data for the C-141 were FW = −18.0 ± 8.0°C (range = −32.3 to −6.8°C) and SW = −12.4 ± 5.3°C (range −21.8 to −3.4°C). The differences between the two aircraft types were significant for mean minimum temperatures in both FW (t = 12.06, df = 44, p < 0.001) and SW (t = 11.80, df = 45, p < 0.001). Additionally, SWs were significantly warmer than FWs in both aircraft types (t-tests for repeated measures; C-130: t = 4.78, df = 9, p = 0.001; C-141: t = 8.60, df = 35, p < 0.001).

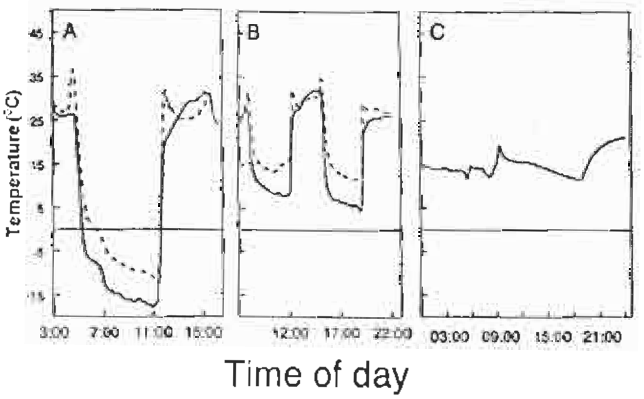

Fig. 1. Representative temperature profiles obtained during flight. A: Wheel-well temperatures for a flight from Guam to Hawaii in a C-141. Cruise altitude was 10,058 m (33,000 ft). B: Wheel-well temperatures for a round-trip flight between Guam and the Federated States of Micronesia. The C-130 reached a cruise altitude of 5182 m (17,000) ft during the first leg and 6706 m (22,000 ft) during the return trip. Solid line = front wheel-well; dashed line = side wheel-well containing auxiliary power unit.

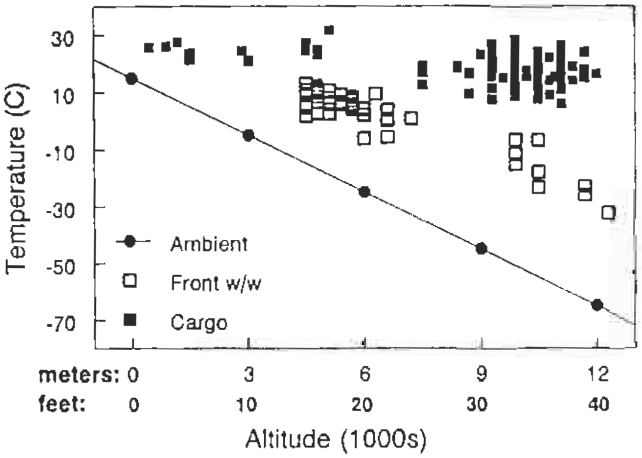

Fig. 2. The relationship of altitude with ambient temperature (calculations from Flight Safety Foundation (1)), minimum temperature measured in cargo compartments of commercial airliners, and minimum temperatures measured in the colder, front wheel-wells of military and civilian aircraft. AQ: 4

For the extensive C-130 dataset (**Fig. 2**), both altitude F2 and flight duration were negatively correlated with minimum temperatures in both FW and SW (duration: partial correlation coefficients exceeded −0.59 and p < 0.001; altitude: partial correlation coefficients exceeded −0.37 and p < 0.03).

As part of the treesnake study, temperature data were also obtained from cargo compartments during 205 passenger flights, encompassing aircraft made by Airbus, Boeing, McDonnell-Douglas, and a variety of others. Total transit duration ranged from 30 min to about 48 h (mean = 9 h) and maximum cruise altitude ranged from 457 m to 12,192 m (1500 ft to 40,000 ft) (mean = 31,400 ft). Minimum temperatures inside the cargo compartments ranged from 5.8 to 31.5°C (mean and standard deviation = 18.6 ± 5.0°C) and were not correlated with either cruise altitude (partial correlation coefficient = −0.169, df = 73, p = 0.147) or OAT (partial correlation coefficient = −0.107, df = 73, p = 0.360) (Fig. 2). However, temperature decreased as trip duration increased and the relationship was significant (partial correlation coefficient = −0.283, df = 73, p = 0.014).

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TABLE I. INFORMATION ON RECENT STOWAWAY EVENTS.*

Date	From	To	Aircraft	Duration (h)	Maximum Altitude (m)	Location	Outcome
19-Apr-66	*France*	*Morocco*	*Caravelle*	*(5)*		*side*	*dead*
14-Apr-72	*US*	*US*	*B-707*	*(5)*	*10700*	*side*	*dead*
10-Jan-86	US	Germany	DC-10	(10)			dead
Jun-89	Russia	UK	B-747	(6)			dead
27-Dec-89		US	B-727			Airstair	dead
Jun-90	Cuba	Spain	DC-10	(10)			2 dead
10-Jul-93	Russia	France		(4)			dead
04-Aug-93	*Colombia*	*US*	*B-747*	*(6)*			*dead*
02-Aug-96	Mongolia	Japan	C-141	5		front	2 dead
Sep-96	Russia	Italy		(5)			dead
14-Oct-96	India	UK		10		front	dead
12-Mar-97	Sri-Lanka	UK		(10)			dead
23-Mar-97	India	UK		(10)			dead
24-Mar-97	Kenya	UK	B747	8	9600	front	dead
01-Oct-97	India	UK		(10)			dead
09-Feb-98	Azeraijan	UK	B767	7		side	dead
23-Dec-98	Antigua	Toronto	L10-11	6			dead
Jan-99	Bangladesh	Saudi Arabia		(6)			dead
05-Jan-99	Bangladesh	India	A310	(3)			dead
02-Aug-99	Guinea	Belgium	Airbus	(10)			2 dead
22-Aug-99	Cuba	UK		(10)		front	dead
19-Sep-99	Cuba	Italy		(12)			dead
26-Jun-00	Holland	US	DC-10	8			dead
25-Dec-00	Cuba	UK	B777	(10)		front	dead
05-Jun-00	Dominican Republic	Sweden	A300	(12)			2 dead
02-Sep-00	Russia	Holland	B737	(4)			2 dead
29-Sep-00	Malaysia	Germany		(12)			2 dead
28-Sep-66	*Colombia*	*Mexico*		*(3)*	*10400*		*live*
14-Nov-86	*Panama*	*US*	*B-707*	*(5)*	*11900*		*live*
24-Feb-90	Trinidad	Antigua	L-1011	(1)			2 live
24-Feb-90	Antigua	Canada	L-1011	5			2 live
04-Jun-93	*Colombia*	*US*	*DC-8*	*3*	*10700*		*live*
14-Oct-96	*India*	*UK*	*B-747*	*10*	*10700*	*front*	*live*
13-Mar-97	India	UK	B747	10	11900		live
1998	China	Japan		3			live
15-Sep-98	Honduras	US	DC-9	(5)	10000	side	live
Jan-99	Senegal	France		5			live
04-Apr-00	US	US	B757	3		cargo	live
05-Aug-00	Polynesia	US	B747	7.5	11800	side	live
13-Nov-00	Germany	Germany	B737	(0.2)			live
24-Nov-00	Vietnam	Vietnam	ATR-72	1.1	5400		live

*All but two, one in the cargo compartment and one in the airstair compartment of a B-727, had hidden in wheel-well compartments. Durations in parentheses are estimates. Information in italics was taken from two published sources (1,7).

Loggers installed in single locations inside two Cessna Citation V luggage compartments for a total of 19 flights showed mean minimum temperature = 6.8°C. Thus, stowaways in cargo compartments of smaller aircraft are likely to be exposed to harsher conditions than in large aircraft.

DISCUSSION

In the aircraft sampled, temperatures in both cargo compartments and wheel-wells were considerably higher than OAT. This is not surprising for cargo compartments, which in modern commercial aircraft are typically designed to maintain pressure and temperature at levels suitable for pets and other delicate items; cargo compartments were usually within the comfort range for both human and non-human stowaways.

Unlike cargo compartments, temperatures inside wheel-wells often dropped well below freezing. Following an early rise in temperature on take-off, presumably due to tire heat (7), temperature plummeted as the aircraft ascended. As cruise altitude was reached, the rate of decrease in wheel-well temperature slowed more than ten-fold (Fig. 1). Contrary to assumptions made in the past based on older aircraft (1,7), minimum values remain about 20°C higher than OAT (Fig. 2). Thus, the risk of hypothermia for stowaways appears smaller than previously thought. Survival chances should be higher in SW, where auxiliary power units help maintain minimum temperatures about 5°C higher than in FW. This should be especially true during longer flights when wheel-well temperatures are even lower.

Based on these findings, the temperatures faced by stowaways in the wheel-wells of modern aircraft will depend primarily on flight length and choice of wheel-well. This allows two predictions to be made. First, that survival rates will be higher for stowaways on relatively short flights; and second, that survival chances of stowaways in side wheel-wells will be higher than in front wheel-wells.

To test these predictions and ascertain the size of the problem, the author conducted a search for information on the Internet, utilizing the keywords "wheel," "well," "aircraft," and "stowaway." The author utilized a variety of search engines (Alta Vista, Excite, FindArticles, Google, GoTo, HotBot, Lexis-Nexis, Lycos, and Yahoo), several prominent news providers (Associated Press, Daily Telegraph, New York Times, and Washington Post), and the sites of the Federal Aviation Agency and the National Transport Safety Board.

The search yielded multiple records of stowaways, most documented by several sources. All survival events were included. Fatalities were included if a body was found in a wheel-well without evidence of mechanical trauma; bodies found after they fell during takeoff or landing were omitted. The remaining 39 wheel-well
T1 events (**Table I**) occurred between 1966 and 2000 and involved 47 people, all men. A single report of a recent stowaway in a cargo compartment was found, and he was reportedly completely unharmed.

AQ:3 Of the 47 stowaways, 15 survived (13 individuals with 2 surviving 2 trips each) and 32 perished. Overall, survivors were aboard shorter flights (mean = 4.8 h, range = 0.2–10 h) compared with fatalities (mean = 7.5 h, range = 3–12 h) and the difference was significant (t-test, t = 2.413, df = 42, two-tailed p = 0.02). Maximum altitude did not significantly differ between survivors and fatalities (n = 10 stowaways; mean altitudes: survivors = 10,350 m, fatalities = 10,150 m; t = 0.126, df = 8, p = 0.836). Although the data qualitatively match the prediction of greater survival in side wheel-wells, the small sample size precludes the identification of significant differences.

Wheel-well stowaways face potentially fatal hypothermia, hypoxia, and decompression (1,2,4,7). However, as the current study demonstrates that temperatures inside wheel-wells are warmer than OAT, it may be worth investigating the possibility that air pressure also differs from the outside environment.

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