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p. 1: "Autumn monitoring..." of birds by Clint Boal, et al.

p. 10: "Diurnal activity patterns of ... stilts..." by Laura Navarrete, et al.

p. 15: "Vertical structure use..." by Iguanas by Chris Cheek, et al.

p. 22: "Non-overlapping..." sheep and Iguanas by Ben Skipper, et al.

p. 31: "... Population density..." of Dwarf Geckos by Krista Mougey, et al.

p. 51: "Thermal biology..." etc. of Dwarf Geckos by K. Allen & R. Powell.

p. 77: "Biodiversité insulaire..." by Robert Powell, et al.

p. 113: "Red imported fire ants..." by Tracy Langkilde & Katriona Shea.

p. 119: "Cymapamphatus..." a new true bug by Thomas Henry

p. 129: "... Cockroaches..." by Wenhua Lu, et al. I saved this for last because these insects, albeit widely despised, are truly wonderful! Only 3 of 21 species are household pests; the other 18 are native natural habit species of dunes to forests, and nifty!

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AUTUMN MONITORING OF RESIDENT AVIFAUNA ON GUANA ISLAND, BRITISH VIRGIN ISLANDS

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Resumen. – Monitoreo de otoño de la avifauna residente in Isla Guana, Islas Virgenes Británicas. – Aunque la región Caribe es considerada un centro de biodiversidad y de gran prioridad en los esfuerzos de conservación ecológica, existe poca información sobre las tendencias poblacionales de aves terrestres en las Indias Occidentales. En este estudio combinamos datos de tres estudios previos cubriendo un periodo de 16 años en una pequeña isla, con minima presencia humana en las Islas Virgenes Británicas. Tomando en conjunto, los estudios presentan patrones temporales de abundancia de aves y como las condiciones ambientales influyen en su detectabilidad. Nuestros datos indican una composición estable de la avifauna. Aunque las abundancias variaron entre los estudios, las mismas especies fueron detectadas con solo raras excepciones. A pesar de la estabilidad en la composición de especies, las aves residentes fueron variables en sus detectabilidades individuales. Las detecciones reflejaron relativamente las tasas de captura para algunas especies, pero fueron muy dife-rentes para otras especies. Sospechamos que esto es debido a diferencias en detectabilidad por comportamiento especifico de cada especie, mediada por condiciones medioambientales tales como la lluvia un mes o varios meses previos a nuestros estudios. Es dificil evaluar la influencia de la sincronización o la cantidad de precipitación sobre las tasas de detección en nuestros estudios, debido en parte a la carencia de una consistente recolección de datos climáticos locales en las Islas Virgenes Británicas. Nuestros estudios sugieren realizar esfuerzos de monitoreo de aves en conjunto con recolección de datos climáticos específicos para cada sitio, lo cual facilitara una mejor interpretación de los datos de estos estudios, y un mejor entendimiento de la respuesta de las aves a los cambios climáticos.

Abstract. – Although the Caribbean region is considered a biodiversity hotspot and a priority for ecological conservation efforts, little information exists on population trends of West Indian landbirds. We combined avian survey data collected from three studies spanning a 16-year period on a small island with a minimal human presence in the British Virgin Islands. Although abundances varied among surveys, the same species were detected with rare exceptions. Despite stability in species composition, the resident landbirds were variable in their individual detectabilities. Survey detections relatively mirrored net captures for some species, but are quite different for others. We suspect that this is likely due to differences in detectability due to species-specific behaviors mediated by environmental conditions, such as rainfall, during the month or months prior to our surveys. It is difficult to assess the influence of timing or amount of precipitation on bird detections rates among our surveys due to a lack of consistent collection of location-specific weather data in the British Virgin Islands. Our study suggests monitoring efforts conducted in concert with collection of site-specific climate data would facilitate improved interpretation of survey data and a better understanding of avian species response to climate mediated changes. *Accepted 11 November 2013.*

Key words: Bananaquit, *Coereba flaveola*, Pearly-eyed Thrasher, *Margarops fuscatus*, avifaunal richness, monitoring, species composition, surveys, British Virgin Islands, Guana Island.

2

INTRODUCTION

The Puerto Rican Bank, consisting of Puerto Rico, the US Virgin Islands, and the British Virgin Islands, is one of ten Endemic Bird Areas of the Caribbean (BirdLife International 2010). Within the Puerto Rican Bank, substantial research and monitoring attention have been directed at resident bird communities (Dugger *et al.* 2000, Faaborg & Arendt 1992, Faaborg *et al.* 1997) and the Nearctic/ Neotropical migrant landbirds wintering in dry forest within the Guánica Biosphere Reserve, Puerto Rico (Dugger *et al.* 2004, Faaborg *et al.* 2007). In contrast, there is a paucity of data for the British Virgin Islands (Mayer & Chipley 1992, Boal *et al.* 2006, McGowan *et al.* 2007). Indeed, there is a well-recognized need for avian monitoring programs among the Caribbean islands in general (Latta 2005, Haynes-Sutton and Wood 2008). Monitoring of avifaunal communities is important to identify the impact of environmental changes, and to facilitate assessments of the loss, habituation, recovery, or expansion of highly vulnerable, often endemic species (Arendt *et al.* 1997, Hilton *et al.* 2003, Dalsgaard *et al.* 2007). Monitoring may be especially important given likely environmental changes that are anticipated to occur in association with changing climate. For example, hurricanes are known to have negative influences on migrant and resident landbirds (Wiley & Wunderle 1993, Wunderle 2005). Hurricane events have increased over the last century (Martin & Weech 2001) and the prognosis is for an increased frequency and intensity of hurricanes due to warmer sea surface temperatures associated with climate change (Emanuel 2005).

Most islands in the Caribbean have experienced various extents of human presence and the influences of anthropogenic activities (e.g., landscape conversion, introduction of non-native species) on avifaunal trends are important factors. However, islands with little human disturbance would allow assessment of environmental influences while keeping the confounding factors of local anthropogenic activities to a minimum. Under this guiding concept, we combined data collected from three different studies spanning a 16-year period on a small Caribbean island with a minimal human presence. The studies were conducted at different times by different researchers so there are slight inconsistencies in methodological approaches. Taken together, however, the studies present a view of temporal patterns in avifaunal abundances and, perhaps more importantly, how environmental conditions may influence detectability.

METHODS

We conducted bird surveys on Guana Island (18°30'N, 64°30'W), a small (3.1 km^2) island approximately 0.5 km immediately north of Tortola, British Virgin Islands (BVI). The BVI are located approximately 150 km east of Puerto Rico. Temperature in the BVI normally ranges from 28–33 °C, with relative humidity fairly constant at about 78% (Lazell 2005). Annual mean rainfall for Guana Island is estimated at 92 cm, but data are limited and the long-term average may be lower (Lazell 2005).

Guana Island is topographically rugged with elevations ranging from sea level to 246m. It is privately owned and has undergone little development or habitat fragmentation. A small resort area occupies approximately 3% of the island; the remainder of the island is a *de facto* nature preserve covered by subtropical vegetation, the majority of which is subtropical dry forest (90%) and mesic ghaut (i.e., drainage) forest (5%) (Lazell 2005). The primary native vegetation on Guana Island is *Tabebuia heterophylla* (Bignoniaceae), *Bursera simaruba* (Burseraceae), *Pisonia subcordata* (Nyctaginaceae), *Conocarpus erectus* (Com-

3

bretaceae), *Plumeria alba* (Apocynaceae), *Acacia muricata* (Fabaceae), and *Coccoloba uvifera* (Polygonaceae) (Lazell 2005).

We used fixed-radius points (Hutto *et al.* 1986) to survey landbirds on Guana Island during the month of October in 1994 (Arendt 1995), 2001 (Wunderle 2001), and 2007–2009 (Boal 2010). Surveyors recorded all birds detected by sight and or sound and classified distance as less than or greater than 25-m from the survey point. Birds in flight were not included in the analyses. Surveys were conducted for 10 min at each point during the 1994 and 2001 surveys, and for 7 min during the 2007–2009 surveys.

We used a hip-chain and biodegradable string to locate survey points at 100-m intervals along parallel transects placed 100 m apart across the entire island in 1994. In 2001 and 2007–2009, we took advantage of a network of trails across Guana Island. The trail system allowed access to all vegetation communities and areas on the island and made surveys more logistically feasible and repeatable given the rugged topography and thick vegetation. A hip-chain was also used in 2001 to locate survey points at 100-m intervals along the trails. In 2007, survey points were paced at 150 pace intervals which, based on GPS coordinates, resulted in survey points located approximately 120 m apart. Survey-point coordinates were recorded with a handheld GPS unit in 2007 and used to survey the same points in 2008 and 2009. Ultimately, the same sections of trail and, hence, the same areas, were sampled in all surveys, which facilitates comparison of data among survey years.

Caribbean birds can be counted during any season, but surveys should be conducted at the same time annually using the same protocol to monitor population changes (Wunderle 1994, Faaborg *et al.* 2000). Surveys of bird populations also need to take into account species-specific detection rates. Distance sampling (Buckland *et al.* 2001) has become a method of choice for estimating avian abundance, density, and population size in context of different detectabilities. However, meeting assumptions for distance sampling can be challenging. A minimum of 75–100 detections per species within a cover type is necessary for estimation of valid detection functions when using point counts (Buckland *et al.* 2001). Furthermore, a critical component of distance sampling is accurate estimation of distance (Buckland *et al.* 2001). Auditory detections can comprise over 80% of songbird detections in tropical forests (Scott *et al.* 1981). Based on trials with song simulation, Alldredge *et al.* (2007a) estimated observers detected only 19–65% of the true bird population, and suggested a lack of control under normal field survey conditions likely makes estimates even more variable. Furthermore, trials have revealed substantial uncertainty in distance estimation based on aural detections and that point count estimates based on distance methods are likely biased (Alldredge *et al.* 2007b).

Failure to meet criteria of distance sampling methodology, such as adequate sample size, and suspicion of bias due to the majority of detections of forest birds being derived from aural cues, compromise use of the method under some conditions and in certain habitat types. Project constraints that limit the number of species whose numbers can be reliably estimated by detectability methods dictate that indices be used as an alternative (Thompson *et al.* 1998). Therefore, we present our data as an index of relative abundance, not actual density. Indices do not allow for precise estimates of population densities, but they do allow for comparisons between years within the same study area (Hutto & Young 2002).

Based on our survey data, we calculated mean number of detections within 25-m fixed-radius points. We used Kruskal-Wallis tests to compare median number of detections within 25 m among years. We conducted these analyses for two variables, the number of individuals and number of species detected, for resident landbird species only. We used multiple comparisons of mean rank to examine differences among years (Siegel & Castellan 1988). We then examined species-specific patterns of detection for those species that were detected ≥ 50 times.

During each October of 2007–2009, CWB operated a banding station on Guana Island. This provided us the opportunity to compare survey detection rates to capture rates. Nets were placed in the same locations along a northeast–southwest ridge on the west side of the island at ca. 70 m elevation each year. All nets were placed in subtropical dry forest and in human-altered areas of the island hotel. As many as 12, 32-mm mesh nets were opened for an average of 422 (± 57 SE) h each year (Boal 2010). The banding station occupied only a small area of the island, whereas surveys were island-wide. However, net captures provide a measure of relative abundance independent of surveys based on aural/visual detections (Faaborg *et al.* 2004). Therefore, for the 2007–2009 data, we compared survey data to net capture rates to assess common patterns in numerical trends. We ranked the relative abundance of each species captured or detected, depending on method, over the three study periods in 2007–2009 to examine similarities or differences between net captures and surveys. This resulted in a ranking of 1–15 (3 years x 5 species) for each method. We then took the absolute values of the difference of the ranks of the two methods for each species within a given year and calculated the 95% Confidence Interval on these numbers. If the two methods are equivalent, the interval would be expected to include zero. Failure of inclusion of zero may indicate detection probabilities varied between methods, among years and species, the methods are equivalent but sampled different populations due to restricted area sampled by the mist-netting, or a combination of these factors.

RESULTS

We analyzed October avian survey data collected at 60 points in 1994, 65 points in 2001, and at 58, 53, and 57 points in 2007–2009, respectively (Table 1). The surveys in 2007–2009 were at the same points each year, but differed in number due to weather or other factors preventing complete surveys of all 58 points.

We detected a total of 17 species across all survey periods (Table 1). There was a significant difference among surveys in terms of total individuals of resident species detected ($H_{4,293} = 101.87$, $P < 0.0001$) and number of resident species detected ($H_{4,293} = 89.97$, $P < 0.0001$). Pairwise comparisons of total detections indicated significant differences ($P < 0.05$) between 1994 and all other years, and between 2001 and 2007, 2007 and 2009, and 2008 and 2009. A pairwise comparison of species detected indicated significant differences ($P < 0.05$) between 1994 and 2007, 2008, and 2009; detections in 2001, 2007, and 2008 were all significantly different from those in 2009. Essentially, 2009 was consistently lower in detections of both total individuals and total resident species compared to all other survey years (Table 2).

Because we restricted our species-specific analysis to only those species for which we had at least 50 detections, our analysis included Bananaquit (*Coereba flaveola*; n = 307), Pearly-eyed Thrasher (*Margarops fuscatus*; n = 306), Caribbean Elaenia (*Elaenia martinica*; n = 70), Zenaida Dove (*Zenaida aurita*; n = 70), and Black-faced Grassquit (*Tiaris bicolor*; n = 54); no other resident landbird was detected 50 or more times.

Detections of the Bananaquit varied among the survey periods ($H_{4,293} = 23.36$, $P =$

5

TABLE 1. Proportion of 25-m radius survey points in which a species was represented by at least one individual during October surveys on Guana Island, British Virgin Islands, 1994, 2001, and 2007–2009. Number of survey points: 1994 - n = 60; 2001- n = 65; 2007 - n = 58; 2008 - n = 53; 2009 - n = 57.

Species	1994	2001	2007	2008	2009
American Kestrel	0	0	0.03	0	0
Mangrove Cuckoo	0.12	0	0.02	0	0
Smooth-billed Ani	0.02	0	0	0	0.02
Scaly-naped Pigeon	0.08	0.11	0.09	0.08	0.04
Zenaida Dove	0.43	0.17	0.12	0.09	0.05
Common Ground-dove	0.15	0	0	0.04	0
Bridled Quail-dove	0.03	0.11	0.05	0.04	0
Green-throated Carib	0.22	0.23	0.03	0.06	0.05
Antillean Crested Hummingbird	0.17	0.05	0.1	0.09	0
Antillean Mango	0.02	0	0	0	0
Gray Kingbird	0.13	0.08	0.03	0.08	0.02
Caribbean Elaenia	0.3	0.18	0.22	0.15	0.11
Pearly-eyed Thrasher	0.87	0.85	0.47	0.38	0.16
Northern Mockingbird	0	0	0	0	0
Bananaquit	0.75	0.57	0.74	0.64	0.46
Yellow Warbler	0	0	0	0	0.02
Black-faced Grassquit	0.12	0.15	0.17	0.19	0.02

0.0001) with differences between 1994 and 2009 ($P = 0.001$) and 2007 and 2009 ($P = 0.0015$). Mean detections of the Bananaquit were similar and highest in 1994 (mean = 1.38 ± 0.13) and 2007 (mean = 1.34 ± 0.14) but lowest in 2009 (mean = 0.56 ± 0.14) (Table 2). Differences among years were more pronounced for the Pearly-eyed Thrasher ($H_{4,\,293} = 102.39$, $P < 0.0001$). The only survey periods between which differences ($P < 0.05$) were not detected among thrashers were those of 1994 and 2001, and 2008 and 2009. In general, detections of the Pearly-eyed Thrasher were highest in 1994 (mean = 1.97 ± 0.12) and progressively decreased to the lowest detection rate in 2009 (mean = 0.16 ± 0.12) (Table 2).

There were no statistical differences among years in detections of Caribbean Elaenia ($H_{4,\,293} = 8.97$, $P = 0.062$), Zenaida Dove ($H_{4,\,293} = 8.17$, $P = 0.080$), or Black-faced Grassquit ($H_{4,\,293} = 9.19$, $P = 0.056$). Detections for the Black-faced Grassquit in 2009 was only 34% of that in 2007 and 32% of that in 2008 (Table 2). Similarly, detections for the Zenaida Dove in 2009 were only 33% of that in 2007 and 26% of that in 2008 (Table 2). Differences among years for elaenias were not as dramatic, but did suggest a consistent decline in detections from 1994 to 2009 (Table 2).

Mist net captures were not consistent among years for most resident species. The Bananaquit was the most frequently captured resident species in all years, with 19.8/100 net-h in 2007, a dip to 13.7/100 net-h in 2008, then up to 16.3/100 net-h in 2009. The Pearly-eyed Thrasher, the second most frequently captured resident species, demonstrated a similar pattern with 11.5 captures/100 net-h in 2007, a drop to only 4.1/100 net-h in 2008, then 9.5/100 net-h in 2009. Captures of the Black-faced Grassquit were similar in 2007 and 2009 (2.9 and 3.4/100 net-h), but almost double in 2008, with 6.3 birds per 100 net-h. The Caribbean Elaenia was the

6

TABLE 2. Average detection numbers/registrations (± SE) of common resident landbirds within 25-m radius plots during October surveys on Guana Island, British Virgin Islands, in 1994, 2001, and 2007–2009.

Year/species	Bananaquit	Black-faced Grassquit	Caribbean Elaenia	Pearly-eyed Thrasher	Zenaida Dove
1994	1.38 ± 0.13	0.13 ± 0.07	0.43 ± 0.07	1.97 ± 0.12	0.55 ± 0.07
2001	0.81 ± 0.13	0.17 ± 0.07	0.23 ± 0.07	1.53 ± 0.12	0.23 ± 0.07
2007	1.34 ± 0.14	0.26 ± 0.07	0.26 ± 0.07	0.83 ± 0.12	0.15 ± 0.07
2008	1.15 ± 0.14	0.28 ± 0.08	0.15 ± 0.07	0.58 ± 0.13	0.19 ± 0.07
2009	0.56 ± 0.14	0.09 ± 0.07	0.10 ± 0.07	0.16 ± 0.12	0.05 ± 0.07

only resident species that demonstrated a consistent decrease in captures, with 2.2, 0.9, and 0.6/100 net-h, in 2007, 2008, and 2009, respectively. Due to the small mesh size of the nets and the large body size of Zenaida Doves which reduced probability of capture, we did not include the species in analysis of mist net captures. In general, Bananaquit and Pearly-eyed Thrasher were captured in greater numbers in 2007 and 2009, with lows in 2008. In contrast, the Black-faced Grassquit was captured in similar numbers in 2007 and 2009, but in higher numbers in 2008.

We found evidence that the methods of surveys and net captures are not equitable in assessing avian abundance. The mean rank was 2.27 (± 1.89) with a 95% Confidence Interval (1.22, 3.31) that did not include zero.

DISCUSSION

Our combined survey data indicate that Guana Island appears to be stable in terms of avifaunal composition. Although abundance varied among surveys (Tables 1, 2), the same species were detected with rare exceptions. Typically, these discrepancies were of species that normally occur at low density, such as American Kestrel (*Falco sparverius*) and Red-tailed Hawk (*Buteo jamaicensis*). However, Arendt (1995) observed an Antillean Mango (*Anthracothorax dominicus*), which has not been detected during surveys since, and Boal (2010) detected the resident Caribbean form of the Yellow Warbler (*Setophaga petechia cruziana*; verified by subsequent capture).

Despite stability in species composition, Caribbean resident landbirds are variable in their individual detectabilities. For example, the Mangrove Cuckoo (*Coccyzus minor*), known for being secretive, had high detectability ratios in 1994 due to calling associate with breeding (Arendt 1995). In contrast, Wunderle (2001) did not detect the species on surveys, and Boal (2010) detected very few, and in only two of three years. T. S. Estabrook (pers. com.) considered the species abundant on Guana Island, however, based on responses to call-playback surveys (which elicit territorial responses) conducted during the same 3-yr period. As Wunderle (2001) suggested, some of these differences may be associated with differences in rainfall prior to the surveys or seasonal hurricane events. The 1994 survey was conducted at the end of a wet period that, presumably, resulted in more species breeding during the survey period (Arendt 1995, Wunderle 2001). The high detection rates Arendt (1995) found for Zenaida Dove and Common Ground-Dove, due largely to their calling associated with breeding, have not been approached in systematic surveys since. When making qualitative comparisons between surveys and net captures in 2007–2009, the trend in survey detections relatively mirrored net captures for

7

Caribbean Elaenia and Black-faced Grassquit. However, survey data for Bananaquit and Pearly-eyed Thrasher are quite different from net capture data. We suspect that this is likely due to species-specific differences in detectability, possibly as a result of behaviors mediated by, as yet uncertain, environmental conditions.

It is difficult to assess the influence of timing or amount of precipitation on bird detection rates among our surveys due to a lack of consistent collection of location-specific weather data in the British Virgin Islands. The closest weather station to Guana Island at the time of our surveys was 40 km to the southeast at Charlotte Amalie on Saint Thomas. Thus, rainfall conditions on Guana Island are derived more from onsite assessments by the researchers during October than by actual measures. The survey in 1994 was conducted during what was considered a wet year, whereas the 2001 survey was conducted at the end of a long dry period (Wunderle 2001). Surveys in 2007, 2008, and 2009 were considered, respectively, normal, wet, and dry.

The Caribbean region has experienced an increase in average annual temperatures over the last century, and is anticipated to experience a further increase of over 2°C this century (U.S. Department of Interior 2010). In addition to increased temperature, a decades-old drying trend is also expected to continue in the Caribbean, resulting in less summer precipitation (Neelin *et al.* 2006, U.S. Department of Interior 2010). Added to this is the expected increase in frequency and severity of tropical storm events due to warming sea waters. These environmental changes may have consequences for birds resident to the Caribbean islands. Even though monitoring is primarily a passive means of identifying population change, and often fails to provide insight as to causes of those changes, it is an important tool for initiating and evaluating conservation plans. As Latta (2005) and Haynes-Sutton & Wood (2008) have stated, monitoring of Caribbean avifauna is sorely lacking. Because environmental conditions are likely to have a substantial influence on both detection and population size of resident landbirds, survey methods need to be suitable for addressing these issues. Our study suggests monitoring efforts conducted in concert with collection of site-specific climate data would facilitate improved interpretation of survey data and a better understanding of avian species response to environmental and climate mediated changes. This would enable robust modeling of time-specific influences of climate conditions on behavior and, therefore, detectability of resident bird species. Such modeling efforts would allow more confidence in interpretation of monitoring data and identification of factors driving population trends.

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9

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10

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DIURNAL ACTIVITY PATTERNS OF BLACK-NECKED STILTS (*HIMANTOPUS MEXICANUS*) DURING THE NON-BREEDING SEASON IN THE EASTERN CARIBBEAN

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Abstract: Diurnal activity patterns of resident Black-necked Stilts (*Himantopus mexicanus*) were observed on Guana Island, British Virgin Islands, during October 2010. Stilts were principally engaged in foraging and idle behaviors. The amount of time engaged in particular behaviors was relatively constant throughout the day, except during mid-afternoon when idleness increased and foraging decreased, with a subsequent increase in foraging in the evening. We speculate that the increase in foraging activity was a result of changing prey activity.

Key words: activity pattern, behavior, Black-necked Stilt, Guana Island, *Himantopus mexicanus*, wetlands

Resumen: PATRONES DE ACTIVIDAD DIURNA DE *HIMANTOPUS MEXICANUS* DURANTE LA TEMPORADA NO REPRODUCTIVA EN LAS ANTILLAS MENORES. Los patrones de actividad diurna de individuos residentes de *Himantopus mexicanus* fueron observados en la isla de Guana, Islas Vírgenes Británicas, durante octubre de 2010. Los individuos estaban ocupados principalmente en conductas de forrajeo e inactivos. La cantidad de tiempo dedicado a conductas particulares fue relativamente constante a lo largo del día, excepto a media tarde cuando se incrementó el descanso y disminuyó el forrajeo con un subsecuente incremento de este último al atardecer. Especulamos que este incremento en la actividad de forrajeo fue el resultado de un cambio en la actividad de las presas.

Palabras clave: conducta, isla de Guana, *Himantopus mexicanus*, humedales, patrones de actividad

Résumé : RYTHMES D'ACTIVITÉ DIURNE DE L'ÉCHASSE D'AMÉRIQUE (*HIMANTOPUS MEXICANUS*) EN DEHORS DE LA SAISON DE REPRODUCTION DANS L'EST DE LA CARAÏBE. Les rythmes d'activité diurne des Échasses d'Amérique (*Himantopus mexicanus*) sédentaires ont été observés sur Guana Island, aux Îles Vierges britanniques, en octobre 2010. La recherche de nourriture et le repos constituaient les principaux comportements des échasses. La durée consacrée à des comportements particuliers était relativement constante au cours de la journée, sauf en milieu d'après-midi où les durées de repos augmentaient et celles de recherche de nourriture diminuaient, suivies par une nouvelle augmentation du temps consacré à la recherche de nourriture dans la soirée. L'augmentation de l'activité de recherche de nourriture pourrait être le résultat de l'évolution des activités des proies.

Mots clés : comportement, Échasse d'Amérique, Guana Island, *Himantopus mexicanus*, rythme d'activité, zones humides

All animals perform a variety of activities, each of which consumes time and energy necessary for survival. Understanding how an organism distributes its time among activities is essential to understanding energy budgets and habitat use (King 1974). Many studies have examined avian activity patterns during the breeding season (Verner 1965, Dwyer 1975, Ettinger and King 1980) but fewer have focused on activity patterns outside of the breeding season.

We studied activity patterns and time allocations of Black-necked Stilts (*Himantopus mexicanus*; hereafter stilts) on Guana Island, located in the eastern Caribbean. Behaviors of this species have been documented in depth (Hamilton 1975) and are easily observed, but remain poorly studied during the non-breeding season (Cullen 1994), including the Caribbean (Wiley 2000). Guana Island provides an opportunity to study the ecology of Caribbean species in a relatively undisturbed and unchanged environment year round.

STUDY AREA AND METHODS

During October 2010, we studied activity patterns of stilts on Guana Island, a privately owned and mostly undeveloped 340 ha island in the British Virgin Islands. The primary vegetation on Guana Island is tropical dry forest (Lazell 2005). Guana Island contains several resident species of waterbirds, including stilts, which typically occupy a large saline pond (hereafter, salt pond) and breed in the surrounding vegetation, near the western shore of the island (Lazell 2005). During our study the stilts occupied a shallow, ephemeral pond in a low-lying area connected to the larger salt pond, separated by vegetation. We did not measure water depth or salinity because we wanted to minimize disturbance and habituation to the stilts, which occupied the pond throughout the entire study duration. We assumed salinity of the ephemeral pond was greater than that of the saline pond, and decreased with distance. Our observations showed water height never went above the tarsometatarsus of the stilts, suggesting water depth in the ephemeral pond was approximately 25–35cm (Robinson 1999).

In order to minimize recording disturbances caused by our presence, we waited 10 min after arriving at the freshwater pond before starting observations. We monitored the behavior of individual stilts from 0600–1800 for 5 consecutive days. Approximately 15–20 individuals occurred at the freshwater pond each day during this period. We observed focal animals from ~20 m using binoculars and recorded individual behavior every 60 sec during a 10-min sample interval, producing 10 sample points per focal animal (Altmann 1974); we sampled a total of 1530 sample points. Our categorized behaviors followed that of Hamilton (1975) and Robinson *et al.* (1999): (1) foraging behaviors which include pecking, plunging, scythe-like sweeps, and walking as part of searching; (2) walking behavior which includes an individual walking from one location to another, or to interact with another bird as opposed to moving as a part of foraging activity; (3) maintenance behavior which includes preening, stretching, head scratching and foot-shaking; (4) idle behavior which includes sleeping and loafing on the shore or in the water; (5) other, which consisted of all activities not included in the above categories; and (6) not visible, which was when an individual was shielded from view by vegetation. Because stilts were unmarked, each observer arbitrarily chose a bird and then sequentially scanned to the left or right to select the next individual for the following sample interval. To minimize pseudoreplication, observers notified each other of which bird was sampled in the previous 10-min sample. Nonbreeding plumages prevented us from determining the sex of individuals. We calculated the percentage of the total time spent in each behavior by all observed.

Foraging behavior and other activity patterns, such as idleness, can be affected by tidal patterns that affect prey availability and behavior (Evans 1976, Connors *et al.* 1981, Wilson 1990). Consequently, we examined tidal charts for the area to assess if tidal patterns may have affected any behavioral categories of stilts during our observation period. Even though all of our observations occurred at one pond, interhabitat and interisland movements on and off Guana Island may have affected our stilt observations at the ephemeral pond.

In addition to observations of behaviors of undisturbed individuals, periodic roadside passage of golf carts nearby (5–20 m) allowed us to assess stilt response to this form of disturbance. We recorded the number of vehicle passes per 10-min sample interval and used a chi-square test (Zar 2010), comparing behaviors recorded within 1 min before the vehicle passed to behaviors within 1 min after the vehicle passed, excluding observations where stilts were not visible, to determine if the passage of vehicles influenced the behavior of stilts.

RESULTS

BEHAVIOR

We sampled a total of 153 birds and collected a total of 1530 sample points (Fig. 1). During diurnal hours stilts spent the majority of daytime foraging (41%) or being idle (32%; Fig. 1). Less time was spent in the four other activities combined (27%): walking between locations (14%); engaging in maintenance behavior (7%); other behaviors (~2%); and not visible (2%). The most pronounced difference in behavior occurred from 1500–1700, a large reduction in foraging and a large increase in idle behavior, followed by a sharp increase (53%) of foraging behavior and a sharp decrease (63%) in idle behavior (Fig. 2). The hourly frequency of walking and activities in the "other" category varied little whereas maintenance behavior fluctuated mildly (Fig. 2). Foraging behavior can be affected by tidal patterns which affect prey availability and behavior. Examining tidal charts for the area (NOAA / NOS 2011) showed, during diurnal hours, high tide occurring at 1200 (~0.27 m) after which tidal levels declined steadily throughout the day until low tide at 1800 (~0.182 m). The frequency of walking and activities in the "other" category varied little throughout the day and maintenance behavior increased somewhat during the hours of 0700, 1300 and 1600, but otherwise remained relatively constant hour to hour (Fig 2).

DISTURBANCE

Vehicles passed by the pond at a rate of 12 / hr. Although a few stilts responded to vehicles by mov-

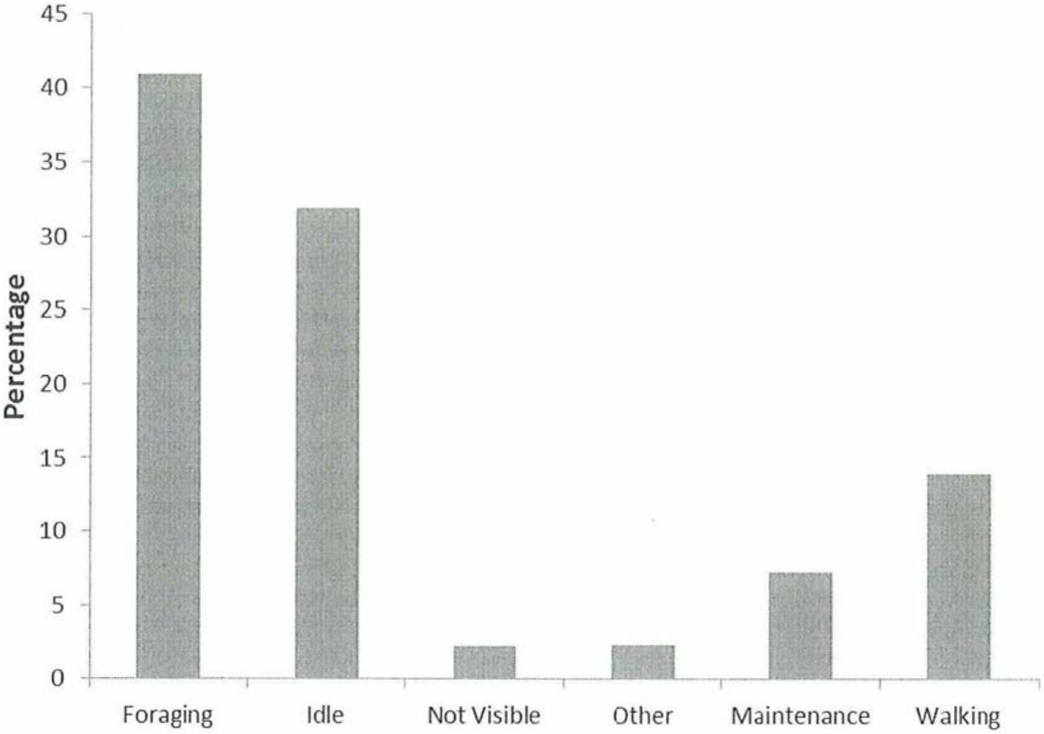

Fig. 1. Composite daytime activity patterns of Black-necked Stilt as a percentage of six behavioral categories during October 2010 on Guana Island, British Virgin Islands. See text for descriptions of behaviors.

ing away or assuming an alert posture, which was recorded as either "walking" or "other," the proportions of five observable activities (foraging, idle, maintenance, walking, and other) performed before and after disturbance were not significantly different ($\chi^2 = 7.12$, df = 4, $P = 0.13$).

DISCUSSION

Regardless of pseudoreplication in our study, Black-necked Stilts on Guana Island during the non-breeding season in autumn clearly spent most daytime hours foraging or idly resting. This result is consistent with an evolutionary strategy of maximizing uptake of energy and minimizing expenditure of energy during the non-breeding season (King 1974). The majority of the behaviors (i.e., walking, maintenance behavior, and those in the "other" category) remained relatively constant throughout the day. The one major change in the frequency of behaviors occurred mid-afternoon when foraging decreased and idling increased, which reversed itself in late afternoon. A number of explanations are available for this behavioral change, including a resource flush and tidal influence (Burger *et al.* 1977, Connors *et al.* 1981, Cullen 1994).

We investigated the possibility that the tidal cycle influenced stilt behavior through prey availability. The closest tidal station to our study area is at St. John Island in the Virgin Islands, approximately 22.5 km SW of Guana Island. Foraging activity among shorebirds usually increases around low tide, due to increased availability of habitat and exposure of prey items (Burger *et al.* 1977). The high spike in foraging activity among stilts occurred at 1700, an hour before low tide. Stilts are visual hunters and are less successful after sunset (Hamilton 1975), which occurred at approximately 1750 during the days we were sampling. The activity lull at 1500 and 1600 could be a necessary rest and digestion period before the large spike in activity at 1700 (Evans 1976). This increase in activity may be correlated to an increase in prey availability in response to tidal influence, which the stilts take advantage of before sundown.

Stilts are known to be aggressive towards people when disturbed during the breeding season (Sordahl 1990, 1996). We expected to see differences in their behavior when disturbed by the vehicles that passed very close to their foraging area at a rate of about 2

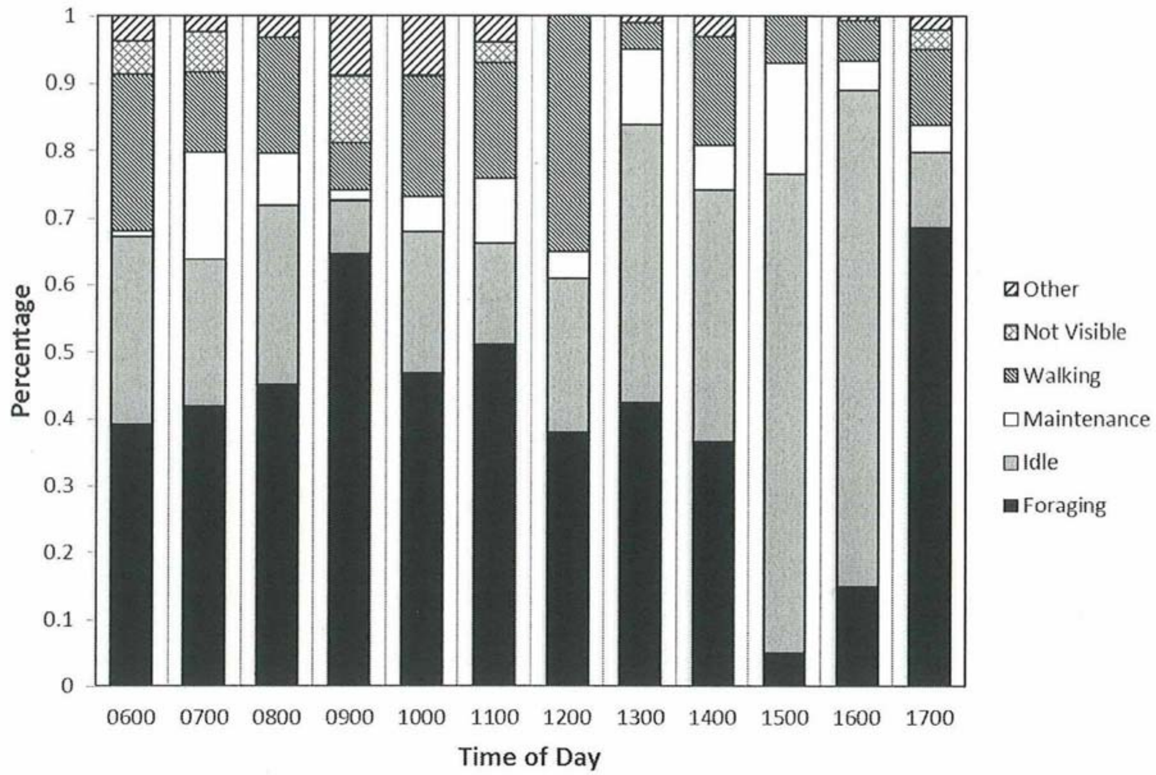

Fig. 2. Hourly daytime activity patterns of Black-necked Stilts as a percentage of six behavioral categories during October 2010 on Guana Island, British Virgin Islands. See text for descriptions of behaviors.

vehicles every 10 min. However, we found no evidence of the birds being disturbed suggesting that the stilts had habituated to the frequent presence of the vehicles.

Understanding how stilts allocate time among different activities during the non-breeding season is very important to understanding their year-round habitat requirements within the context of seasonal interhabitat use and movements. We assume the stilts were found in the smaller overflow pond because the larger pond where they are normally seen became too deep for successful foraging. The results of this study can be used to further investigate the energy budgets of stilts in the non-breeding season.

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14

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CONSERVATION AND NATURAL HISTORY

Vertical structure use by the Stout Iguana (*Cyclura pinguis*) on Guana Island, BVI

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Abstract.—The Stout Iguana (*Cyclura pinguis*) is a critically endangered species endemic to the Puerto Rico Bank and currently restricted to the British Virgin Islands (BVI). Our study on Guana Island, BVI, focused on vertical structure use. Based on previous incidental observations, we hypothesized that Stout Iguanas use vertical structures and that adults and juveniles use such structures differently. In October 2011, we documented movement and vertical structure use by adult ($n = 4$) and juvenile ($n = 11$) iguanas with tracking bobbins. We recorded structure types used, heights attained on structures, distances between structures, and structure sizes. We found that Stout Iguanas used vertical structure more than previously documented. Trees comprised a significantly greater ($P < 0.001$) proportion of structures used by juveniles than by adults, whereas rocks comprised the greatest proportion of structures used by adults. In addition to differential structure use, juveniles climbed significantly higher (2.4 vs. 0.9 m on average; $P < 0.001$) than adults. We found no difference in the diameter or distance between structures used by adults and juveniles. Our results suggest that vertical structure use may be an important habitat element for free-ranging juvenile Stout Iguanas. Habitat management that provides vertical structure may be advantageous for the conservation of this species.

The Stout Iguana (*Cyclura pinguis*; Fig. 1) is endemic to the Puerto Rico Bank and has been listed as critically endangered (Mitchell 1996, USFWS 1999). When Stout Iguanas were first described in 1917, the species was restricted to the flat and sandy island of Anegada (British Virgin Islands, BVI; Fig. 2). The common name "Anegada Iguana" is also in frequent use, despite subfossil evidence found in caves and in middens that indicates the species once inhabited much or all of the Puerto Rico Bank (Pregill and Olson 1981, Stephen 2012). The reduced distribution of Stout Iguanas was likely due to the habitat loss caused by rising sea levels and the introduction of non-native herbivores and direct predation by humans (Pregill and Olson 1981, Lazell 2005).

Anegada is flat (highest elevation < 10 m), highly sandy, and the eastern two-thirds of the island consist of mostly exposed limestone rubble (D'Arcy 1975). Introduced predators, competition with non-native mammalian herbivores, and habitat loss have all contributed to an extensive decline of the Stout Iguana population on the island (Mitchell 1999, Bradley and Gerber 2005, Perry and Gerber 2011). Mitchell (1999) estimated only 164 individuals persisted into the early 1990s. While a headstarting program continues on Anegada, eight iguanas were introduced to privately owned Guana Island (Fig. 3) in 1984 in an effort to conserve the species (Goodyear and Lazell 1994). Guana Island is dedicated to tourism and has become a *de facto* nature preserve. Anegada, which is inhabited by about 200 people, has more anthropogenic disturbance than Guana. Guana also differs dramatically from Anegada in its volcanic origins, steep topography (highest elevation 245 m), and a more complex vegetative community (Lazell 2005). The difference in geology, soils, and vegetation initially led to concerns that the iguana introduction would fail. However, the introduced population has done extremely well on Guana (Perry and Mitchell 2003, Perry et al. 2007) and has since served as the source for several subsequent introductions to other islands in the BVI (Perry and Gerber 2011).

Guana Island offers a multitude of vertical structures such as trees, vines, and large boulders (Fig. 4) that are mostly absent on Anegada (Fig. 5). Use of habitat elements not currently available on Anegada could partially explain the population decline of Stout Iguanas there and the observed popu-

16

Fig. 1. Adult Stout Iguana (*Cyclura pinguis*). Photograph by Doug Bell.

Fig. 2. Aerial photograph of Anegada Island. Photograph by Krista Mougey.

17

Fig. 3. Aerial photograph of Guana Island. Photograph by Krista Mougey.

lation growth on Guana. We therefore focused our study on two questions: (1) What types of vertical structures do iguanas use on Guana, and (2) how do juveniles and adults use these structures differently?

Materials and Methods

We tracked adult and juvenile Stout Iguanas that had been captured by hand and fitted with thread bobbins (Wilson 1994) for up to four days. Bobbins (200 m of string) were placed inside a balloon that had been coated with a rubber spray to form a rigid exterior (Performix© Plasti-Dip). The coated balloons were then glued anterior to the base of the tail on each iguana. The device weighed less than 5% of animal mass. We released iguanas at capture sites within 24 hours and attached the end of the bobbin string to a fixed object. Upon release, juvenile iguanas usually only ran 1–2 m. Adults tended to flee farther after release and often went straight to a burrow, but were usually active again within a short period. We consequently assumed that iguanas resumed normal behavior shortly after release.

We monitored each string at least once per day and noted the location of the animal if the string was not yet completely dispensed. After the bobbin was completely dispensed or the string was broken, we measured the linear distance traveled by each iguana. We omitted one string that was so fragmented that analysis was meaningless. We recorded the distance between vertical structures (defined as objects on which the iguana climbed more than 15 cm above the ground), maximum height reached on each structure, type of structure used (trees [live woody vegetation], other vegetation [cacti, vines, logs, stumps, and brush piles], rock [boulders, and rock piles], and cement structures), and the diameter at breast height (DBH) of trees used.

Fig 4. Typical vegetation on Guana Island illustrating the difference in vegetation when compared to Anegada (Fig. 5). Photograph by Krista Mougey.

Fig 5. Typical Vegetation on Anegada Island. Photograph by Krista Mougey.

We tested for differences in observed height on vertical structure used between juvenile and adult iguanas with a Wilcoxon rank test and used a two-sided Fisher's exact test to assess differences between adults and juveniles in the types of vertical structure used. Means are given ± one standard error. Data were analyzed using software R version 2.15.1 (R Development Core Team 2008). All use of live animals was conducted under Texas Tech University Animal Care and Use Protocol 10068-09.

Results and Discussion

We measured a total distance of 407 m of string for juveniles (n = 11) and 192 m for adults (n = 4). Types of structures utilized by adult and juvenile iguanas were significantly different (Fisher's exact test, $P < 0.001$; Fig. 6). Adults mainly used rocks and low vegetation. Conversely, juveniles primarily used trees (Fig. 7) when climbing above ground level and often were observed in trees during inactive periods (900–1500 h), as previously suggested by Gebert (2011). The average maximum heights attained by adults (0.9 ± 0.2 m) and juveniles (2.4 ± 0.2 m) also differed significantly ($W = 327.5$, df = 53, $P < 0.001$; Fig. 8). Juveniles also were observed in the canopy during twilight hours (5 individuals, 12 observations) and presumably passed the inactive nocturnal period in these arboreal locations.

Juvenile and adult iguanas also differed in structure choice during inactive periods. Juveniles spent inactive periods in trees (n = 5), whereas adults tended to use burrows (n = 3) near structures such as boulders and brush piles. During our brief study we observed adult bobbin string coming in and out of individual burrows multiple times, indicating repeated use within a single day. We suspect that adults spend the majority of the day in the burrows and leave only a few times to feed, thermoregulate, and conduct social interac-

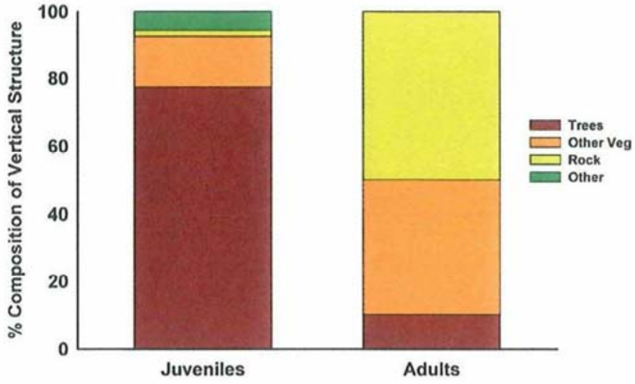

Fig. 6. Percent composition of vertical structure used by adult and juvenile Stout Iguanas. A total of 53 structures were used by juveniles and nine by adults.

Fig. 7. Juvenile Stout Iguana with tracking bobbin utilizing a tree limb. Photograph by Krista Mougey.

tions. Iguanas also may enter burrows to avoid humans traveling nearby. Additional studies of burrows would be desirable, as the substrate on Guana (volcanic rock) is substantively different from the limestone cavities available on Anegada and throughout much of the range of the genus *Cyclura* (Bradley and Gerber 2005).

The mean total distance of string measured was 36.6 ± 18.7 m for juveniles and 47.9 ± 13.7 m for adults. The mean distance between vertical structures used was similar for adults (8.4 ± 1.7 m) and juveniles (8.6 ± 1.4 m), but our observations indicated that the method of movement between structures differed. Adults moved almost exclusively along the ground between structures. In contrast, string from juvenile iguana bobbins was usually observed on vertical structures, indicating movement along vines and shrubs to move between trees. Trees used by adults (DBH 40 ± 18 cm) were larger than those used by juveniles (11 ± 3 cm), but small samples (only two adults used trees) precluded statistical analysis. However, the difference in body size and mass of juveniles (approximately 60 g) and adults (typically 1–6 kg; Perry et al. 2007) could preclude adults from using small trees or traveling in the canopy as juveniles commonly do.

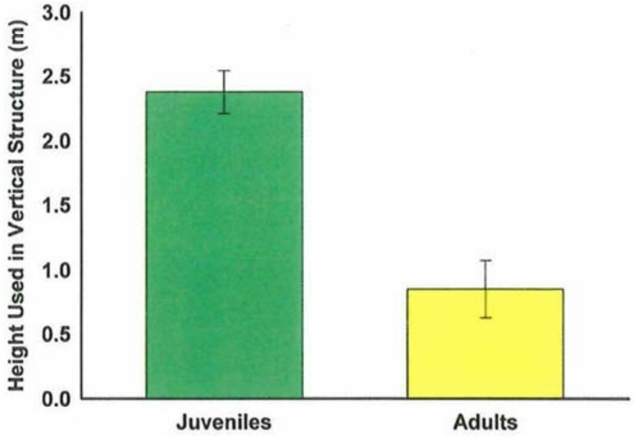

Fig. 8. Mean height used on vertical structures by adult and juvenile Stout Iguanas.

Thermoregulation is an important activity for Stout Iguanas, which maintain a high body temperature during active periods (Lemm and Alberts 2012). The presence of juveniles well above ground during inactive periods may be related to availability of sunlight early and late in the day, when the forest floor is already shaded. Use of vertical structures allows juvenile iguanas to bask later into the evening and earlier in the morning, presumably allowing them to sustain high body temperatures, increasing metabolism, digestion, and growth rates (Troyer 1987). In addition, the use of tree canopies by juveniles during inactive periods could be an evolved behavior for avoiding predators. Vertical structure use is likely advantageous for avoiding native daytime predators such as Puerto Rican Racers (*Borikenophis* [formerly *Alsophis*] *portoricensis*; LeVering and Perry 2003), as well as introduced predators such as feral cats (Bradley and Gerber 2005).

Habitat composition differs greatly between the low-lying, limestone island of Anegada and the much higher volcanic Guana Island. On Anegada, where relatively little vertical structure exists, juveniles mostly use sandy scrub areas that have little tall vegetation (D'Arcy 1975). As Stout Iguanas were only known from Anegada until fairly recently, and as many species in the genus *Cyclura* typically are found on low-lying limestone islands (Bradley and Gerber 2005), assuming that Anegada provided ideal habitat for iguanas was reasonable. However, our data suggest that this species is well suited, and perhaps even adapted, to the richer vegetation diversity and volcanic geology typical of the rest of the BVI (Fig. 9). *Cyclura pinguis* is the most basal member of its genus and is not greatly differentiated genetically from a clade including the genera *Iguana*, *Sauromalus*, *Ctenosaura*, *Conolophus*, and *Amblyrhynchus* (Malone et al. 2000). These are Central and South American species typically found in relatively dry or edge habitats (Burghardt and Rand 1982), as are many modern *Cyclura*. Central America, where *Iguana*

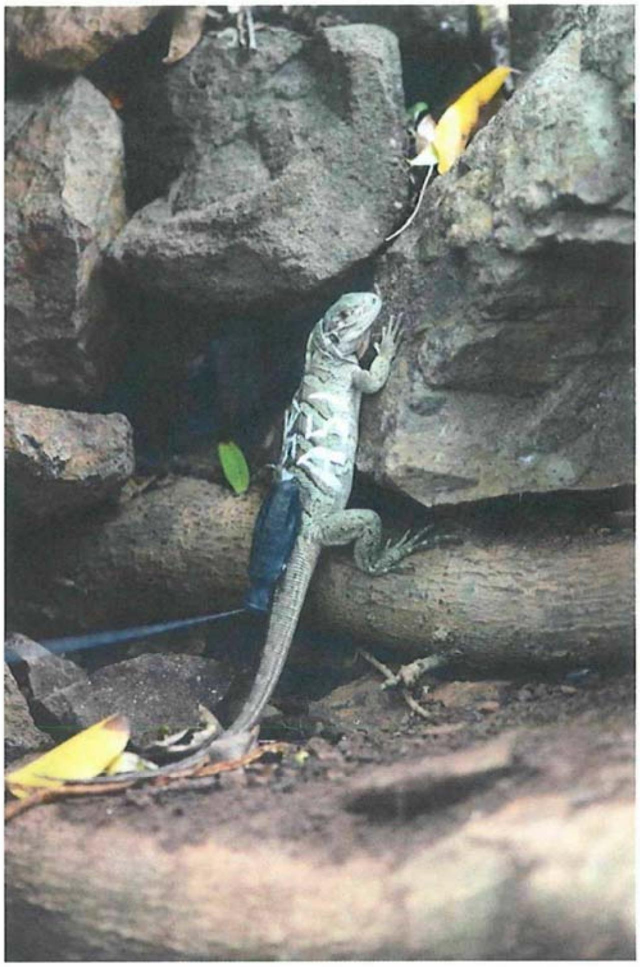

Fig. 9. Juvenile Stout Iguana with bobbin using vertical rock structure. Photograph by Doug Bell.

and *Ctenosaura* are found, is primarily volcanic (Malzer and Fiebig 2008). This also is the case for the Galapagos Islands, where *Conolophus* and *Amblyrhynchus* are found (White et al. 1993). In fact, although many Caribbean islands on which *Cyclura* are found are overlain with limestone, other Caribbean islands where other iguanas are found are of volcanic origins (Powell et al. 2005). When the ancestors of *C. pinguis* arrived in the Puerto Rico Bank some 33–35 million years ago (Stephen 2012), they therefore would have likely shared the ancestral state of *not* being limestone specialists. We consequently suggest that Stout Iguanas should perhaps be considered a refugee species (*sensu* Kerley et al. 2012) on Anegada, already confined to suboptimal habitats when early reports were published. This interpretation also could help explain the success of repatriated populations on Guana and Necker Islands (Perry and Gerber 2011).

Given that published observations from Anegada, starting with the work of Carey (1975) and continuing today (Lemm and Alberts 2012), have almost exclusively been limited to adults, that the importance of vertical structure to the species on that island had not been addressed is not surprising. Protecting and revegetating core iguana areas on Anegada, as called for by previous authors (Perry and Gerber 2011, Mitchell et al. 2011), would likely be highly efficacious for conservation efforts there. Removal of non-native herbivores from Anegada and other islands where they might be affecting iguana habitats and diets is a feasible management option (Island Conservation, 2006), and could be a part of any revegetation plan and is fully compatible with the existing species recovery plan (Burton and Bloxam 2006).

Acknowledgments

We thank J. Lazell for sharing his insights and the staff of Guana Island for technical assistance. We also thank Katrina Street, Matthew Gifford, and Robert Powell for their assistance in capturing iguanas. The Conservation Agency provided financial support through a grant from the Falconwood Foundation. The use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government. This is manuscript T-9-1247 of the College of Agricultural Sciences and Natural Resources, Texas Tech University.

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21

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22

IRCF REPTILES & AMPHIBIANS
CONSERVATION AND NATURAL HISTORY

Non-overlapping Distributions of Feral Sheep (*Ovis aries*) and Stout Iguanas (*Cyclura pinguis*) on Guana Island, British Virgin Islands

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Abstract.—Stout Iguanas (*Cyclura pinguis*) remain one of the most critically endangered reptiles in the world. Factors contributing to that status include habitat loss, predation by introduced species, and competition with introduced herbivores. On Guana Island, British Virgin Islands, the presence of feral sheep (*Ovis aries*) has been a hypothesized detriment to iguanas. Using motion sensitive cameras, we documented the distribution of feral sheep on Guana Island in 2010. We also quantified the impact of feral sheep on ground vegetation by comparing plant abundance at long-term sheep exclosures and areas where sheep were absent to areas where sheep were present. Finally, we compared sheep distribution to iguana distribution on the island. The co-occurrence of sheep and Stout Iguanas was less than expected, indicating possible competition. Although we detected no difference in vegetative cover between areas where sheep were present and absent, the long-term exclosures showed that the exclusion of sheep allowed the abundance of many plant species to increase. Our data support the hypothesis that feral sheep are altering the abundance of ground-level vegetation and limiting iguana distribution on the island.

Five principal factors contribute to species endangerment: Natural causes, over-hunting, introduced predators, non-predatory invasives, and habitat alteration (Fisher et al. 1969). Hunting, predator introduction, and habitat alteration have received considerable attention in both the popular and scientific press. The more subtle but no less profound effects of non-predatory invasive species such as herbivores have received less attention. Introduced herbivores may outcompete native species for resources or negatively affect them by altering the habitat (Lowney et al. 2005). Herbivorous reptiles appear to be particularly sensitive to the effects of introduced herbivorous mammals. As an example, Cuban Ground Iguanas (*Cyclura nubila*) now compete with deer (*Odocoileus* spp.) and feral goats (*Capra hircus*) at Guantanamo Bay, Cuba (Roca and Sedaghatkish 1998). That competition forced iguanas to move farther while foraging and juveniles to disperse greater distances and suffer greater mortality. Similarly, Stout Iguanas (*C. pinguis*) altered their diet and declined in numbers in response to feral livestock grazing on Anegada Island, British Virgin Islands (BVI; Mitchell 1999). Feral livestock

Fig. 1. The distribution of Stout Iguanas (*Cyclura pinguis*) and feral sheep on Guana Island (British Virgin Islands) is largely disjunct. Photograph by Robert Powell.

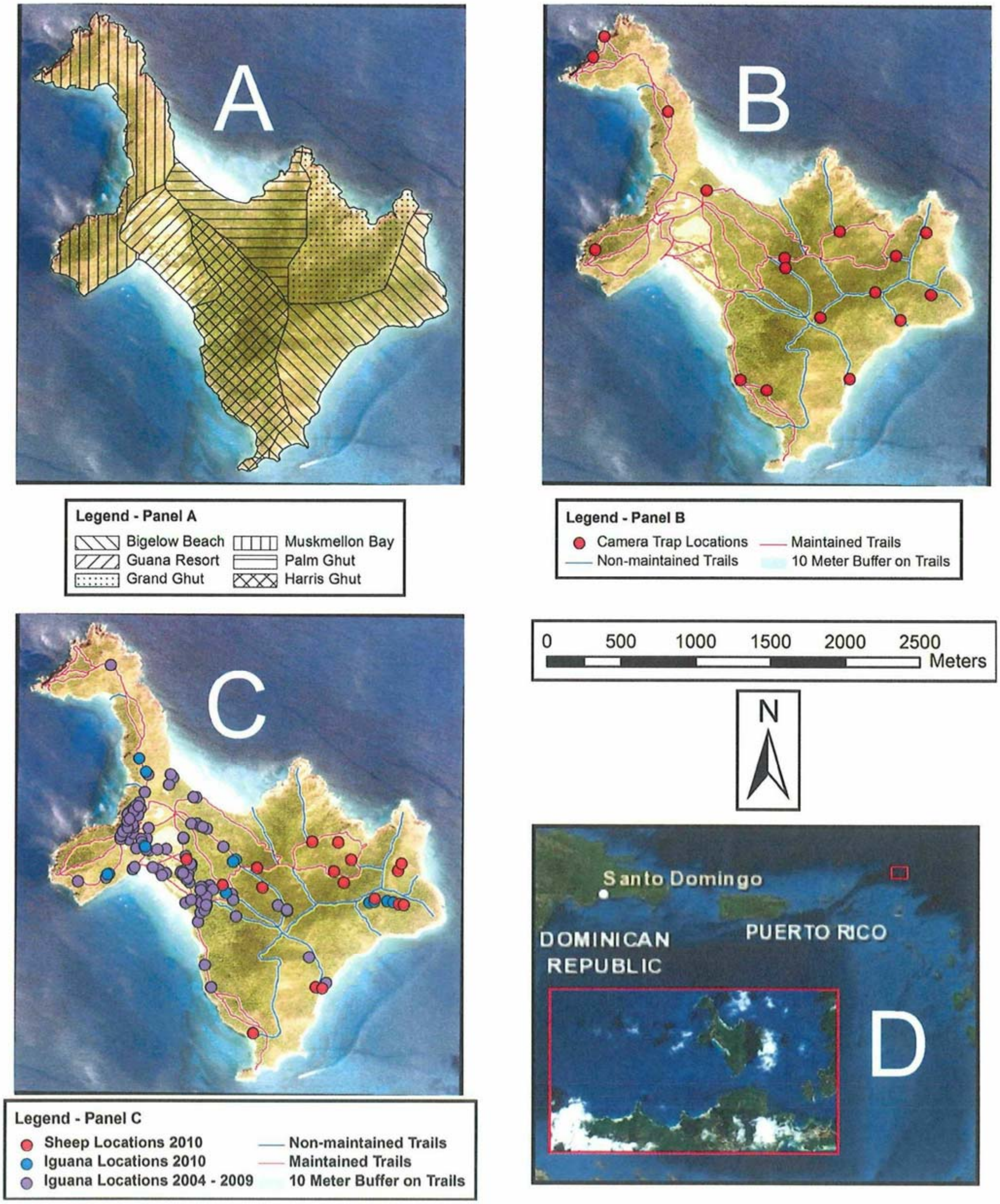

Fig. 2. Sampling effort of: (A) Subdivision of Guana Island into 6 units; (B) locations of cameras traps (red dots) along the trail system (red = maintained trails, blue = non-maintained trails, light blue = 10 m buffer of all trails) of Guana Island; (C) 2010 locations of encountered sheep (red dots), 2010 locations of encountered iguanas (blue dots), 2004–2009 locations of iguanas; (D) location of Guana Island within the greater Caribbean region. Note: scale bar for figures A, B, and C only.

Table 1. Ground cover composition at locations where sheep were and were not detected. "Green vegetation" represents pooling of all living plant material.

		Mean ± SD*	n**	%***
Sheep Absent	Green Vegetation	1.05 ± 3.55	25	4
	Litter	73.76 ± 18.56	25	74
	Rock and Soil	15.60 ± 15.60	25	22
Sheep Present	Green Vegetation	2.93 ± 7.69	50	12
	Litter	73.64 ± 14.43	50	74
	Rock and Soil	7.32 ± 9.33	50	14

* Mean ± SD of encounters of each ground cover type per 100 sample points.

** Number of forest floor photos analyzed. Each photo had 100 sample points.

*** Percentage of cover type with all samples pooled.

also has been shown to be responsible for negative effects on other species of rock iguanas (Lemm and Alberts 2012).

The Stout Iguana is listed as Critically Endangered and Endangered by the IUCN (2004) and the U.S. Fish and Wildlife Service (1999), respectively. By the 1980s, Stout Iguanas were known to occur only on Anegada Island, where they were in rapid decline (Mitchell 1999). Concern for the species' persistence prompted the translocation of eight individuals from Anegada to Guana Island, BVI. A decade later, Goodyear and Lazell (1994) found that the Guana population (Fig. 1) was persisting, but had not achieved an island-wide distribution. Goodyear and Lazell (1994) suggested that competition with feral sheep (*Ovis aries*), still found on Guana Island despite several eradication attempts (Lazell 2005), might have been the cause of the limited expansion by Stout Iguanas. The iguana population has grown considerably (Perry and Mitchell 2003), but a disjunction between Stout Iguana and sheep distributions appears to remain (Anderson et al. 2010). Further, previous researchers have noted the existence of a browse line where sheep are common (G. Perry and C. Boal, pers. obs.). Nonetheless, no concerted effort has previously been made to compare the distributions of the iguana and sheep on the island. We therefore sought to quantify the distribution of both Stout Iguanas and feral sheep on Guana Island to determine if the two species' distributions are indeed non-overlapping. In addition, we sought to quantify the impacts of sheep browsing on island vegetation. Effects of sheep on the vegetation would provide a mechanistic explanation to support the hypothesis that feral sheep are negatively influencing iguana distributions.

Methods

Guana Island is a privately owned 340-ha island located less than 1 km north of Tortola, BVI (Fig. 2D). The island functions as a resort, although much of it is undeveloped, mostly free of human disturbance, and covered in dry tropical forest. Lazell (2005) provided a detailed overview of the island's natural history.

We subdivided Guana Island into six units (Fig. 2A) using ArcGIS 9.2 (ESRI 2006, Redlands, California). Four of the six units (Bigelow Beach, Grand Ghut, Harris Ghut, and Palm Ghut) are natural watersheds. The Guana Resort was defined as the area of the island receiving heavy human traffic. The remainder of the island was pooled into the Muskmellon Bay unit. We created a digital model of Guana Island consisting of 309 100 x 100-m grid cells (Fig. 3A). Steep terrain prevented us from sampling 168 of the 309 grid cells (Fig. 3B), and we do not consider these areas further. Based on field observations (see below), each grid cell was coded as having sheep, iguanas, neither, or both. The amount of overlap between sheep and iguanas was determined by comparing the number of grid cells with occurrence of both species to what would be expected (i.e., joint probability) from the portion of cells occupied by sheep and by iguanas.

We used seventeen motion sensitive cameras (Reconyx model RM30, Holmen, Wisconsin) to passively sample feral sheep and Stout Iguanas. In October 2010, within 10 m of the existing trail system of the island (Fig. 2B), we used a random number generator to determine possible camera placements. The number of camera locations placed in each of the six pre-determined units was determined by the relative size of each unit: Bigelow Beach, Grand Ghut, and Muskmellon Bay each received four cameras, Palm Ghut received three cameras, and Harris Ghut received two cameras (Fig. 2B). We did not place any cameras within the Guana Resort unit, as island staff informed us that the level of human traffic precludes the occurrence of sheep. Cameras were attached to trees 1 m above ground, orientated to provide the least

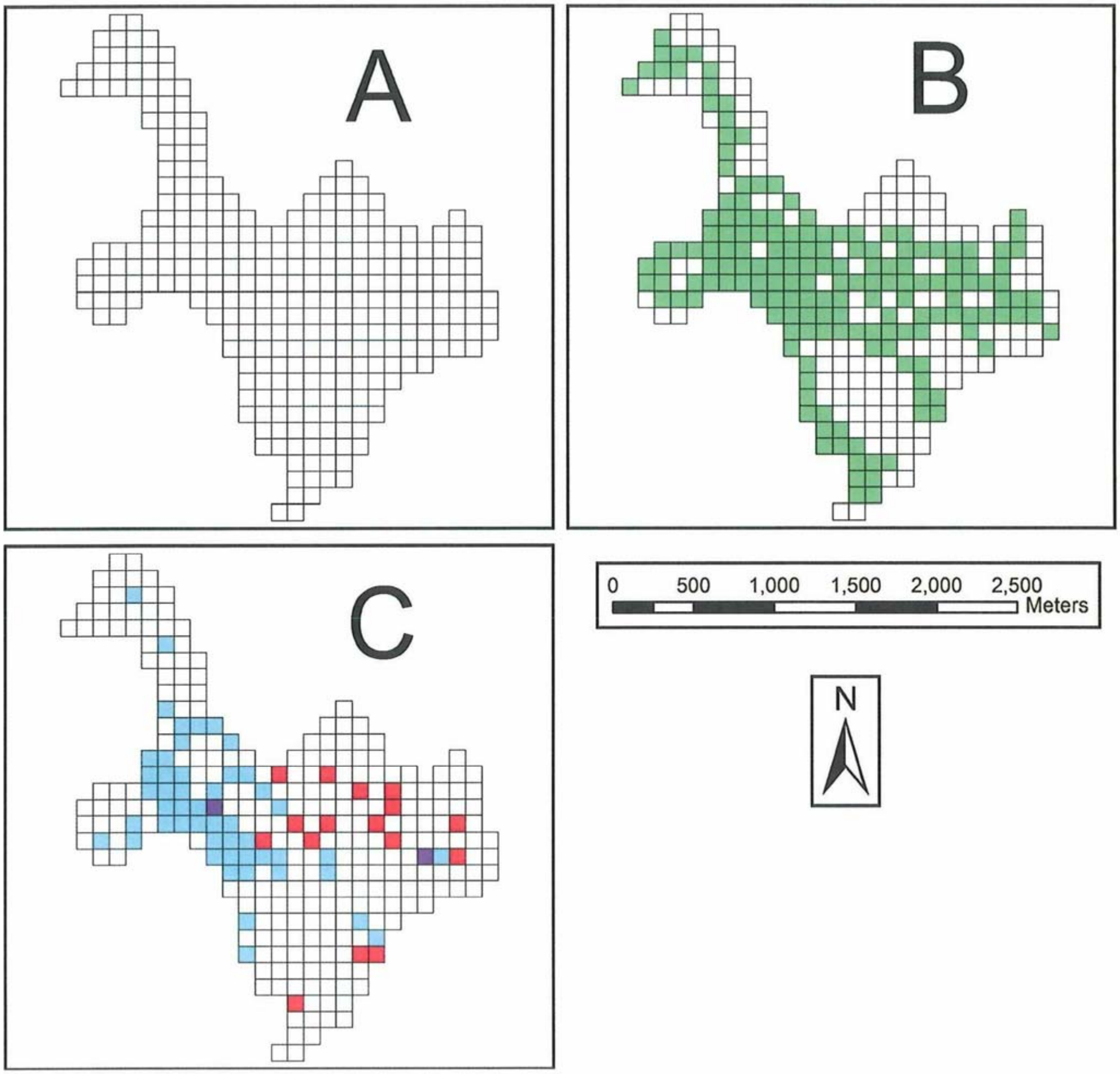

Fig. 3. (A) Subdivision of Guana Island into 309 100 x 100 m cells; (B) sampled cells (green); (C) sampled cells containing sheep (red), iguanas (blue), and sheep and iguanas (purple).

obstructed view, and programmed to record for three days. They then were moved to a new, pre-determined location. Additionally, we recorded the locations of chance encounters of sheep and iguanas during repeated hikes throughout the island. Indirect evidence of sheep presence, such as scat and sound, also were recorded. For iguana distributions, we incorporated all 159 previously recorded (2004–2009) locations (G. Perry, unpubl. data).

We assessed vegetation density by measuring vertical vegetative visual obstruction (hereafter, visual obstruction) at camera-trap locations. Using a 1-m Robel pole (Robel et al. 1970) segmented into 10-cm bands, we recorded visual obstruction at a distance of 1.8 m from the pole in each of the cardinal directions to the nearest 25%. To quantify ground cover, we took digital photographs of the forest floor at the pole location and 1.8 m from it in each of the cardinal directions. Photographs were taken from a height of 1 m. We analyzed photographs using SamplePoint (Booth et al. 2006), which superimposes 100 regularly spaced points on each photograph. At each point we recorded the cover type: Vegetation, litter, or open soil/rock. Wet conditions, such as those experienced by the BVI in the months just before

Table 2. Common plant species inside and outside of exclosures on Guana Island.

Species*	Common name**	Family	Growth habit***
Amyris elemifera	Sea Torchwood	Rutaceae	TR/SH
Bursera simaruba	Gumbo Limbo	Burseraceae	TR/SH
Capparis spp.	Caper	Capparaceae	TR/SH
Eugenia spp.	—	Myrtaceae	TR/SH
Guapira fragrans	Black Mampoo	Nyctaginaceae	TR/SH
Krugiodendron ferreum	Leadwood	Rhamnaceae	TR/SH
Macfadyena unguis-cati	Catclaw Vine	Bignoniaceae	VI
Opuntia repens	Roving Pricklypear	Cactaceae	SS/SH
Tragia volubilis	Fireman	Euphorbiaceae	VI/FB

* Taxonomy from Lazell (2005)

** Common names from USDA NRCS (2013)

*** Growth habit from USDA, NRCS (2013). FB = forb/herb, SH = shrub, SS = subshrub, TR = tree, VI = vine

our study (G. Perry, unpubl. data), can produce high plant densities regardless of browsing by feral sheep. Additionally, sheep are likely to be attracted to locations where vegetation is available. Thus, simple comparisons of locations with and without sheep could provide uninformative results. We therefore supplemented our findings with numbers obtained from two fenced sheep exclosures on the island and their paired, un-fenced control sites. These exclosures were established in 1997–98 and the abundance of nine plant species was measured following establishment and again in 2004 and 2010 (Table 2). They thus provide a long-term comparison of how sheep could be affecting the vegetation.

We used chi-square tests (Zar 2010) to examine differences between ground cover where sheep were present and absent. To examine differences in visual obstruction, we used *t*-tests to compare values recorded at each 10-cm band of the Robel pole in areas where sheep were present to the corresponding segment where sheep were absent. All statistical analyses were performed with R 2.13.0 (R Development Core Team 2011).

Results

Our cameras recorded sheep at five locations and a single iguana at one location (Fig. 2C). During hiking, we encountered sheep and iguanas (Figs. 4–6) at 12 and 53 other locations, respectively. Of the 168 grid cells sampled, we detected iguanas only in 28.6% (n = 48) of cells, we detected sheep only in 9.5% (n = 16) of cells, and we detected both iguanas and sheep in 1.2% (n = 2) of cells (Fig. 3C). Neither we nor previous researchers detected iguanas within the Grand Ghut watershed, which had the greatest number of sheep detections (Fig. 2C). The observed co-occurrence of iguanas and sheep was less than half the value expected based on the probabilities of sighting either species (2.7% or 5 cells).

At camera-trap locations, ground cover differed significantly between areas where sheep were and were not detected ($\chi^2 = 187.16$, df = 2, $p < 0.001$). The litter component of ground cover did not vary between areas where sheep were and were not detected, but the proportion of green vegetation and rock and soil did, with a greater percentage of green vegetation being observed in areas where sheep were detected (Table 1). Visual obstruction did not significantly differ between locations where sheep were and were not detected by cameras (Fig. 7; $p > 0.05$ in all cases).

Of the nine woody and herbaceous plants monitored in and outside of the exclosures, four species (*Amyris elmifolia,*

Fig. 4. Feral sheep were most often detected by camera traps at night and only on the eastern side of the island.

Fig. 5. Immature Stout Iguanas were most commonly encountered near the Guana Resort. This individual was marked with white paint to facilitate identification during a concurrent study. Photograph by Ben Skipper.

Bursera simarubra, Capparis spp., and *Tragia volubilis*) clearly increased in abundance when sheep were excluded (Fig. 8). Two other species (*Krugiodendron ferreum* and *Macfadyena unguis-cacti*) displayed stronger increases in abundance inside exclosures compared to outside, although some overlap in standard deviations exists (Fig. 8). *Eugenia* spp. and *Guapira fragrans* abundance seemed less affected by the exclosures, although trends show both increasing inside the exclosures (Fig. 8). One species, *Opuntia repens*, remained approximately stable over the 10-year observation period inside the exclosures, but declined sharply outside of exclosures. No monitored species declined in the exclosures when compared to control plots.

Discussion

Since their re-introduction almost 30 years ago, Stout Iguanas have established a self-sustaining population on Guana Island (Goodyear and Lazell 1994, Perry and Mitchell 2003, Anderson et al. 2010). However, prior researchers (Goodyear and Lazell 1994, Anderson et al. 2010) hypothesized that competition with feral sheep for available browse may limit iguana distribution on the island. Our data support this hypothesis. Iguanas and sheep are much less likely to co-occur than would be expected, suggesting that occurrence of sheep in some of the eastern portions of the island precludes iguana presence. We did encounter several iguanas (both adults and juveniles) at the eastern end of the island, where they had not previously been seen. We believe this represents a wider search effort, but it could represent an expansion of the population compared to the surveys of Goodyear and Lazell (1994) and Anderson et al. (2010).

A possible explanation for the lack of overlap between iguanas and sheep, consistent with Mitchell's (1999) observations on Anegada and studies of other species in the genus

Fig. 6. Large, mature Stout Iguanas were rarely encountered far from the Guana Resort. Photograph by Rebecca Perkins.

Cyclura (Lemm and Alberts 2012), is reduction in available forage for iguanas due to browsing by feral sheep. Although previous researchers (W. Anderson, pers. comm.) have observed a prominent browse line in areas occupied by sheep, we detected no difference in visual obstruction between areas with and without sheep detections. Possibly, the 1.8-m distance from which we recorded visual obstruction was insufficient to assess accurately the effects of browsing. More importantly, perhaps, Guana Island received above-average precipitation in the months before our study (G. Perry, pers. obs.), which could have allowed the vegetation to recover from browsing pressure. Guana Island experienced drought in 2009, which could have rendered the effects of browsing more pronounced, whereas in 2010, high rainfall may have rendered signs of browsing unobservable. Consistent with that interpretation, browse damage was obvious again in 2011, another dry year (G. Perry, pers. comm.).

We did not find differences in visual obstruction between camera-trap locations where sheep were and were not documented. Somewhat counterintuitive is that camera-trap locations where sheep were detected had a greater proportion of green vegetation than those where sheep were not detected. However, such differences might not be unexpected for two reasons. First, our study was conducted during a wet spell, when vegetation is relatively lush and regrowth is rapid. Second, sheep are likely to be attracted to available forage or avoid areas denuded of vegetation, and thus may preferentially be found at locations with more remaining vegetation. Our comparisons of sheep exclosures to un-enclosed control

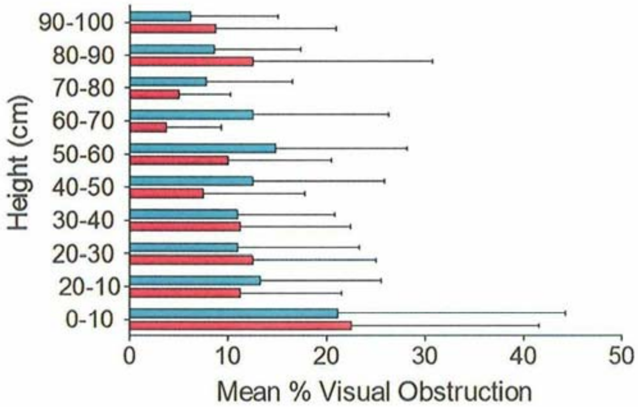

Fig. 7. Mean (± SD) percent visual obstruction measured of vegetation at camera trap locations, red bars indicate camera trap locations where sheep were detected; blue bars indicate areas where sheep were not detected.

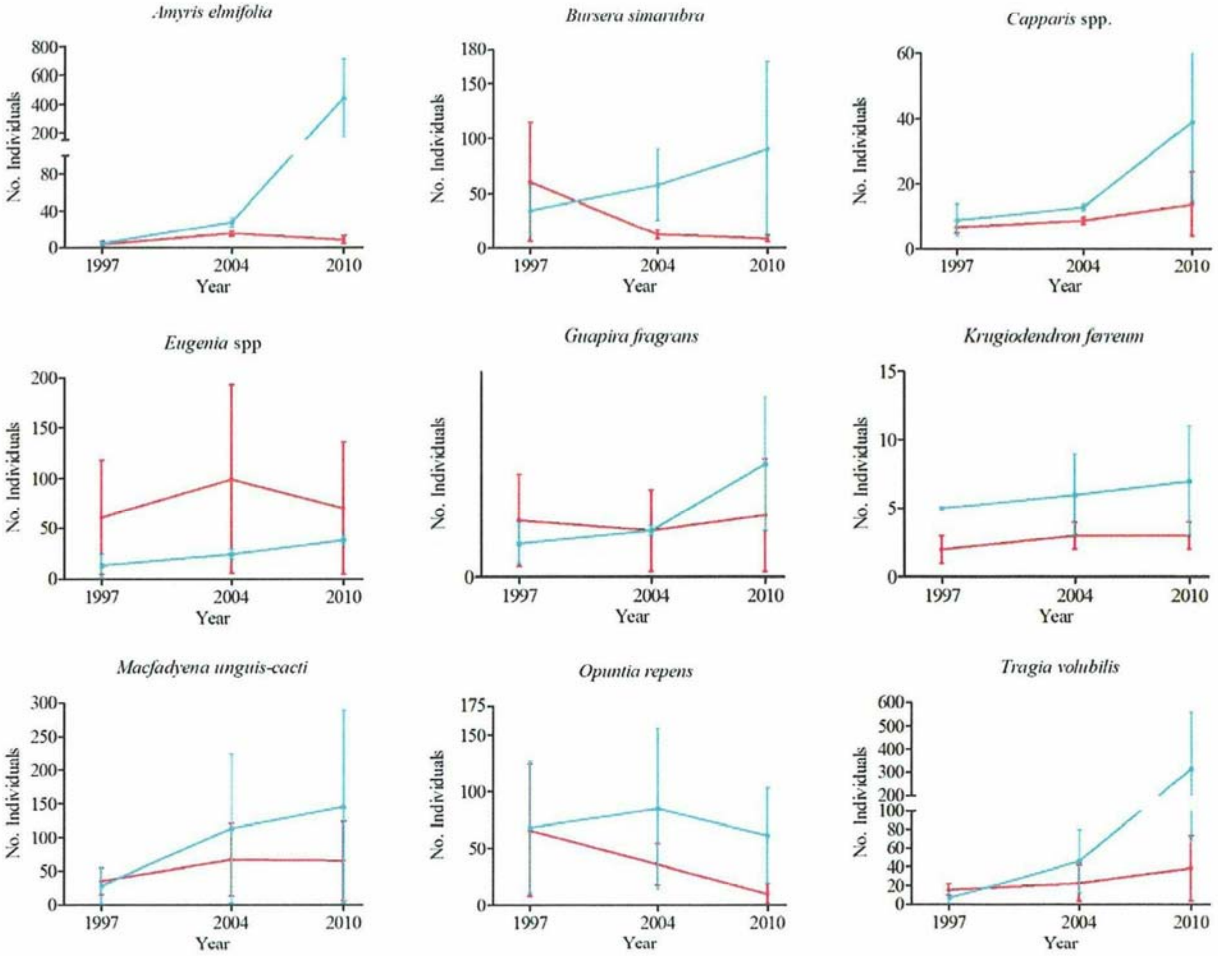

Fig. 8. Mean (± SD) number of individuals of nine plant species monitored from 1997/1998 to 2010. Blue lines represent plants within exclosures. Red lines represent plants outside of exclosures.

plots provided further evidence. We saw marked increases in four plant species, weaker increasing trends in another four species, and no declines inside exclosures.

Our study supports previous suspicions (Goodyear and Lazell 1994, Anderson et al. 2010) that feral sheep limit the distribution of Stout Iguanas on Guana Island. This is a source of concern, as the Guana population is one of the largest populations of the species and its survival may be critical to the long-term existence of *C. pinguis*. Although our short-term assessment of vegetation (assessments at camera-trap locations) did not reveal clear differences in vegetative structure in areas where sheep were and were not detected, assessments at the long-term exclosures did indicate that exclusion of sheep can have a positive effect on the vegetative community. Further exclusion of feral sheep through removal would likely be beneficial to Stout Iguanas by providing an opportunity for more complete expansion of the current distribution into the eastern half of the island. Sheep removal also could be of value to the island's vegetation, some of which is of significant conservation value (Procter and Fleming 1999, Lazell 2005). Other species that depend on the vegetation, such as invertebrates and birds, also could be affected positively by such management practices.

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30

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Herpetological Conservation and Biology

METHODOLOGICAL AND ECOLOGICAL FACTORS AFFECTING POPULATION DENSITY ESTIMATES IN THE DWARF GECKO *SPHAERODACTYLUS MACROLEPIS*

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Abstract.— Cryptic species such as the minute, leaf-litter dwelling *Sphaerodactylus macrolepis*, are notoriously difficult to accurately sample. We compared the efficacy of sampling techniques commonly used for population estimation in order to address three main questions: (1) How do density estimates of *S. macrolepis* obtained using transect searches compare to those from small plot clearing techniques? (2) How do density estimates from small-scale sampling techniques compare with those obtained from large total removal plots previously conducted on the same island? And (3) do gecko densities vary as a function of habitat type? Small plots and less time-consuming transects produced estimates of gecko densities (0.22 and 0.20 geckos m^2, respectively) that were statistically indistinguishable. Unsurprisingly, both provided much lower density estimates than those previously reported from large-scale total removal plots (5.28

geckos m^2). Gecko densities were significantly positively correlated with leaf litter depth and varied among vegetation types. The highest recorded densities were obtained in beach strand vegetation, and intermediate numbers were recorded in dry, ghut, and palm forests, and in some orchard areas. Sites lacking leaf litter, such as pastures and sandy beaches, were devoid of geckos. As land conversion and development continue throughout the Caribbean and native forest is converted to ecosystems that offer less leaf litter, *S. macrolepis* populations may be impacted.

Key Words.—Caribbean; density; Dwarf Gecko; removal plots; sampling methodology; *Sphaerodactylus macrolepis*; techniques comparison; transects

INTRODUCTION

Accurately estimating the abundance and density of free-ranging organisms is a fundamental but difficult component of ecological research. Numerous methods have been developed to derive such estimations (Heyer et al. 1994; Braun 2005). The choice of sampling method varies among target organisms and sampled environment, and is often influenced by practical considerations. Methods that provide counts of all individuals in the sampling area are the most statistically defensible, but are typically time-, labor-, and cost-intensive. Alternative methods that measure relative abundance and density suffer from inherent biases and limitations (Petranka and Murray 2001), but are nonetheless commonly used because they are easier to implement.

Geckos of the genus *Sphaerodactylus* are among the smallest living terrestrial vertebrates (MacLean 1985; Hedges and Thomas 2001). They are cryptic leaf-litter dwellers, and although they are common throughout the Caribbean, they are often difficult to study because of their secretive lifestyles (Rodda et al. 2001). Abundance estimates of *Sphaerodactylus* are most often conducted via either transect searches (typically applied to questions of presence/absence or relative abundances; e.g., Hensley et al. 2004; Bentz et al. 2011) or small-plot sampling techniques (e.g. Nava et al. 2001). However, few quantitative data exist comparing the efficacy of these two techniques to each other, or to actual densities derived from the more defensible but time-consuming large-scale total removal plots. Thus, a primary question for this study was (1) how do density estimates of *S. macrolepis* populations obtained using transect searches and small plot clearing techniques compare?

We conducted our study on Guana Island, British Virgin Islands. The biotic community of Guana has been the subject of numerous studies (Lazell 2005), including a total removal plot project that measured the absolute densities of terrestrial reptiles (Rodda et al. 2001). The highlight of this study, conducted in two habitat types, was the discovery that *S. macrolepis* (Fig. 1) reached the densest populations ever measured for a terrestrial vertebrate. The existence of those data allowed us to also ask (2) how density estimates from our small-scale sampling techniques (transect searches and small-plot samples) compare with those obtained from large total removal plots previously conducted on the same island. Finally, with the methodological issue settled, we also asked (3) how *S. macrolepis* densities vary as a function of vegetative community type and physical site characteristics?

MATERIAL AND METHODS

Study site.— Our study was conducted on Guana, a 340 ha privately owned island in the British Virgin Islands that is managed as both an exclusive Caribbean resort and as a wildlife sanctuary (Lazell 1996, 2005). The interest of the owners in conservation and their desire to maintain guest privacy has spared much of Guana from the intense land conversion that is common throughout the West Indies (Ricklefs and Bermingham 2008). Development on the island has been sparse and primarily limited to three small areas utilized by the resort, covering < 5% of total land area. Narrow and mostly unpaved trails allow foot access to various parts of the island.

Vegetative communities.— We divided Guana into seven vegetation community types: dry forest, ghut (i.e., mesic) forest, palm forest, beach strand, sandy beaches, human-cultivated grassy vegetation, and human-cultivated orchard vegetation. The island is predominantly covered by tropical dry forest, which stretches from near sea level to the peak of the island at 246 m and is characterized by thin rocky soils, moderately open canopies, and dry understories with shallow leaf litter layers (Lazell 2005; Thomas and Devine 2005). Deciduous trees such as acacia species, elephant trees (*Pisonia subcordata*), and gumbo-limbos (*Bursera simaruba*) are common overstory plants, as are large dildo cacti (*Pilosocereus royenii*). The understory generally contains a community of spiny shrubs, agave plants, and small cacti, but the density of this layer varies between locations (Rodda et al. 2001; Lazell 2005). Rocky ravines, locally known as ghuts, channel runoff during the wet seasons and hold more hydrophilic species, denser canopy covers, and heavier concentrations of undergrowth. The forest floor near the ghuts is more heavily shaded and moister than in standard dry forest, so succulents such as cacti and agaves are generally replaced by more herbaceous and shrubby growth. The ground is typically quite rocky and leaf litter depth is highly variable. Palm forest is limited to the north side of the island and is characterized by the presence of *Sabal causiarum*, an indigenous fan palm. Guana's final forest community, beach strand, is found in flat coastal areas near sea level and forms the buffer between the coastline beaches and the interior of the island. The vegetation in this community is typically dominated by sea grape (*Coccoloba uvifera*). The density of the canopy allows little light and wind penetration, creating relatively moist understory conditions with dense leaf-litter (Rodda et al. 2001; Lazell 2005; Thomas and Devine 2005). In addition to the four forest types, the island also has sandy beaches and human dominated sites. Beaches were defined as the typically < 20 m wide area between the waterline and the beginning of the beach strand vegetation. Human-cultivated vegetation types were subdivided into mowed grassy areas and cultivated orchards.

Sampling methods.—During October 2007 we sampled 187 sites located along the Guana island trail systems. Each vegetation community was sampled in proportion to its frequency of occurrence on the island, as estimated from previously developed GIS layers. Sampling sites were placed at least 20 m apart to avoid pseudoreplication.

The first 109 sites were used for comparisons of small-scale sampling methods. Each site was sampled using two 0.25 m^2 plots and one linear transect. Quadrats (41 cm x 61 cm frames) were placed 3 m away from the edge of the trail, on alternate sides, and 10 m apart. To prevent geckos from escaping from our quadrats, we firmly and rapidly pressed a reinforced frame into the soil upon arrival, recording any geckos escaping under the frame during the placement process. In each quadrat we measured leaf litter depth approximately 10 cm in from each corner of the frame, and then averaged the results to derive mean leaf litter depth for the plot. We then carefully removed all the leaf litter and other items within the quadrat, and recorded all encountered geckos. We also recorded GPS location (later used to obtain elevation from a topographical GIS map); the type of trail (paved road, unpaved vehicular road, or a pedestrian path of high, medium, or low use); slope (taken with a compass-mounted clinometer); aspect (estimated by compass bearing); and canopy cover (using a spherical concave densitometer). Transects (10 m long x 1 m wide) were parallel to and located approximately 1 m farther off the trail than the plots, to avoid any disturbance caused by the plot sampling process. A single individual counted all geckos moving in the area within 50 cm of either side of the transect, shuffling his or her feet in the leaf litter in an effort to disturb all geckos present, as done in other studies (e.g., Hensley et al. 2004; Bentz et al. 2011). Occasionally, the rugged terrain made surveying the full 10 m impossible or unsafe, and in such instances a shorter transect (always > 3m) was surveyed. Leaf litter depth, slope, aspect, and canopy cover measures were taken at four equidistant points and averaged across the transect. From these data we calculated gecko density for comparison to quadrats both within and across vegetation community types.

Transects were found in initial comparisons to be less-time consuming and to provide comparable gecko densities to quadrats. We therefore used this technique to sample 78 additional sites during the second portion of the study. The density estimates derived from the original 109 transects were combined with the addition 78 samples and estimates from all 187 transects were used to compare gecko density as a function of vegetative community and physical site characteristics.

Statistical methods.— We used paired *t*-tests to compare the mean of the densities of *S. macrolepis* obtained in the two quadrats at each location to those estimated from the matched transect. To explore the possibility of habitat-related differences in method efficacy, we conducted a similar analysis on the subset from each vegetation type. We used an analysis of variance (ANOVA) to examine the relationship between *S. macrolepis* density and site characteristics such as elevation, leaf litter depth, canopy cover, slope, aspect and habitat/vegetation type. If the ANOVA identified statistically significant differences ($P < 0.05$), we used Fisher's LSD procedure for post-hoc comparisons. We conducted all statistical analyses in SPSS version 16.0 (SPSS Inc., Chicago, Illinois, USA) with an alpha level of 0.05.

RESULTS

Methods Comparisons.—We cleared 218 small removal plots (total area: 54.5 m^2), walked 109 matched transects (total area surveyed: 1079 m^2), and observed a total of 227 geckos during the course of our methods comparison study. Of the 227 geckos observed, 12 were recovered from within plot frames and the remaining 215 were seen during visual transect surveys. Small-scale plot clearing and transect walking provided statistically indistinguishable estimators of gecko density in each habitat (Fig. 2) and in all habitats combined (0.22 ± 0.06 and 0.20 ± 0.03 geckos m^2 respectively; $P > 0.05$). However, estimates obtained using transect methodology had lower variability and were also more time efficient, requiring approximately one to two minutes to complete, rather than the five to 10 minutes needed per quadrat.

Ecological Determinants of S. macrolepis Density.—We used data from the entire 187 transects sampled to evaluate the ecological determinants of gecko density. Of the environmental characteristics measured at each site, only vegetation type (ANOVA; $F = 3.843$, df = 6, $P = 0.001$) and leaf litter depth ($F = 21.441$, df = 1, $P < 0.001$) were significantly related to *S. macrolepis* population density (Fig. 3). Combined, these two factors were highly predictive of gecko density, accounting for approximately 40% of the total variation in population density estimates ($R^2 = 0.43$, df =179, $P < 0.0001$). Of the six major vegetation types represented on the island, the highest density of geckos was found within the *Cocoloba*-dominated beach strand, a habitat characterized by shade, deeper leaf litter, and presumably a moister environment. We found intermediate gecko densities in dry forest, ghut forest, and palm forest habitats, but also in human-cultivated orchard. The orchard was a mix of open grassy paths and planted trees, and leaf litter depth varied greatly. In high litter areas, we recorded some of the highest gecko densities on the island. However, the landscaped areas outside of the litter patches were largely devoid of geckos, thus reducing the overall habitat average. Although geckos do use grassy edge habitats and will move through grass-dominated areas between more appropriate habitat patches (Robert Powell, pers. comm.), no geckos were seen in these grassy areas during the course of this study, nor were there any sightings of geckos in the beach habitat.

DISCUSSION

Methods Comparisons.— Our study highlights the importance of understanding the strengths and limitations of methodologies commonly used in the study of wildlife density and habitat associations. The estimates of *S. macrolepis* density we obtained from small scale plots and transects were very similar, indicating that both are similarly appropriate in terms of data quality. Since a transect takes about 20% as long to complete as a quadrat, linear transects offer a more cost-, labor-, and time-effective method for sampling the relative abundance of *S. macrolepis*. Most likely, the method is also appropriate for additional species of *Sphaerodactylus* and similar leaf-litter dwellers.

The results we obtained were consistent across methods, but both methods have limitations. Transects provide estimates that ignore the unknown detectability of geckos in the area surveyed, and small quadrats may allow an unknown but potentially larger fraction of the geckos to escape before the barrier is placed down. Large removal plots offer a more accurate method for assessing the population density of organisms. Using 10 x 10 m total removal plots, Rodda et al. (2001) found an average of 1.34 geckos m^2 in their dry forests sites on Guana Island and an average of 5.28 geckos m^2 in their beach strand sites. These numbers are an order of magnitude greater than what we found in the same habitats. As these studies were conducted a decade apart, *S. macrolepis* densities may have changed substantively, perhaps as a result of differences in ambient conditions. However, this seems unlikely to be the entire explanation, especially in light of the differences in employed methodologies. Rodda et al. (2001) installed more substantial barriers and used a 10 X 10 m design which greatly decreases edge effects, compared to our 0.25 m^2 plots. Transects are perhaps even more prone to un-recorded lizard escapes prior to the start of counting, but both of our methods, which are designed for portability, limited man-power, and rapid results, are prone to detectability problems minimized by the Rodda et al. (2001) design. Despite the lower cost and time investment required by our study, the overall area we sampled was greater than that sampled by Rodda et al. (2001). Unfortunately, the inherent biases and limitations of our techniques make the findings less rigorous. We believe that findings from studies relying on the methodologies we evaluated should be construed to represent relative, as opposed to actual, population densities. If the vegetative communities sampled differ too much in detectability, even that level of inference may not be defensible. Further study comparing the time efficient methods we evaluated with more rigorous methods such as those used by Rodda et al. (2001) would provide additional insights. Regrettably, the distance-sampling approach increasingly used in wildlife studies cannot be used in this case because one of the most basic assumptions – that all animals on the transect line are detected (e.g., Buckland et al. 1993) is obviously not met.

Ecological Determinants of Density.— Although our data can most likely not be used to establish absolute population density values, we believe that our protocol and the nature of the habitats we studied make inferences about relative densities valid. Our *S. macrolepis* population density estimates were only significantly associated with vegetation type and leaf litter depth. These results are consistent with several studies that found vegetation and litter depth to be important to *Sphaerodactylus* species (e.g., Genet et al. 2001; Lopez-Ortiz and Lewis 2004; Steinberg et al. 2007). Our findings support those of Rodda et al. (2001), who found the population density of *S. macrolepis* in Guana's beach strand environment to be higher than in other habitats, and those of MacLean and Holt (1979), who reported similar observations from St. Croix in the US Virgin Islands. Deep leaf litter likely offers a predictably moist microhabitat to this minute species, something that may be absent in many places in the British Virgin Islands (Perry et al. 1999, 2000).

Contrary to our expectation, the estimated population density of *S. macrolepis* was not correlated with canopy cover. We measured 100% canopy cover in most dry forest and beach strand plots, although dry forest generally has a more open canopy, greater light penetration, and less leaf litter, than the more densely-canopied beach strand (Lazell 2005). Overestimation of canopy cover is a known problem with spherical concave densitometers in forested habitats (Cook et al. 1995), and may have led to this counter-intuitive finding.

Conservation Implications.— Tropical dry forest is one of the world's most rapidly disappearing habitats (Janzen 1988). Of about 470,000 km^2 of forest remaining in the Caribbean a decade ago, less than 550 km^2 was dry tropical forest (FAO 1993). In Puerto Rico, about 80% of forest cover had been lost by 1900. Of the remaining forest area, only a tiny fraction is dry forest, most of it unprotected (Harcourt and Sayer 1996). About 97% of remaining tropical dry forest is at risk from human activities, resulting in calls for dry forest remnants to be given high conservation priority (Miles et al. 2006). Unfortunately, poor legal protection and increased fragmentation of dry tropical forests puts them at high risk from human disturbance and ongoing deforestation (Brooks et al. 2002; Portillo-Quintero and Sánchez-Azofeifa 2010). As land conversion, urbanization, and de-forestation continue throughout the West Indies, it becomes increasingly important to understand the potential impacts of human activities on native wildlife (Genet et al. 2001; Germano et al. 2003).

The rapid rate of habitat loss and the ongoing arrival of invasive species in the Caribbean (Powell et al. 2011) are likely to lead to extensive herpetofaunal declines and extinctions unless native species can utilize human-dominated refugia. Although some members of the Caribbean herpetofauna are able to utilize human-altered habitats that simulate facets of the native environment (Henderson and Powell 2001), many cannot. We found high *S. macrolepis* densities in some human-cultivated vegetation, such as the island's orchard, but not others, such as mowed grassy areas. Fortunately, *S. macrolepis* is a common species found on many islands (Perry and Gerber 2006, 2011). Even though declines are likely as new anthropogenic developments take place, the outlook for the species remains good. However, other congeners, such as *S. parthenopion* in the BVI (Perry and Gerber 2006) and multiple species throughout the Caribbean (Corke 1992), have limited distributions and are already believed to be at risk. The study of which species can coexist with humans and how such coexistence can be enhanced – essentially, urban ecology – thus has great urgency in this region.

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FIGURES

FIGURE 1. *Sphaerodactylus macrolepis* shown in *Coccoloba* leaf litter and in hand for scale

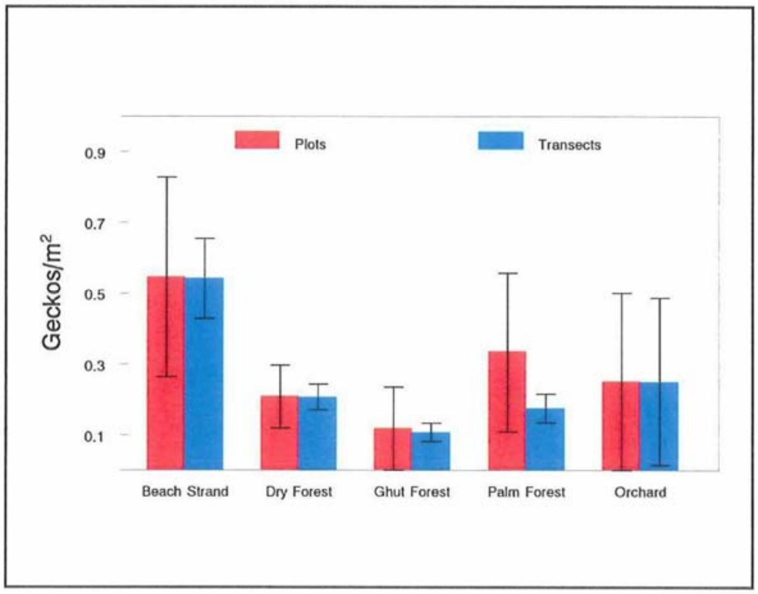

FIGURE 2. Mean number and SE of *S. macrolepis* m^2 for each sampling technique in the major forest types of Guana Island. The difference was not statistically significant in any forest type.

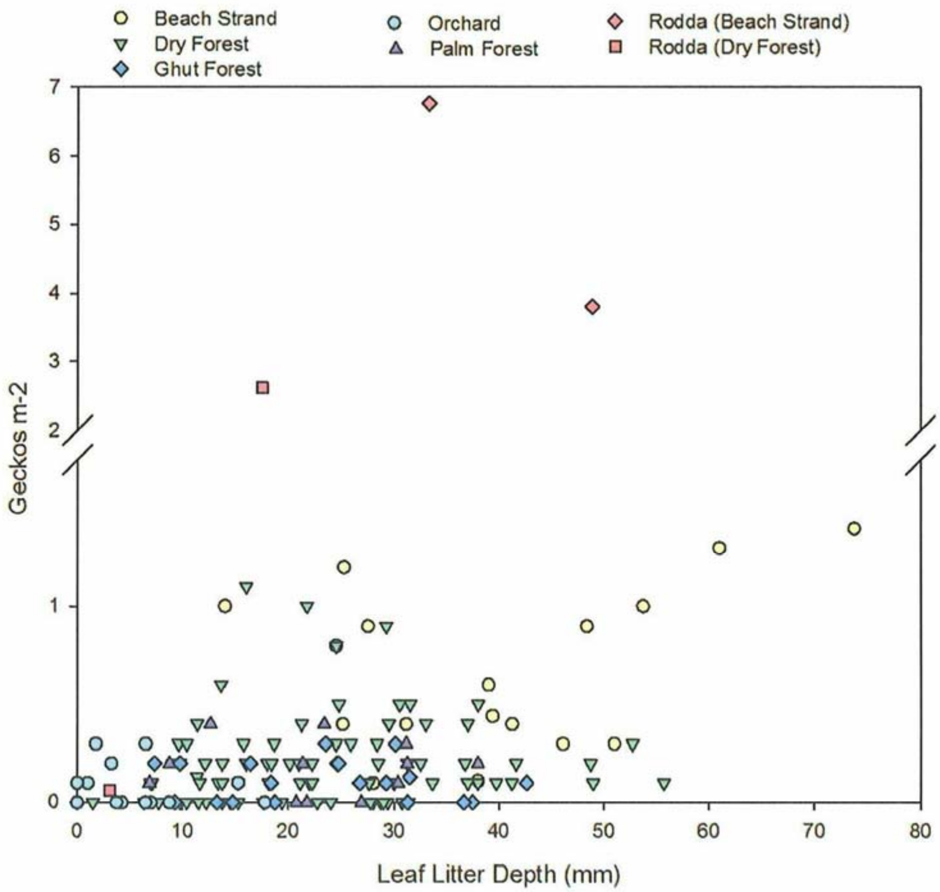

FIGURE 3. Correlation between leaf litter depth and the number of geckos per m^2 for each relevant vegetation community on Guana Island compared with the gecko density estimates of Rodda et al. (2001).

Herpetological Conservation and Biology

THERMAL BIOLOGY AND MICROHABITAT USE IN PUERTO RICAN EYESPOT GECKOS (*SPHAERODACTYLUS MACROLEPIS*)

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Abstract.—**The thermal environment of ectotherms affects every aspect of their life history and many ectotherms must keep their body within an optimal temperature range through some form of thermoregulation. Because of the small size of geckos in the genus *Sphaerodactylus*, they have been assumed to be thermoconformers, but their size also renders them extremely susceptible to overheating and desiccation. We used a thermal gradient to find the preferred temperature of *S. macrolepis* in the lab and thermal imaging and data loggers to explore their thermal ecology and microhabitat selection in the field. Our data suggest that all of the microhabitats available within our study sites are outside of the preferred temperature of *S. macrolepis* during the hottest parts of the day. The layer of leaf litter closest to the ground had the highest humidity and lowest, most stable temperatures. However, geckos ranged into a nearby grassy field where temperatures and humidity were sub-optimal. Although these geckos quickly conform to the temperature of**

their microhabitat, they appear to adjust activity periods to coincide with optimal environmental temperatures.

Key words.—activity time; body temperature; humidity; Puerto Rican Eyespot Gecko; rapid heat exchange; *Sphaerodactylus macrolepis*; thermal environment; thermal imaging

INTRODUCTION

Every aspect of the life history of ectothermic animals is directly affected by body temperature (Stevenson et al. 1985; Shine et al. 1997). Consequently, the ability to keep body temperatures within an optimal range is essential for survival (Gans and Pough 1982). Ectothermic reptiles often accomplish this through behavioral thermoregulation. Such behaviors include changes in activity time (e.g., Huey and Pianka 1977), shuttling between sun and shade (Cowles and Bogert 1944), and changes in posture (e.g. Muth 1977). However, some ectotherms are thermoconformers and exhibit few thermoregulatory behaviors.

Body size directly affects the ability of an ectotherm to thermoregulate. Heat transfer theory predicts that larger animals will exhibit greater differences between body and environmental temperatures than smaller animals and that this is largely attributable to thermal inertia (Muth 1977). The effects of convective heat loss also are much greater for smaller organisms as a result of their small surface area to volume ratio, making them more likely to be thermoconformers (Stevenson 1985).

Puerto Rican Eyespot Geckos (*Sphaerodactylus macrolepis*; Fig. 1) are small tropical sphaerodactylids (~34–35 mm SVL; Rice et al. 2005) distributed across the Puerto Rican Bank (Schwartz and Henderson 1991). Because of their small size, sphaerodactyls exhibit high surface area to volume ratios and are highly susceptible to desiccation (Leclair 1978; Snyder 1979; Nava 2006; Steinberg et al. 2007). Snyder (1975) determined that 94% of total water loss in *S. macrolepis* was cutaneous. Because of this high susceptibility to desiccation, sphaerodactyls frequently are restricted to cool, moist microhabitats (Steinberg et al. 2007).

Maintaining relatively low body temperatures would appear to be important for sphaerodactyls to avoid overheating or excessive desiccation. However, largely because of their diminutive size and the resulting difficulty in using conventional field methods to obtain body temperatures, no studies have determined whether these geckos are thermoregulators or thermoconformers. In this study, we used thermal imaging technology to test the hypothesis that their small size leaves them no alternative but to be thermoconformers. We also determined if these small ectotherms use microhabitat selection and/or adjust activity times to avoid suboptimal environmental temperatures, and how their size affects their ability to exchange heat rapidly with the environment.

MATERIALS AND METHODS

Study Sites.—We conducted this study on Guana Island, British Virgin Islands, from 13–18 October 2013. Two primary study sites (ca. 3 x 3 m) were located near coordinates 18°28'31.86"N 64°34'33.32"W (WGS84) in coastal seagrape (*Coccoloba uvifera*) between White Beach and a mowed grassy area (Fig. 2). Both sites were characterized by shaded *Coccoloba* litter on a sandy substrate. In addition, we regularly monitored a 180-m transect (18°28'31.86"N 64°34'33.32"W to 18°28'26.45"N 64°34'27.52"W) along the grassy side of the forested area.

Preferred Temperatures.—We determined preferred temperatures in an air-conditioned laboratory on 9–11 October by placing 14 (seven male and seven female) *Sphaerodactylus* *macrolepis* captured on Guana Island in October 2012 individually into a thermal gradient with a temperature range of 21.1–38.9 °C. Because some sphaerodactyls tend to avoid bright lights, we placed a dark-purple filtered heat light over and a heating pad under a 20-gallon aquarium with a uniformly dry sand substrate. We conducted all trials between 1230 and 1830, recorded thermal images of each individual after 45 min, and changed the sand substrate after each trial to avoid the possible effects of scent marking.

Thermal Environment.—We placed 14 ibuttons (DS1922L and DS 1923-Hygrochron; Embedded Data Systems, Lawrenceburg, Kentucky, USA) at varying depths in the leaf litter at both sites and in different microhabitats representing varying degrees of shade and sun exposure along the transect. Microhabitats included the top, middle, and bottom of leaf litter, in dense grass on a dirt substrate, on open sand, in thin grass on a sand substrate, and under leaves on grass. Ibuttons were programmed to record temperature data to 0.5 °C every half an hour. We collected temperature data for five days at the study sites and temperature for one full day and two half days along the transect. We also collected humidity data to 0.001% RH every ten minutes for one full day and two half days in the two sites and along the transect for six ecologically relevant microhabitats including the top and bottom of leaf litter, dense grass on a dirt substrate, open sand, thin grass on a sand substrate, and under leaves on grass.

Activity Periods.—On the assumption that active geckos would be visible on the surface of the litter, we counted the number of lizards observed on the surface during five minute periods on 15 October at 0700, 0900, 1100, 1330, 1530, and 1730.

Observations of lizards in the grassy area at varying distances from the forest edge triggered questions of how far away from shade they would move and at what times they would do so. We recorded the distance of lizards from the forest edge at 0730, 0930, 1130, 1400, 1600, and 1800 on 15 October and opportunistically on the previous and following days. We measured distances in centimeters from where a gecko was first sighted in the short grass to the closest shaded site with elevated vegetation (i.e., trees or shrubs). For each sighting, we recorded time of day, degree of insolation, sex of the lizard, and the type (dense grass, sand, sand/grass, and grass/leaves) and temperature of the substrate. When possible, we recorded thermal images of the gecko.

Body Temperatures.—We used a TiR FLUKE thermal imaging camera (Fluke Corp., Everett, Washington, USA) to record thermal images of geckos and substrates and used "SmartView" thermal imaging software (Fluke Corp., Everett, Washington, USA) to analyze them. We recorded date, time, location, and sex of the gecko for each image.

Heating and Cooling Rates.—We generated heating and cooling curves at ambient temperatures on an artificial substrate (a large plastic container) on 17–18 October. We placed three adult geckos under a heat lamp for one minute until they reached temperatures of 34–35 °C and three juveniles for 30–40 sec until they reached temperatures of 31–35 °C. We also placed six adult and three juvenile geckos in a refrigerator for 3–4 min until they reached temperatures of 21–22 °C. We subsequently monitored the temperatures of each gecko on a substrate at ambient temperature using the FLUKE thermal imaging camera until the gecko was no longer visible on the camera screen (i.e., it had reached ambient temperature). We recorded sex, SVL (the distance from the tip of the snout to the vent in mm), time, temperature, time elapsed until an individual reached ambient temperature, and then marked each gecko to assure that no individual was subjected to heating or cooling more than once.

Statistical Analyses.—We preformed Shapiro-Wilk tests to determine whether data were normally distributed. We used student's t-tests, χ^2 analyses, linear regression, and ANOVA to test our hypotheses on normally distributed data and a Mann-Whitney U-test on data that were not normally distributed. We analyzed all data in R statistical programming language (R version 3.0.2; R Development Core Team, www.r-project.org/). All means are presented ± 1 SD. For all statistical tests, $\alpha = 0.05$.

RESULTS

Body Temperatures.—Mean preferred temperature for *Sphaerodactylus macrolepis* in the lab was 25.34 ± 2.65 °C, with that of males (24.91 ± 2.50 °C) slightly but not significantly lower than that of females (25.77 ± 2.93 °C; two sample *t*-test; $t = -0.588$, df = 12, $P = 0.567$). However, geckos in the field conformed to temperatures in the leaf litter that were outside their preferred temperature range for most daylight hours (Fig. 3; Fig. 4).

Thermal Environment.—All microhabitats available to geckos in leaf litter at our study sites and along our transect were outside the preferred temperature at some times of day (Fig. 5). Even the deepest layer of leaf litter was warmer than preferred temperature between 1200 and 1730. All microhabitats, however, were within the preferred range between 2300 and 0800 (Fig. 5). Humidity was significantly different across all six of the tested microhabitats on 17 October (ANOVA; $F = 65.38$, $P < 0.0001$). Humidity was both highest and most stable under the leaf litter throughout the day (mean 97.92 ± 0.98% RH). Humidity on top of the leaf litter had the lowest average (78.39 ± 9.31% RH), and humidity on sand was the most variable (79.67 ± 21.30% RH). Between 2100 and 0800, humidity remained high and stable across all microhabitats (on litter: 86.23 ± 2.41% RH, under litter: 98.48 ± 0.81% RH). However, during the day, between 0800 and 2100, it became much more variable (sand: 64.68 ± 18.62% RH; under litter: 97.43 ± 0.87% RH).

Activity Time.—Unless disturbed, geckos were not active on the surface of leaf litter during the day. Therefore, we assessed the number of geckos found in clumps of grass or under leaves in the field along the transect throughout the day. Gecko activity away from deep shade was low (essentially zero on sunny days) until 1800 when it increased dramatically (Fig. 6). Juveniles were more likely than adults to venture away from shade during the early morning and evening (Fig. 6), but differences were not significant. Distances from the shaded vegetation throughout the day exhibited a small spike beginning around 0700 and a larger increase in the evening beginning at 1800, the latter corresponding to the increase in the total number of geckos found in the grassy area (Fig. 7). Distances of juveniles and adults from shaded vegetation did not differ significantly (Mann-Whitney U; $W = 307.5$, $P = 0.106$).

Microhabitat Selection.—Active microhabitat selection was evident along the transect where geckos had to choose between dense grass, sand, sand/grass, and grass/leaves ($\chi^2 = 12.35$, $P = 0.006$). Geckos most frequently chose dense grass and grass covering sand. All but one gecko were in shade or observed under cloudy conditions or before the sun rose above a hill to the east and sunlight reached the area. Microhabitats utilized by juveniles and adults differed significantly along the transect, with adults more frequently in dense grass ($\chi^2 = 7.20$, $P = 0.007$) and juveniles more frequently in grass/sand ($\chi^2 = 6.23$, $P = 0.013$). Although grass/sand was significantly warmer than dense grass (paired *t*-test; $t = -14.86$, df = 143, $P < 0.00001$), grass/sand had significantly higher humidity throughout the day (paired *t*-test; $t = -32.82$, df = 143, $P < 0.00001$). A greater but non-significant proportion of adults than juveniles were encountered venturing out into the grassy area (adults: 28, Juveniles: 17, $\chi^2 = 2.689$, $P = 0.101$).

Heating and Cooling Rates.—The mean heat gain rate of artificially cooled adults (0.717 ± 0.221 °C/min; Fig. 8a) was significantly less than that for juveniles (1.286 ± 0.509 °C/min;

paired *t*-test; *t* = -2.438, df = 7, *P* = 0.045). No significant association was evident between the rate of cooling and SVL in adults or juveniles (linear regression; adults: *F* = 2.818, *P* = 0.169; juveniles: *F* = 10.31, *P* = 0.192); however, this is likely attributable to small sample sizes (adults: n = 6, juveniles: n = 3). The mean heat loss rate of artificially heated adults (0.649 ± 0.093 °C/min; Fig 8b) did not differ significantly from that of juveniles (1.089 ± 0.379 °C/min; *t*-test; *t* = -1.950, df = 4, *P* = 0.123). We observed no significant association between adult or juvenile SVL and the rate of heat loss (linear regression, adult: *F* = 00.101, *P* = 0.804; juvenile: *F* = 2.807, *P* = 0.343), but this also might have been a reflection of small sample sizes (adults: n = 3 and juveniles: n = 3). Heating and cooling rates for adults or juveniles did not differ significantly (*t*-test; adults: *t* = 0.495, df = 7, *P* = 0.636; juveniles: *t* = 0.537, df = 4, *P* = 0.620).

DISCUSSION

Although thermal camera images cannot precisely measure internal body temperatures, our data strongly suggest that the *Sphaerodactylus macrolepis* at our study site conformed to the temperatures of the microhabitat. Preferred temperature (25.34 °C) was lower than expected given the available environmental temperatures, but similar to the preferred temperature of 25.3 °C for *S. kirbyi* on Union Island, St. Vincent and the Grenadines (Bentz et al. 2011). Environmental temperatures were higher than preferred temperature during much of the day, even under the leaf litter where these geckos spend much of their time. This suggests that they restrict activity to periods when suitable temperatures are available, possibly becoming nocturnal when both temperature and humidity are closer to optimal. Although preferred temperature and activity temperature often are coadapted in lizards, this pattern does not apply to many geckos (Huey et al. 1989). Therefore, to what extent these high environmental temperatures affect the physiology of sphaerodactyls is unknown, and no information is available on the performance curve of this species or any lizard in the genus *Sphaerodactylus.*

Because of their small size and susceptibility to desiccation, cool moist microhabitats are extremely important to the thermal ecology of these geckos. Choosing habitat that is protected from direct sunlight by a dense forest canopy and deep leaf litter is a tactic commonly used by sphaerodactyls to avoid overheating and desiccation (Lopez-Oritz and Lewis 2004). We determined that deep leaf litter was the most stable thermal environment with the highest, most stable humidity and was closest to the preferred temperature throughout the day. However, we also found individuals ranging away from apparently critical microhabitats into an exposed grassy area, but largely before sunrise, after rain, or during cloudy periods. This was unexpected as grass was deemed unsuitable habitat for *S. nicholsi* (Lopez-Oritz and Lewis 2004) and *S. levensi* (Meier and Noble 1990), and we could find no previous records of *Sphaerodactyus* active in open grassy fields. Why adults primarily utilized dense grass over a dirt substrate and juveniles were more commonly encountered in sparse grassy cover over a sand substrate is unclear. Since grass on sand remained well outside the preferred temperature for a greater part of the day than dense grass and provided less cover, we doubt that thermal factors or predator avoidance are responsible. However, humidity in grass on sand was significantly higher than in dense grass, and we speculate that humidity might be more critical to the survival of juveniles than an optimal thermal environment.

In general, *Sphaerodactylus* geckos exhibit diurnal activity patterns (e.g., *S. becki* [Powell 1999], *S. nicholsi* [Lopez-Oritz and Lewis 2004], *S. kirbyi* [Bentz et al. 2011]), although Nava et al. (2001) indicated that *S. parvus* activity on Anguilla peaked between 1900 and 2100. The round or oval pupils found in all geckos in the genus *Sphaerodactylus* suggest that they evolved to be primarily diurnal (Röll 2001). In our study sites, we saw no *S. macrolepis* on top of the leaf litter during the day unless the litter was disturbed. However, geckos were in the field along the transect during the day when it was cloudy, after a rain, or in well shaded areas. The small increase in both numbers of geckos (particularly juveniles) in the grass and their distance from the forest edge during the morning at 700–800 and a larger increase in the evening at 1600 are suggestive of crepuscular peaks in activity. These increases in activity correspond more closely with environmental temperatures approaching the preferred temperature than with humidity levels rising to those in the microhabitat under the leaf litter. We did not collect data before sunrise or after dark, so we cannot say whether activity continued into or through the night, but these geckos appear to adjust their activity patterns to take advantage of times when environmental temperatures are close to the preferred temperature.

Not surprisingly, juveniles gained heat significantly more quickly than adults, but differences in cooling rates were not significant. The difference between heating and cooling rates was not significant for either adults or juveniles, and neither was significantly affected by SVL. These results correspond with those of Frasier and Grigg (1983), who suggested that heating and cooling rates are unimportant to thermoregulation in small lizards because they are unable to control them physiologically like larger ectotherms. Although unable to control heating and cooling rates, the capacity to heat and cool quickly allows small ectotherms to opportunistically exploit limited optimal environmental temperatures by means of rapid heat exchanges (Frasier and Grigg, 1983).

Due to small size and secretive habits, our knowledge of the thermal biology of sphaerodactyls lags far behind that of many other ectotherms. Although this study confirms assumptions that these diminutive geckos conform rapidly to temperatures of the microhabitat, gain and lose heat quickly, and apparently exploit microhabitats that provide optimal temperatures and tolerable humidity levels at least during some periods, it raises additional questions regarding how small ectotherms deal with environmental temperatures that frequently exceed apparent optima and what thermal limits can be exceeded when foraging in presumably inhospitable microhabitats. These questions become increasingly important when we consider that global changes in climate are likely to exacerbate the apparent discrepancies between preferred and available temperatures. Consequently, we need to explore the nature of performance curves in sphaerodactyls, how changes in temperature affect physiological function, and how available environmental temperatures affect their distributions in nature and activity periods throughout the year.

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FIGURE 1. Adult female Puerto Rican Eyespot Gecko (*Sphaerodactylus macrolepis*). Individuals rarely ventured onto the surface of leaf litter except when disturbed. Photograph by Robert Powell.

FIGURE 2. Google Earth® image of White Beach on Guana Island (British Virgin Islands), showing the dense seagrape (*Coccoloba uvifera*) stand separating the beach from a regularly mowed grassy area. The two white Xs mark the approximate locations of the two study sites (18°28'31.86"N 64°34'33.32"W; WGS84) and the white line marks the approximate location of the transect paralleling the seagrape stand.

FIGURE 3. Body temperatures of *Sphaerodactylus macrolepis* at site 1 compared to temperatures at the top and bottom of the leaf litter on 15 October 2013. Body temperatures of geckos are represented by solid dots, temperatures at the top of the leaf litter by circles, and temperatures at the bottom of the leaf litter by squares. The dotted line represents the mean preferred temperature and the gray bar one standard deviation on either side of the mean.

FIGURE 4. Thermal images taken from each of the field sites and the transect on 15 October 2013. Smart View Thermal Imaging software was used to place the marker over the gecko and analyze the body temperature (°C). Body temperature is shown for a gecko at: (A) Site 1 at 0925; (B) Site 2 at 1600; and (C) in the transect at 1420. Temperature ranges are represented by color gradients with red being the warmest and purple the coolest relative to the average temperature in the rest of the image. Geckos are at lower temperatures than their backgrounds because they had moved out of deep grass or litter after being disturbed.

FIGURE 5. Thermal environments available to *Sphaerodactylus macrolepis* on and in the leaf litter at site 2 and in ecologically relevant microhabitats along the transect throughout the course of the day on 17 October 2013.

FIGURE 6. Numbers of geckos found along the transect throughout the day on 15 October 2013. White bars represent adults and black bars represent juveniles. A significant difference ($\chi^2 = 5.00$, $P = 0.025$) between adults and juveniles at 1100 is denoted by the asterisk (*).

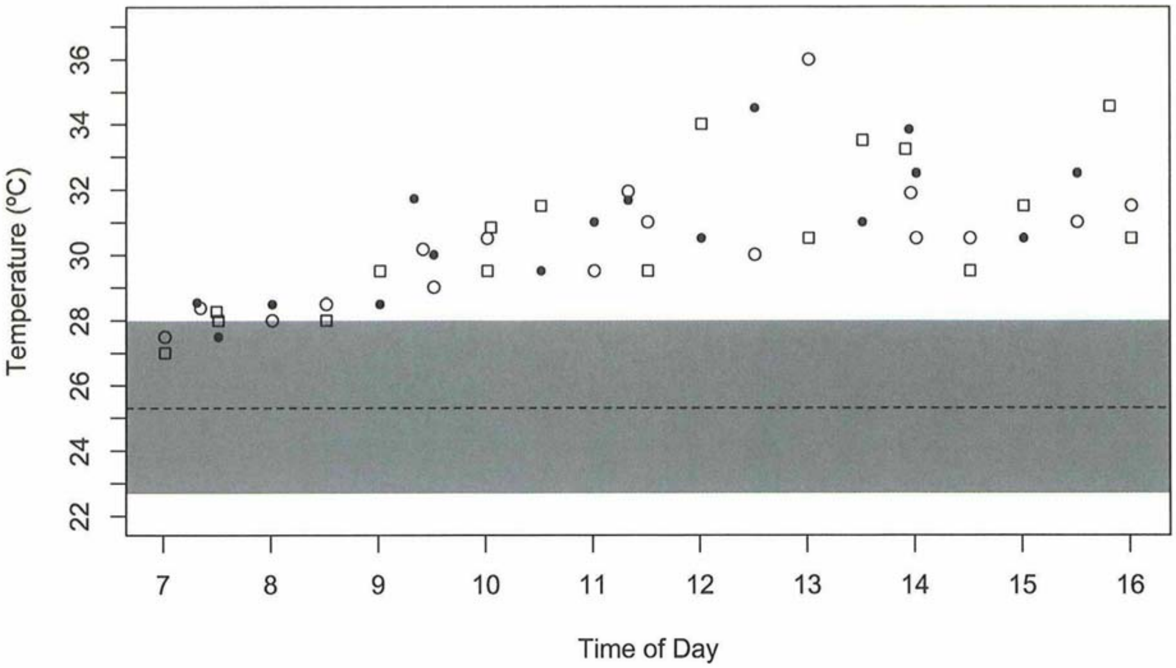
FIGURE 7. Distances of geckos along the transect from the nearest point of shaded forest cover on 15 October 2013.

FIGURE 8. Thermal images of heating and cooling trials. Each series shows a thermal image from the beginning, middle, and end of each trial. The marker is placed over the gecko and the body temperature (°C) is indicated. Series (A): cooling trials. Series (B): warming trials. The color range represents temperatures relative to the average temperature of the rest of the image with red being warmer and purple being cooler.

Figure 1.

Figure 2.

Figure 3.


Temperature (ºC)
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Time of Day

Figure 4.

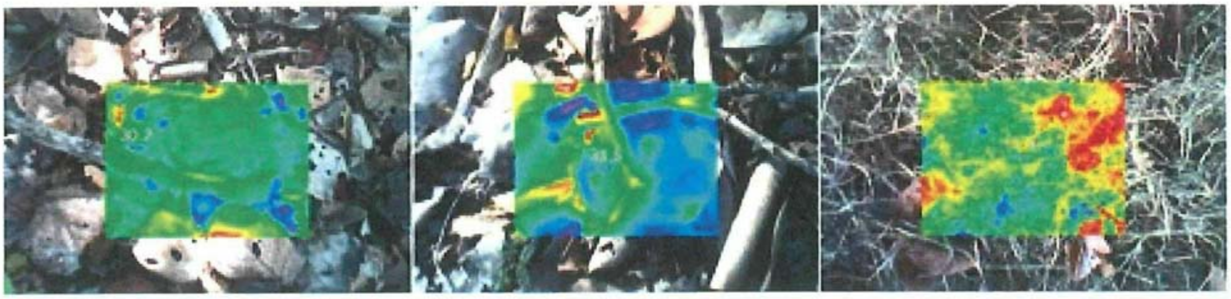
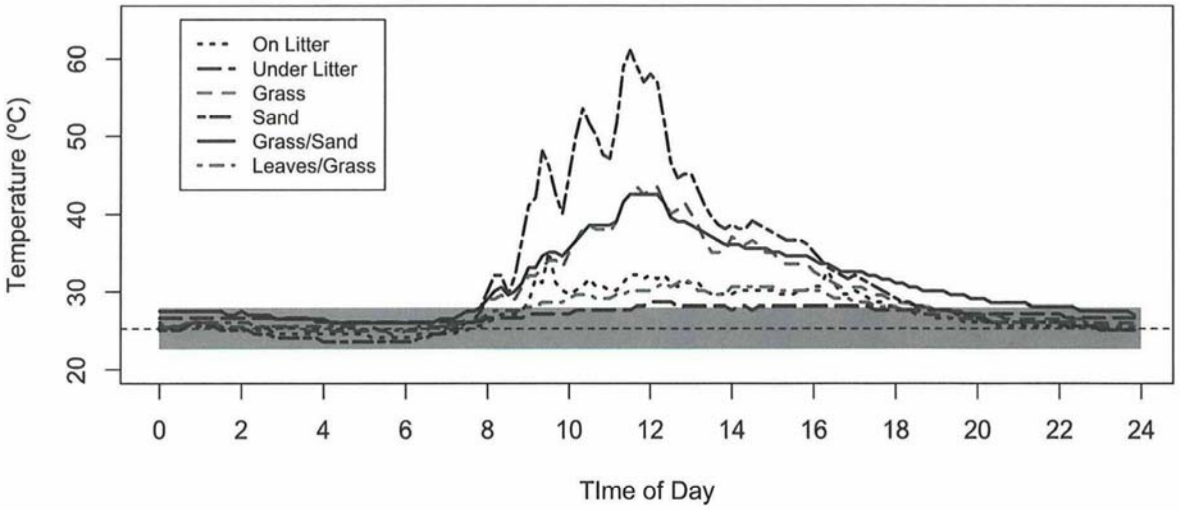


Figure 5.


On Litter
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Sand
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Leaves/Grass
Temperature (ºC)
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TIme of Day

Figure 6.

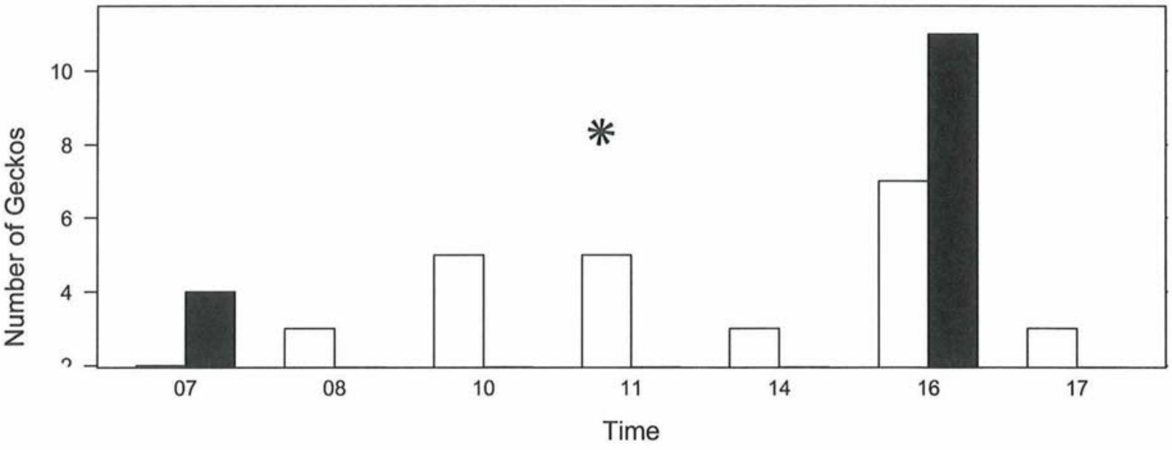

Figure 7.

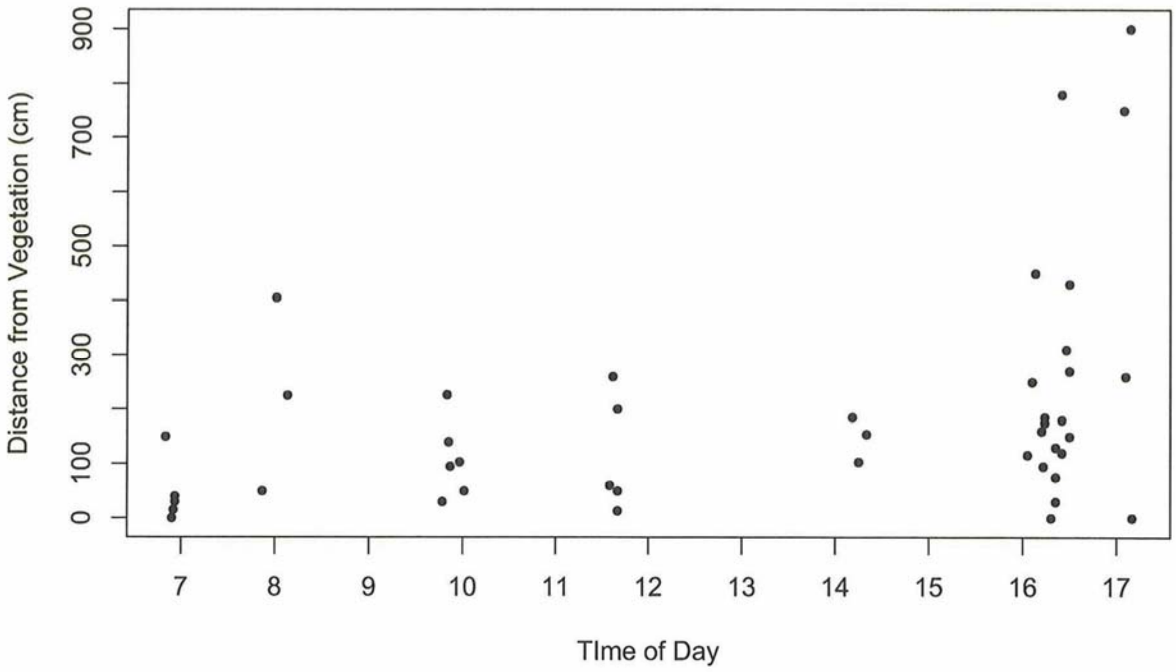
Distance from Vegetation (cm)
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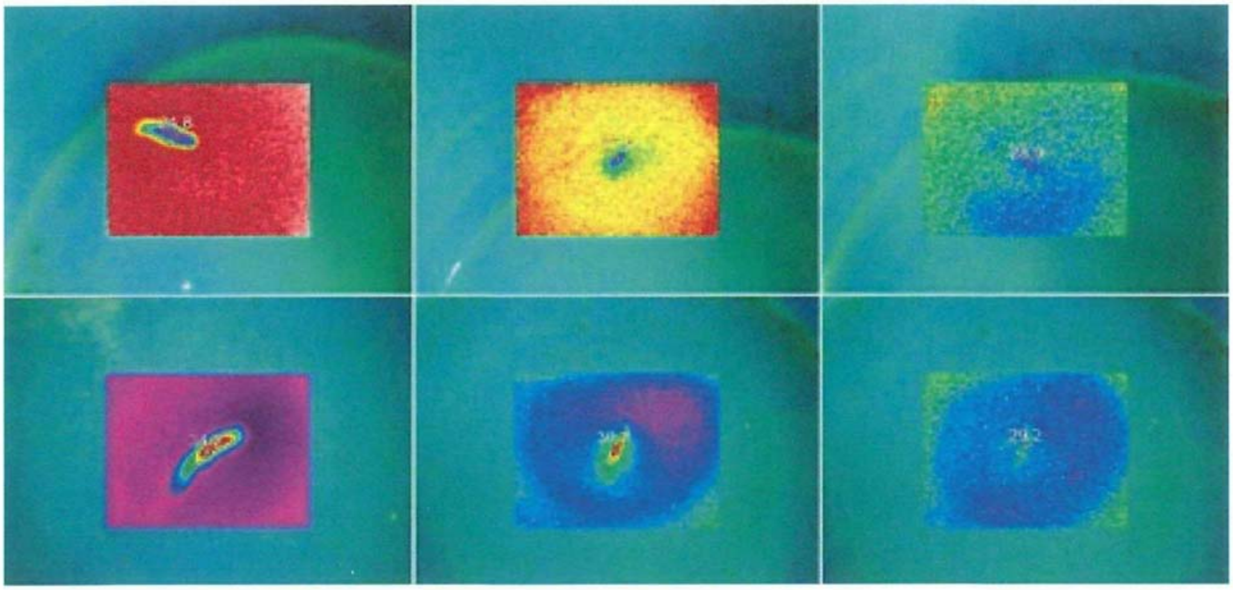
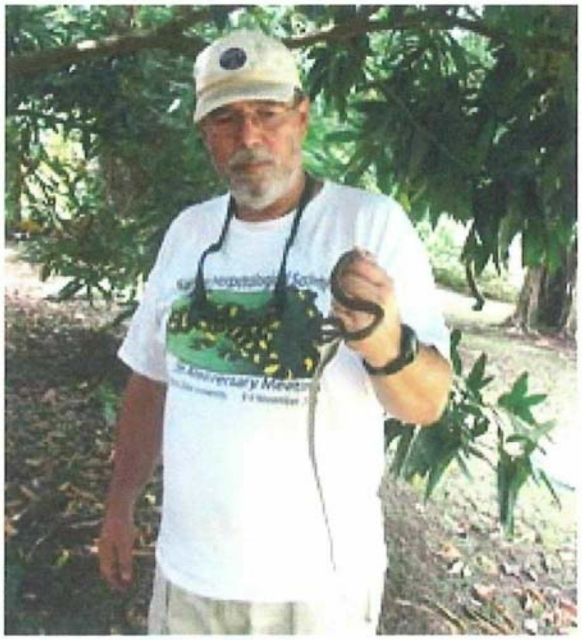
Figure 8.



Kaitlin E. Allen graduated in 2009 from Truman State University where she studied the diet of insular Boa Constrictors and the behavior of *Sphaerodactylus* geckos. She is currently working on her Master's degree in biology at Villanova University studying the effects of elevation on evolutionary processes in African skinks. She is broadly interested in behavior, ecology, and phylogeography of reptiles. Photograph by Mariel Sorlien.



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Photograph by David S. Steinberg.

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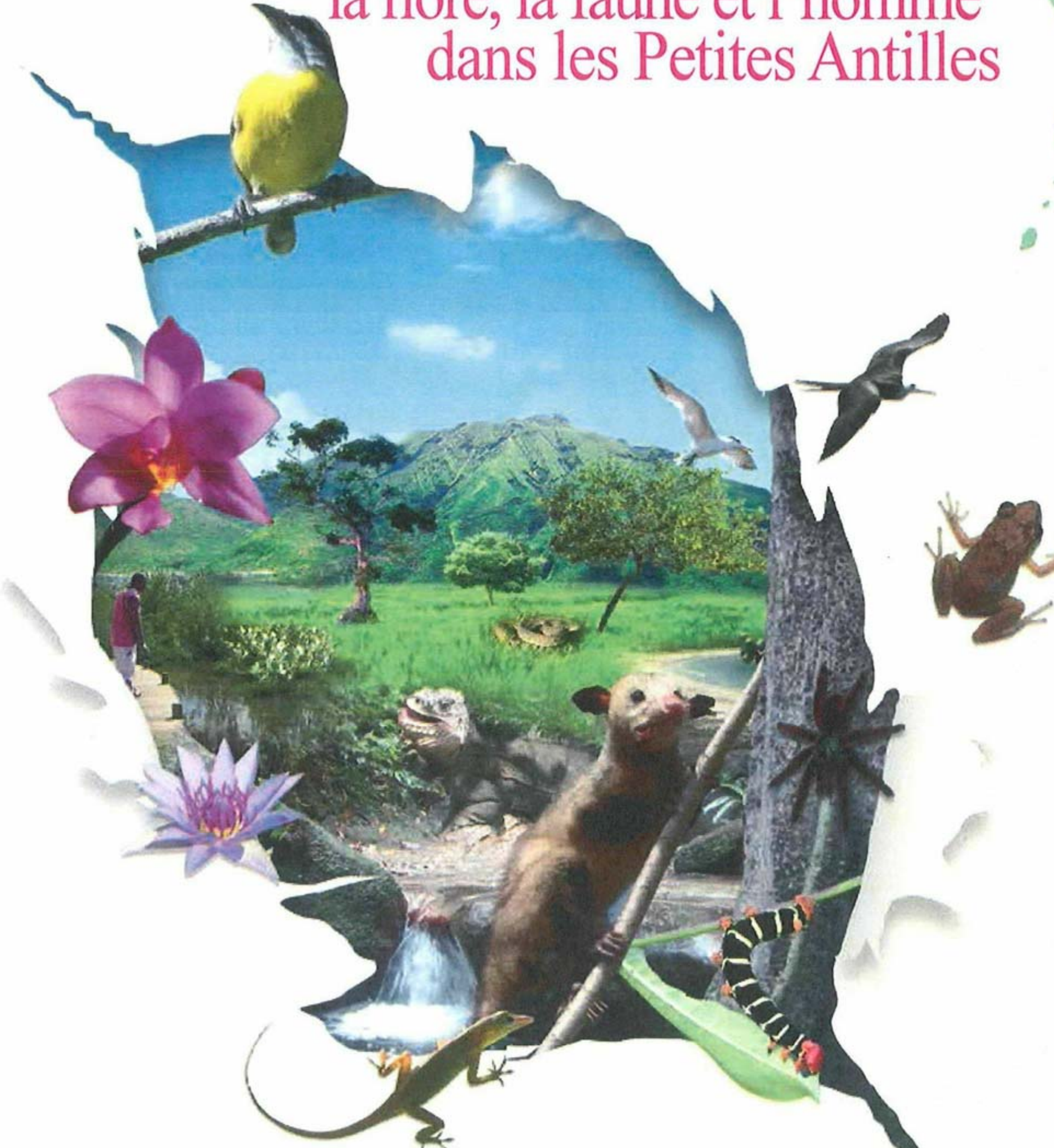

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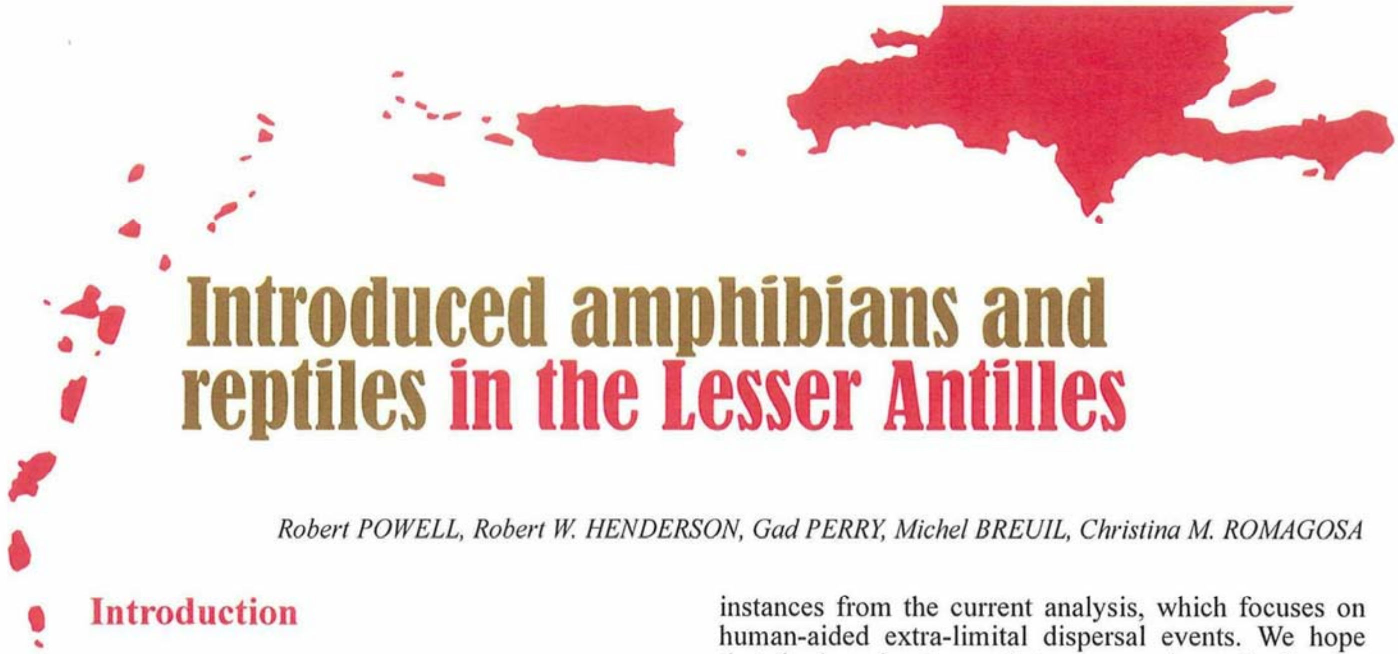


Introduced amphibians and reptiles in the Lesser Antilles

Robert POWELL, Robert W. HENDERSON, Gad PERRY, Michel BREUIL, Christina M. ROMAGOSA

Introduction

Dispersal is a common and natural phenomenon, although long-distance dispersal is typically rare (Nathan *et al.*, 2003; Trakhtenbrot *et al.*, 2005). Human-aided dispersal is becoming increasingly common, and often occurs over great distances. The number of amphibians and reptiles being moved to non-native locations is growing (Lever, 2003; Kraus, 2009; Powell *et al.*, 2011), as are reports of their ecological and economic impacts (e.g., Bomford *et al.*, 2009), despite the inadequate attention paid to documenting them (McGeoch *et al.*, 2010). Globally, human-transported non-native species are among the top three causes of biodiversity loss (Clavero and García-Berthou, 2005; McGeoch *et al.*, 2010), and non-native reptiles and amphibians are known to cause both ecological and economic problems.

The Lesser Antilles (LA), with extensive tourism in many areas and limited local production of essential items such as food and building materials, are at especially high risk. Herpetological introductions in the region are not new. Felix-Louis L'Herminier, as director of the "Jardin de naturalization de la Guadeloupe" in the early 19th century, had a goal of introducing and acclimating new species to the island (Breuil, 2002, 2003). Among the species he attempted to establish were three turtles, *Kinixys erosa*, *Kinyxis homeana*, and *Pelusios castaneus*, which are native to western Africa and which he might have purchased from slave traders. In addition, his son, François-Joseph, visited Puerto Rico and caught *Trachemys stejnegeri*, which was liberated in Marie-Galante, where his father was a chemist in 1802. Other 19th-century reports include Schomburgk (1848), Feilden (1889), and Boulenger (1891). Modern reports are numerous and highly dispersed, despite efforts of Lever (2003) and Kraus (2009) to collate them. Our goal in this paper is to summarize what is known about herpetological introductions in the region, the mechanisms that allow them, and their effects in this wide geographical area.

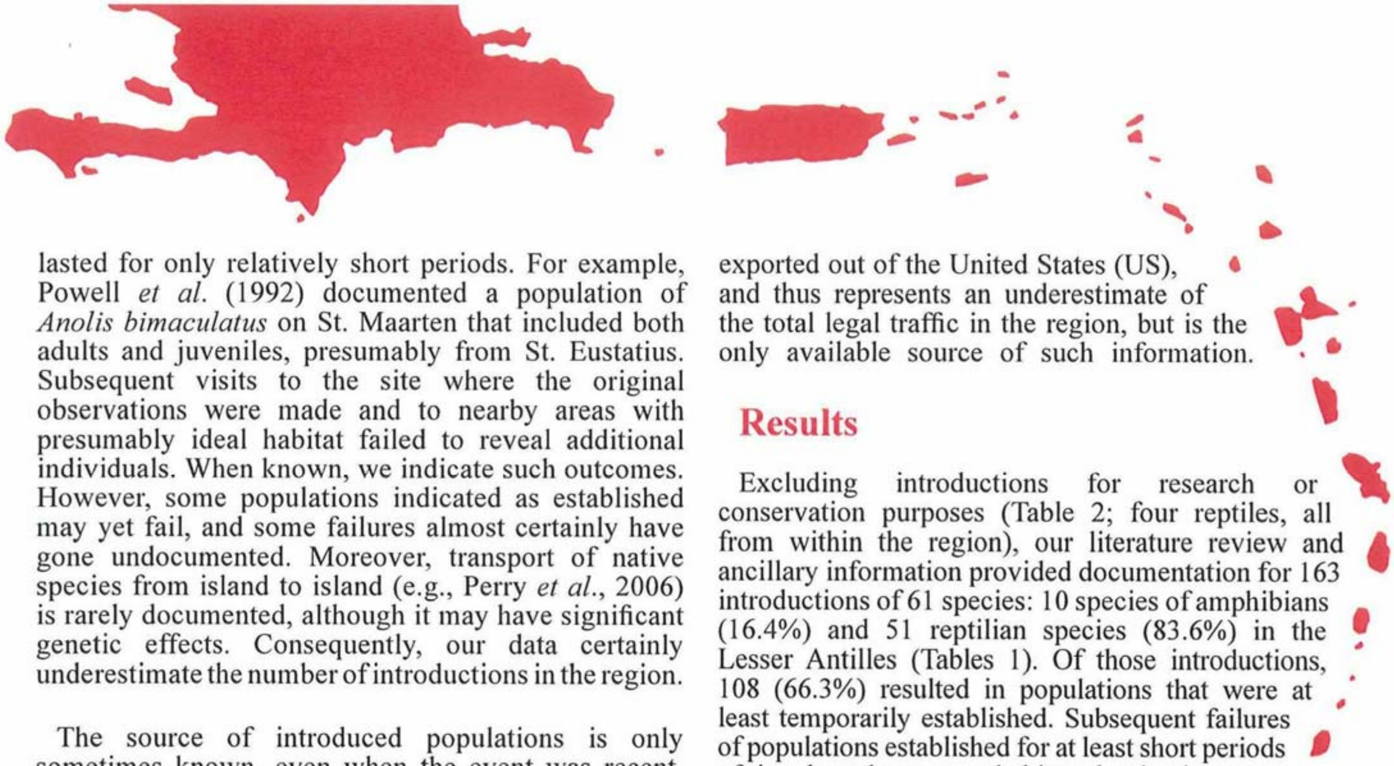
By their nature, islands are more isolated than mainland sites, yet overwater dispersal still occurs naturally (e.g., Censky *et al.*, 1998). We exclude such instances from the current analysis, which focuses on human-aided extra-limital dispersal events. We hope that the broad patterns that emerge—in particular, the primacy of a small number of arrival mechanisms—will encourage a coordinated regional policy response and help reduce negative economic and ecological impacts.

Materials and Methods

In order to develop an overview of all introductions of amphibians or reptiles in the region, we exhaustively reviewed the pertinent literature, much of which was reviewed previously in Kraus (2009), Henderson and Powell (2009), and Powell *et al.* (2011). In fact, this survey is a geographically restricted portion of the latter (which covered the greater Caribbean), complemented with new records and information. Unfortunately, records of "benign" non-native arrivals and dispersal are notoriously incomplete (McGeoch *et al.*, 2010). We therefore supplemented the literature accounts with our own personal experiences, collected over several decades of working in the region, and with additional information from well-informed persons working or residing in the region.

We organize our text taxonomically. Written accounts identify (when known), the arrival mechanism (often as identified in Kraus, 2009), and whether this was a one-time arrival, a repeated incursion, or an established population. However, the origins of some populations—whether they arrived naturally or were human-mediated—remain uncertain. Locations are detailed in Tables 1 and 2, which also provide citations in order to assist readers seeking information regarding the sources or fates of introductions unrelated (Table 1) and related to (Table 2) conservation and research efforts. To avoid duplication, we do not consistently distinguish arrivals to single islands within island groups or banks (e.g., satellites of major islands, the Grenadines, the Guadeloupean Archipelago) from arrivals to an entire island group.

Not all introductions are successful. Reports of one-time arrivals (e.g., Powell *et al.*, 2005) are uncommon in the literature, although they provide valuable information on vectors, propagule pressure, and times of arrival. In some instances, we report the presence of ephemeral populations, although many



lasted for only relatively short periods. For example, Powell *et al.* (1992) documented a population of *Anolis bimaculatus* on St. Maarten that included both adults and juveniles, presumably from St. Eustatius. Subsequent visits to the site where the original observations were made and to nearby areas with presumably ideal habitat failed to reveal additional individuals. When known, we indicate such outcomes. However, some populations indicated as established may yet fail, and some failures almost certainly have gone undocumented. Moreover, transport of native species from island to island (e.g., Perry *et al.*, 2006) is rarely documented, although it may have significant genetic effects. Consequently, our data certainly underestimate the number of introductions in the region.

The source of introduced populations is only sometimes known, even when the event was recent. Generally, we are even less certain of sources for older introductions. For example, Amerindians and early European colonists almost certainly intentionally transported tortoises (*Chelonoidis carbonaria*) and iguanas (*Iguana iguana*) from the mainland to islands or from one island to another (e.g., Censky, 1988; Powell, 2004b; Powell *et al.*, 2005). Descendants of those animals might have interbred with animals descended from ancestors that arrived via natural over-water dispersal and animals introduced more recently, many in association with the burgeoning pet trade. Because of this complex and poorly documented history, whether particular populations of some species were established with human mediation cannot be determined with any certainty. Similarly, house geckos (*Hemidactylus mabouia*) are of African origin (e.g., Kluge, 1969; Vanzolini, 1978). Whether American populations were established as a consequence of natural trans-Atlantic dispersal (see discussion in Mausfeld *et al.*, 2002) or were human-mediated is unknown (e.g., Hedges, 1996). Late Quaternary fossils on Guadeloupe (Pregill *et al.*, 1994) are indicative of a prolonged presence in the region, although Breuil (2002, 2009) noted that only one species of gecko (*Thecadactylus rapicauda*) was known from the region at the time of colonization. However, once established in the Western Hemisphere, populations might have dispersed naturally to Caribbean islands; and such dispersal might have been facilitated by human activities or extant populations might be descendants of ancestors arriving by both means. Herein, we omit the species from our list of introduced populations, with the implicit assumption that at least some of the Lesser Antillean populations are natural, although they might frequently be supplemented with individual stowaways.

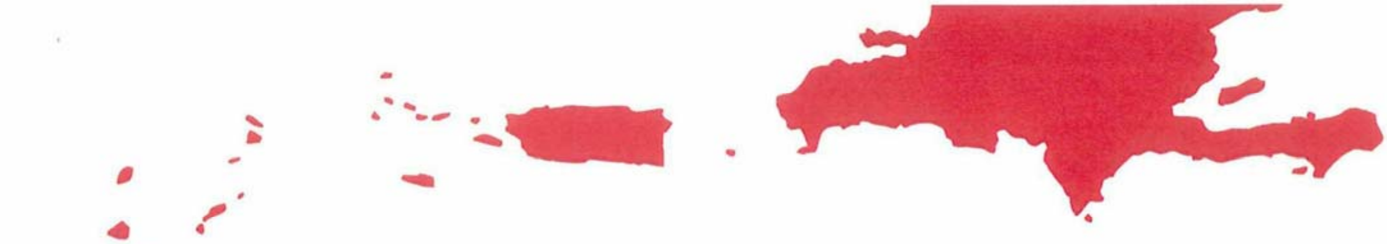
We obtained data on the live animal trade during the years 1998-2008 from the United States Fish and Wildlife Service (USFWS) Law Enforcement Management Information System (LEMIS) database. This database only records animals coming into or exported out of the United States (US), and thus represents an underestimate of the total legal traffic in the region, but is the only available source of such information.

Results

Excluding introductions for research or conservation purposes (Table 2; four reptiles, all from within the region), our literature review and ancillary information provided documentation for 163 introductions of 61 species: 10 species of amphibians (16.4%) and 51 reptilian species (83.6%) in the Lesser Antilles (Tables 1). Of those introductions, 108 (66.3%) resulted in populations that were at least temporarily established. Subsequent failures of populations established for at least short periods of time have been recorded in only nine instances (plus one introduction for research purposes). Nine species (14.8%) were native to other Lesser Antillean islands and 52 (85.2%) presumably were native to areas outside the region. Most of the latter originated in the Western Hemisphere (n = 41, 78.8%), but 11 (21.2%) were from the Eastern Hemisphere. Some of those might have been established by individuals from regional captive-breeding programs supplying the international live animal trade, and some Caribbean populations of *Rhinella marina, Iguana iguana,* and *Gymnophthalmus underwoodi* might be native, but their exact origins remain unclear. A growing number of introductions (n = 19, 11.7% of all introductions) represents introduced species that became established in Florida and were then secondarily introduced into the region. All are attributable to three species (*Osteopilus septentrionalis, Anolis sagrei, Ramphotyphlops braminus*), but other species prominent in the pet trade (e.g., *Iguana iguana*) might also have originated from introduced populations in Florida.

Most species have become established on only one or two islands, but at least 15 species have been introduced to three or more islands or island groups in the region. Although many of the introduced populations are limited to human-dominated habitats, such as urban areas, at least some (e.g., *Rhinella marina, Eleutherodactylus johnstonei, Iguana iguana*) have successfully invaded natural habitats. Known effects on native species in the region include predation, competition, hybridization, confounding conservation/education programs, and possibly introducing alien disease vectors.

Strays (documented arrivals of one or a few individuals with no evidence of reproduction) represent 33.7% (n = 55) of all documented introductions. These include nine introductions of amphibians and 46 of reptiles, plus two amphibian and three reptilian introductions for which the status is unknown and which are presumed to have been strays. Including those would increase the percentage to 36.8% of all introductions.



Although some introduced populations stem from multiple arrivals and the origins of many are unknown, primary pathways for introduction include inadvertent arrivals in cargo and ornamental plants (ca. 80). However, a substantial number are associated with the pet trade (ca. 30). Some of the latter might have been intentional, but most releases were probably accidental. Tortoises (*Chelonoidis carbonaria*) and iguanas (*Iguana iguana*) are widely distributed throughout the region, and many populations probably have mixed origins, with some tracing their ancestry back to individuals that arrived via natural over-water dispersal, intentional introductions by Amerindians and early European colonists, inadvertent releases of pets, or some combination thereof (e.g., Censky, 1988; Powell, 2004b). Complicating matters further are recent intentional inter-island introductions such as that of *C. carbonaria* onto St.-Barthélemy from Saba after World War II (Breuil, 2004).

Although some unintentional introductions occurred more than a century ago, most are more recent. Intentional introductions generally fall into four broad categories: for food (an undetermined percentage of arrivals of *I. iguana, C. carbonaria*, and turtles in the family Emydidae), for pest control (predominantly *R. marina*), research (*Anolis pogus* on Anguillita; Roughgarden *et al.*, 1984), and conservation (*Iguana delicatissima* on Îlet à Ramiers off Martinique; Breuil, 2009; *Cnemidophorus vanzoi* on Praslin Island off Maria Major near St. Lucia; Dickinson and Fa, 2000; *Alsophis sajdaki* on Green and Rabbit islands off Antigua; Daltry, 2007, 2011). Unlike recent conservation and research-related introductions (all after 1980), intentional introductions for food and biocontrol almost always occurred earlier, most of the latter during the 19th century. A fifth category of intentional introductions might become more prevalent as animal dealers or even hobbyists seek to establish local populations of species.

The live animal trade

Although the LA have never been a large legal export market for amphibians and reptiles for the United States, a surprisingly large number of animals are shipped from the US to the Caribbean (**Table 3**), the Caribbean to the US (**Table 4**), and from the Caribbean to the US and then onward, including back to the Caribbean (**Table 5**). Between 1998 and 2009, nearly 29,000 amphibians and reptiles were exported each year from the US to the Caribbean. A large percentage of these species do not occur in the region either naturally or as previously introduced populations. Many obviously are being shipped to serve the pet/aquarium trade. Turtles, which almost certainly represent a combination of animals destined for the pet trade and those destined ultimately for food markets (many in eastern Asia), were shipped in the largest numbers, including 12,300 *Pseudemys* sp. sent to the Netherlands Antilles (no indication of whether these are the Leeward or Windward islands of that nation).

Countries within the LA have exported introduced amphibians and reptiles to the United States, as well as countries within the European Union and Asia. Like exports from the US, most supply the pet/aquarium trade and many are not known to occur in the region.

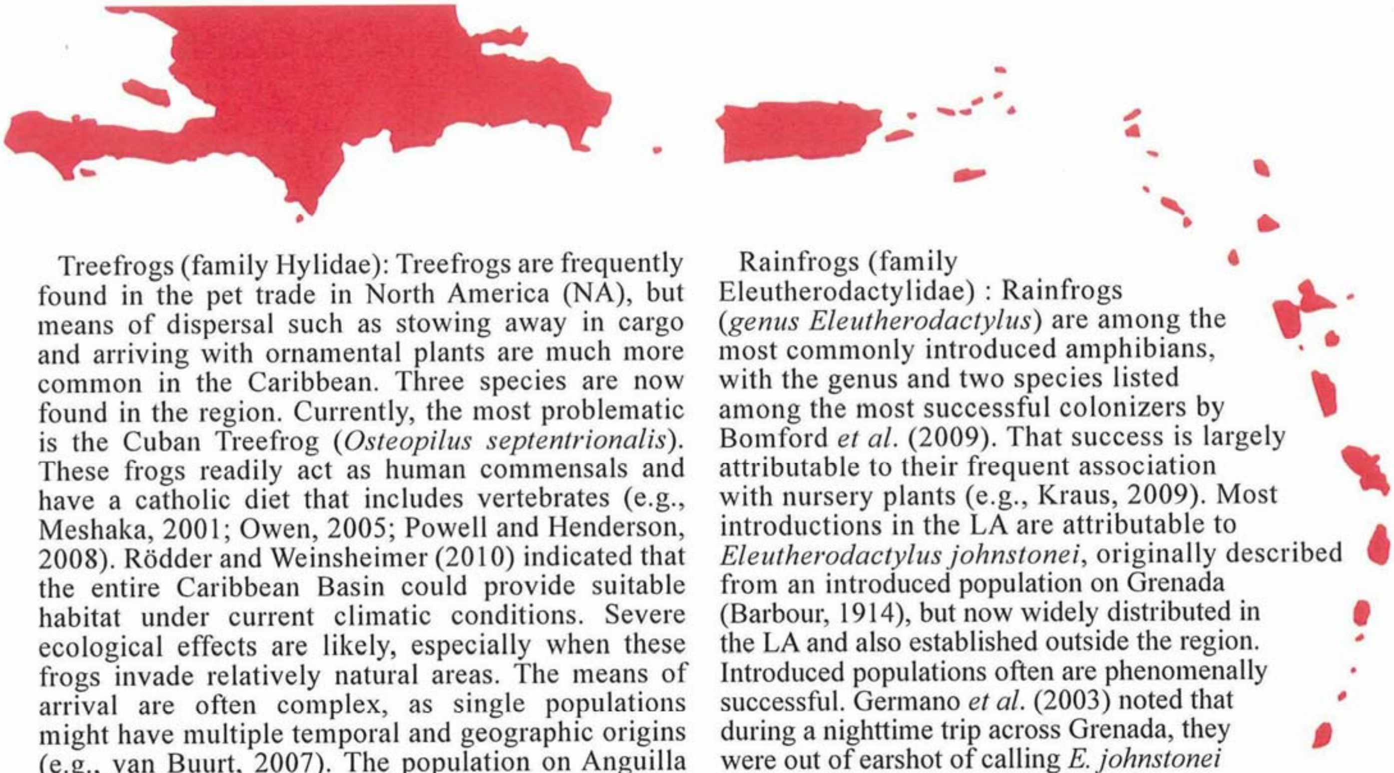
Barbados accounts for 27 (32.5%) and the Netherlands Antilles for 47 (56.6%) of the 83 documented species exported to the LA from the US (**table 3**). Although a market for pets exists in both nations, active animal vendors are based in those countries, suggesting that many of the exported animals are destined for markets elsewhere. Of 18 species imported from the region into the US (**table 4**), most come from Barbados (11, 61.1%).

Taxonomic patterns: Amphibians

Although some urodeles and a diversity of frogs are exported to the Caribbean from the US, all amphibians introduced in the region to date have been frogs belonging to four families: Bufonidae, Eleutherodactylidae, Hylidae, and Leptodactylidae. Relatively few genera are represented, all from within the Americas. Inadvertent introductions via the nursery trade are the most frequent mechanisms of arrival, although stowaways in cargo are common, as are a few species arriving via the pet trade and as a consequence of historical intentional releases for food or biocontrol.

True toads (family Bufonidae): The Cane Toad (*Rhinella marina*), native to the Neotropics, has been intentionally introduced for biocontol of insect pests in many parts of the world. Although it rarely fulfills that purpose, it feeds voraciously on almost everything else (e.g., Wolcott, 1937; Lynn, 1940; Long, 1974; Breuil, 2002; Meshaka and Powell, 2009), with broad ecological impacts reported from Australia, Florida, and Hawaii (e.g., Esteal, 1981). Wilson *et al.* (2010) also reported negative effects on native predators, describing mortality in endemic and threatened Jamaican Boas (*Epicrates subflavus*) after ingesting Cane Toads.

The Cane Toad is widely established in the LA and some populations might be traced to founders that arrived naturally via over-water dispersal (Henderson and Powell, 2009). These toads are ubiquitous on many islands (e.g., Mallery *et al.*, 2007 for St. Vincent). However, populations have failed to become established on islands that provide few opportunities to breed, such as Anguilla (Hodge *et al.*, 2003; Hodge *et al.*, 2011) and Union Island in the Grenadines (J. Daudin, pers. comm.). These toads are common commensals, often utilizing human-created habitats such as parks, gardens, and resort grounds (Powell and Henderson, 2008) and exploiting the artificial night-light niche (Perry *et al.*, 2008).



Treefrogs (family Hylidae): Treefrogs are frequently found in the pet trade in North America (NA), but means of dispersal such as stowing away in cargo and arriving with ornamental plants are much more common in the Caribbean. Three species are now found in the region. Currently, the most problematic is the Cuban Treefrog (*Osteopilus septentrionalis*). These frogs readily act as human commensals and have a catholic diet that includes vertebrates (e.g., Meshaka, 2001; Owen, 2005; Powell and Henderson, 2008). Rödder and Weinsheimer (2010) indicated that the entire Caribbean Basin could provide suitable habitat under current climatic conditions. Severe ecological effects are likely, especially when these frogs invade relatively natural areas. The means of arrival are often complex, as single populations might have multiple temporal and geographic origins (e.g., van Buurt, 2007). The population on Anguilla was traced to containers of ornamental plants from Florida, and a small population had been present for several years before generating wide attention after a series of particularly wet years during the late 1990s. At that time, the frogs spread from localized sites (often on resort grounds) to much of the island, where they used various sources of water, including cisterns associated with residences, for breeding (Townsend *et al*., 2000; Hodge *et al*., 2003). A similar scenario played out on St.-Barthélemy, where an initial association with resorts was documented by Breuil (2002), Breuil and Ibéné (2008), and Breuil *et al*. (2009). Populations elsewhere have exhibited similar patterns, remaining relatively obscure until propitious weather conditions (often associated with hurricanes) result in a population explosion. Cuban Treefrogs were relatively rare on St. Maarten/St.-Martin in the 1980s, but had become almost ubiquitous by the early 1990s (e.g., Powell *et al*., 1992). Similarly, frogs were infrequently encountered on Antigua until they became a plague during a relatively short period in the late 1990s and early 2000s (Daltry, 2007, 2011; R. Powell, unpubl. data). Spread of this species continues (e.g., Powell, 2006, 2007 on Saba, presumably from St. Maarten). In dry years, frogs are less evident (Powell and Henderson, 2008; Hodge *et al*., 2011), and some populations on Anguilla have shrunk as a consequence of a regional drought in 2009 (Hodge *et al*., 2011).

Scinax ruber has become established in Martinique and St. Lucia, but the means of arrival remain largely uncertain. The population of this SA native on St. Lucia appears to have resulted from cargo stowaways (Kraus, 2009). The closely related *S. x-signatus*, also SA in origin, was recently reported on several islands in the Guadeloupean Archipelago (Breuil, 2004; Breuil and Ibéné, 2008) and on Martinique (Breuil, 2011). The latter now has two species of *Scinax*; interactions between these two exotic species will be interesting to study. These treefrogs were discovered in a new bungalow built three years ago on Martinique using a kit delivered in a container imported directly from Brazil (Breuil *et al*., 2010a).

Rainfrogs (family Eleutherodactylidae) : Rainfrogs (*genus Eleutherodactylus*) are among the most commonly introduced amphibians, with the genus and two species listed among the most successful colonizers by Bomford *et al*. (2009). That success is largely attributable to their frequent association with nursery plants (e.g., Kraus, 2009). Most introductions in the LA are attributable to *Eleutherodactylus johnstonei*, originally described from an introduced population on Grenada (Barbour, 1914), but now widely distributed in the LA and also established outside the region. Introduced populations often are phenomenally successful. Germano *et al*. (2003) noted that during a nighttime trip across Grenada, they were out of earshot of calling *E. johnstonei* for only a few seconds in the most densely developed center of St. George's, and Mallery *et al*. (2007) found calling frogs at every site they sampled on St. Vincent. The nursery trade and stowaways appear to be the primary vectors for dispersal.

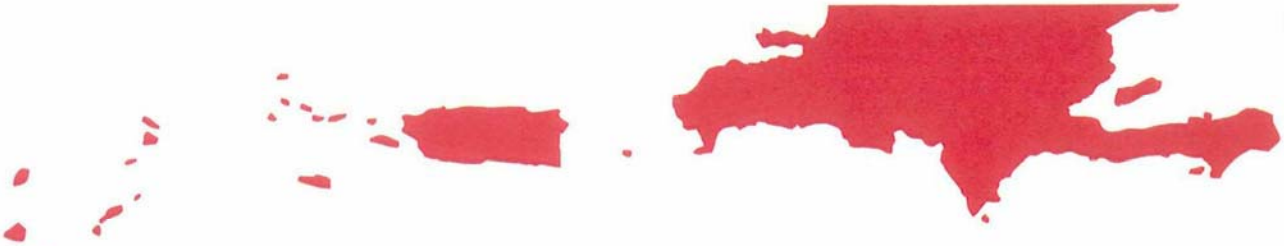
Eleutherodactylus martinicensis from Antigua, Guadeloupe, Dominica, and Martinique was established on St.-Barthélemy as a result of the nursery trade (Kaiser, 1992) and on St. Maarten/St.-Martin, either via the nursery trade or as a stowaway in other cargo (Breuil, 2002).

Neotropical frogs (family Leptodactylidae): Native to the Caribbean, the very robust "Mountain Chicken" *(Leptodactylus fallax*) has been introduced on Grenada, Jamaica, Martinique, and Puerto Rico, presumably intentionally as a delicacy (Kraus, 2009). All attempts ultimately failed, although the introduction to Martinique might date to Amerindians (Breuil and Ibéné, 2008; Breuil *et al*., 2009). Ironically, this species is rapidly declining in its native range (e.g., Garcia *et al*., 2007). Recent work (Yanek *et al*., 2006; Camargo *et al*., 2009) suggested that *L. validus*, long believed to be native to St. Vincent and Grenada, was in fact introduced into the LA with early human arrivals.

Taxonomic patterns: Reptiles

A variety of reptilian taxa has arrived in various Caribbean locations, and disconcertingly large numbers of those have become established. A large proportion of these species is of regional origin, although some originated in the Eastern Hemisphere. The two primary paths of arrival appear to be stowaways in cargo and, more recently, the pet trade, although other sources have been reported.

Crocodilians (families Alligatoridae and Crocodilidae): Such large and obvious animals might seem unlikely to be invasive, since they are not likely to stow away unnoticed. The only observations of



non-native crocodilians in the region are of strays (e.g., "an undetermined caiman from Guiana" on Martinique; Breuil, 2009), none of which have become established. In general, such arrivals remain uncommon, both in terms of numbers and geographic scope.

Tortoises (family Testudinidae): South American tortoises in the genus *Chelonoidis* tend to be large and are introduced primarily via the pet trade or as ornamentals, although their willingness to consume fecal matter renders them useful for cleaning latrines or chicken pens (e.g., Pinchon, 1967). Daudin and de Silva (2007, 2011) indicated that locals in the Grenadines scorn them as food for that very reason. The status of *C. carbonaria* populations on many islands remains unclear (e.g., Censky, 1988; Hodge *et al.*, 2003; Powell *et al.*, 2005; Powell and Henderson, 2005; Fields and Horrocks, 2009), with the ancestors of some likely arriving via natural over-water dispersal, whereas those of others might have been introduced by Amerindians or early colonial Europeans (perhaps for food), and others being more recently moved for ornamental value (e.g., Breuil, 2002; Powell *et al.*, 2005; Lorvelec *et al.*, 2007, 2011). Individuals from Barbados are exported regularly to supply the pet trade (Fields and Horrocks, 2009). The closely related *C. denticulata*, originally from SA, is introduced on Guadeloupe (Pritchard and Trebbau, 1984; Breuil, 2002), although only escaped individuals are known (i.e., no feral population exists). *Centrochelys sulcata*, from northern Africa, is known as a stray on Martinique (Breuil, 2009). Early 19th-century attempts to establish two species of *Kinixys* (*K. erosa* and *K. homeana*) on Guadeloupe failed (Breuil, 2002, 2003).

Pond turtles (family Emydidae): Pond turtles of several species are common in the pet trade, which is the primary vector for their worldwide spread, although some populations are exploited for food (e.g., Powell, 2003). *Graptemys pseudogeographica*, from NA, is known as a stray on Martinique (Breuil, 2009). *Trachemys scripta*, another NA species, is widely established. This is one of the most common species in the pet trade and also is marketed for food, to such an extent that multiple arrivals at any given location are not unlikely. Many Caribbean populations, such as those in Barbados (Horrocks and Fields, 2011), Guadeloupe (Schwartz and Thomas, 1975; Lescure, 1979; Schwartz and Henderson, 1988, 1991; Breuil, 2002; Breuil *et al.*, 2010), Marie Galante (Breuil, 2002), Martinique (Servan and Arvy, 1997; Breuil, 2002), and St. Eustatius (Powell *et al.*, 2005), appear to be strays and are unlikely to have extensive impacts on native species. Even where abundant (e.g., St. Maarten/St.-Martin; Powell *et al.*, 2005), severe ecological effects are unlikely where no native congeners occur.

Another member of the genus, *Trachemys stejnegeri*, from the Greater Antilles, has become established in Les Îles de Saintes and on Marie Galante (Seidel and Adkins, 1987; Seidel, 1988; Ernst and Barbour, 1989; Breuil, 2002, 2003; Breuil *et al.*, 2010). An introduction on Dominica apparently failed (Fritz, 1991; Seidel, 1996; Kraus, 2009), and the species is known only as a stray on Guadeloupe (Breuil, 2002, 2003; Breuil *et al.*, 2010). The status of *Terrapene carolina* on Martinique (Breuil, 2009) is unknown, but it is likely to have been a stray. This terrestrial member of the family originated in NA and LA populations almost certainly are pet-trade related.

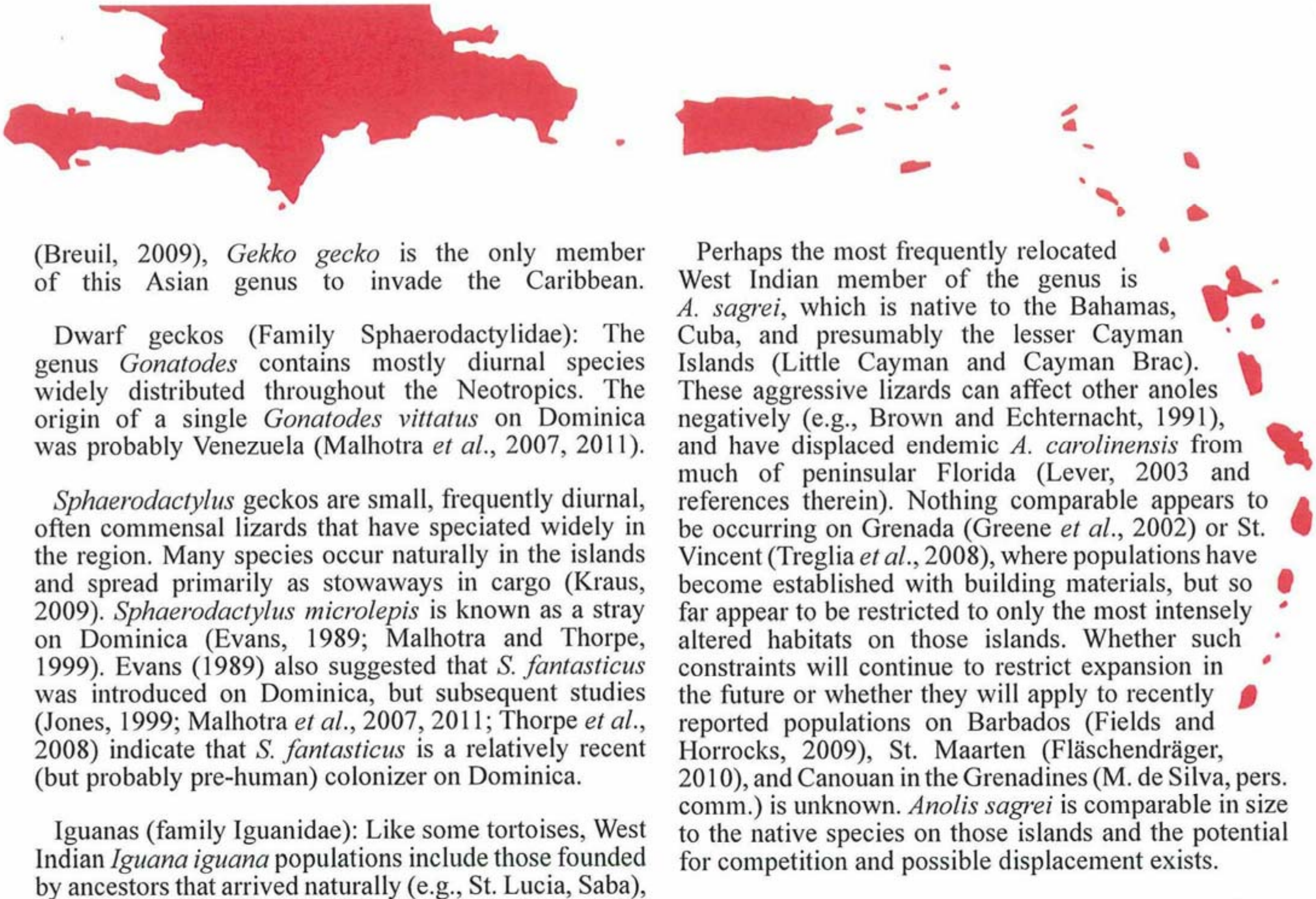
Afro-American side-necked turtles (family Pelomedusidae): *Pelusios castaneus* is African in origin and not uncommon in the pet trade. Lescure (1979) indicated that the exact source of the population established on Guadeloupe (e.g., Lescure, 1979, 1983) remains unclear, but Breuil (2002, 2003) indicated that it was introduced intentionally by L'Herminier in the early 19th century.

Austro-South American side-necked turtles (family Chelidae): No documented explanation exists for the single *Phrynops geoffroanus* found on Anguilla (Hodge *et al.*, 2011).

Geckos (family Gekkonidae): Many geckos are common human commensals that have become widely distributed around the globe. The genus *Hemidactylus* and four species (one of which is known from the LA), all originally from the Eastern Hemisphere, are included among the most successful colonizers (Bomford *et al.*, 2009). The most widely distributed "house gecko" within the region, *H. mabouia*, is found on many islands, where it is essentially ubiquitous on buildings and walls (e.g., Howard *et al.*, 2001). Origins are uncertain (e.g., Kluge, 1969; Powell *et al.*, 1998); although some insular populations might have arrived via natural over-water dispersal from SA (or even Africa), others probably arrived with humans, and some populations are likely mixtures of both. Breuil (2009) recommended studies using molecular markers to identify the origins of insular populations in the region. Because of uncertainty regarding the origins of LA populations, we omitted the species from table 1.

Hemidactylus palaichthus was long considered a Neotropical endemic (Kluge, 1969), with populations in northeastern SA, adjacent continental islands, and on the Maria Islands off St. Lucia (Powell, 1990). Originally thought to be derived from *H. brookii haitianus*, which is now known to be conspecific with African *H. angulatus* (Weiss and Hedges, 2007), its current systematic status is uncertain. Whether the Maria Island population is of natural or anthropogenic origin is unknown.

Intentionally introduced on Martinique (Henderson *et al.*, 1993) and now also known from Guadeloupe



(Breuil, 2009), *Gekko gecko* is the only member of this Asian genus to invade the Caribbean.

Dwarf geckos (Family Sphaerodactylidae): The genus *Gonatodes* contains mostly diurnal species widely distributed throughout the Neotropics. The origin of a single *Gonatodes vittatus* on Dominica was probably Venezuela (Malhotra *et al.*, 2007, 2011).

Sphaerodactylus geckos are small, frequently diurnal, often commensal lizards that have speciated widely in the region. Many species occur naturally in the islands and spread primarily as stowaways in cargo (Kraus, 2009). *Sphaerodactylus microlepis* is known as a stray on Dominica (Evans, 1989; Malhotra and Thorpe, 1999). Evans (1989) also suggested that *S. fantasticus* was introduced on Dominica, but subsequent studies (Jones, 1999; Malhotra *et al.*, 2007, 2011; Thorpe *et al.*, 2008) indicate that *S. fantasticus* is a relatively recent (but probably pre-human) colonizer on Dominica.

Iguanas (family Iguanidae): Like some tortoises, West Indian *Iguana iguana* populations include those founded by ancestors that arrived naturally (e.g., St. Lucia, Saba), some of which might now be distinct at the species level (Malone and Davis, 2004; Powell, 2004b). Other founders were transported by Amerindians or early colonists, have arrived recently, or represent mixtures of the above (Powell, 2004b; Henderson and Powell, 2009). Although some early introductions presumably were for food (e.g., Grant, 1937), the pet trade is the primary vector for many of the more recent introductions (Powell, 2004b). These animals pose a threat to endemic Lesser Antillean populations of *I. delicatissima*, with which they hybridize (e.g., Breuil and Sastre, 1994; Day and Thorpe, 1996; Breuil, 2000, 2002; Breuil *et al.*, 2007, 2010). A population of *I. delicatissima* was introduced from Îlet Chancel to Îlet à Ramiers (Martinique) for conservation purposes (Breuil, 2009).

Anoles (family Dactyloidae): Anoles are highly diverse (e.g., Losos, 2009), quite adaptable, and often function as human commensals. Many species in the region exploit buildings, ornamental plants, and the night-light niche (e.g., Henderson and Powell, 2001, 2009; Perry *et al.*, 2008; Powell and Henderson, 2008). Some are colorful and available in the pet trade (e.g., Kraus, 2009), but nearly all introductions within our region were inadvertent and attributable to stowaways in cargo such as building materials and ornamental plants.

Anolis cristatellus is native to the Puerto Rico Bank and was the only anole that made the list of most successful colonizing species (Bomford *et al.*, 2009). These anoles have recently been introduced into Dominica (Malhotra *et al.*, 2007, 2011), where they are expanding their range and displacing endemic populations of *A. oculatus* along the dry leeward coast, and to St.-Martin (Breuil *et al.*, 2010).

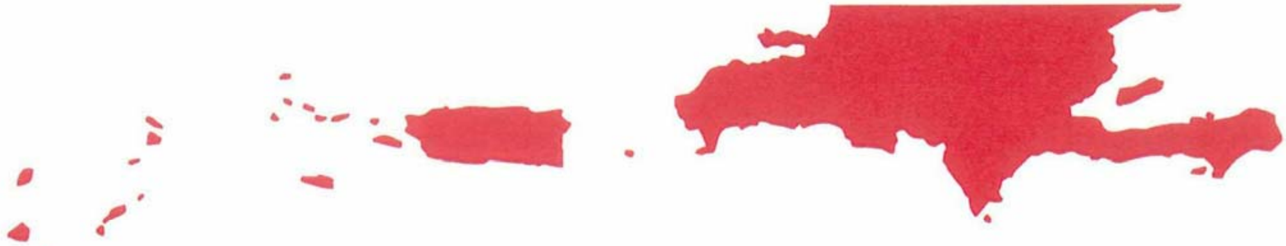
Perhaps the most frequently relocated West Indian member of the genus is *A. sagrei*, which is native to the Bahamas, Cuba, and presumably the lesser Cayman Islands (Little Cayman and Cayman Brac). These aggressive lizards can affect other anoles negatively (e.g., Brown and Echternacht, 1991), and have displaced endemic *A. carolinensis* from much of peninsular Florida (Lever, 2003 and references therein). Nothing comparable appears to be occurring on Grenada (Greene *et al.*, 2002) or St. Vincent (Treglia *et al.*, 2008), where populations have become established with building materials, but so far appear to be restricted to only the most intensely altered habitats on those islands. Whether such constraints will continue to restrict expansion in the future or whether they will apply to recently reported populations on Barbados (Fields and Horrocks, 2009), St. Maarten (Fläschendräger, 2010), and Canouan in the Grenadines (M. de Silva, pers. comm.) is unknown. *Anolis sagrei* is comparable in size to the native species on those islands and the potential for competition and possible displacement exists.

Populations of *A. carolinensis*, a NA native, have become established inside and outside of the Caribbean. Although the pet trade has been implicated in many instances (Kraus, 2009), the Anguillian introduction appears to be a consequence of arrival with nursery plants (e.g., Eaton *et al.*, 2001; Hodge *et al.*, 2003). *Anolis extremus* from Barbados and *A. wattsi* from Antigua are both established on St. Lucia, where they interact with each other and with endemic *A. luciae* (Lazell, 1972; Gorman, 1976; Henderson and Powell, 2009). The introduction of *A. bimaculatus* in St. Maarten (Powell *et al.*, 1992) appears to be one of the few documented colonization failures in the region (Powell *et al.*, 2005). Researchers intentionally introduced *A. pogus* from the Anguilla Bank onto Anguillita (Roughgarden *et al.*, 1984). That introduction eventually failed.

Ground lizards (family Teiidae): Lizards in the genus *Ameiva* are common on many Caribbean islands. Some species become habituated to human presence and many can be found in urban settings (Henderson and Powell, 2001; Powell and Henderson, 2008). *Ameiva ameiva*, which occurs naturally on the Grenada and St. Vincent island banks, has been documented on Barbados (Fields and Horrocks, 2009), presumably, however, originating from Trinidad.

Cnemidophorus vanzoi was intentionally introduced to Praslin Island from nearby natural populations, for investigative and conservation purposes (Dickinson and Fa, 2000). The population appears to have successfully colonized its new habitat.

Worm lizards (family Gymnophthalmidae): Gymnophthalmids, most occurring



in CA or SA, usually are small and many are associated with leaf-litter or live underground (Avila-Pires, 1995). *Gymnophthalmus pleii* is a Lesser Antillean endemic and *G. underwoodi*, which occurs on a number of Lesser Antillean islands, might have reached many of them via natural over-water dispersal (Powell, 2011). However, at least some populations, certainly those in the central and northern LA, are introduced (Powell, 2011), and some might be competing with or even displacing native populations of *G. pleii* on Martinique (Breuil, 2009) or Dominica (Turk *et al.*, 2010). This species is parthenogenetic (e.g., Cole, 1975; Hardy *et al.*, 1989; Cole *et al.*, 1990), which facilitates colonization because single individuals can establish new populations (e.g., Schwartz and Henderson, 1991; Hodge et *al.*, 2003; Powell *et al.*, 2005).

Amphisaenians (family Amphisbaenidae): Two records of *Amphisbaena fuliginosa* from SA, presumably strays, are known from St. Lucia and Grenada (Murphy *et al.*, 2010).

Blindsnakes (family Typhlopidae): Usually small and spending most of their lives underground, blindsnakes are unfamiliar to the general public and practically unheard of in the pet trade. However, they easily stow away in planters and often are spread by the ornamental plant trade. Originally from Asia, the Flowerpot Snake (*Ramphotyphlops braminus*) might be the most widely distributed snake in the world. The family Typhlopidae, genus *Ramphotyphlops*, and species *R. braminus* top the respective lists of most successful colonizing taxa (Bomford *et al.*, 2009). Since the first report of the species on Anguilla (Censky and Hodge, 1997), it has been documented widely in the Caribbean, including recent reports from St. Christopher (Orchard, 2010), Barbados (Fields and Horrocks, 2009; Horrocks and Fields, 2011), Guadeloupe (Breuil and Ibéné, 2008; Breuil, 2009), Mustique (M. de Silva, in litt., 2009), and St. Eustatius (Powell, 2011). A parthenogenetic species, it appears to be ideally pre-adapted to dispersal by humans (e.g., McKeown, 1996). West Indian populations are almost certainly derived from the introduced population in Florida.

Boas (family Boidae): Boas are common in the pet trade, which is the primary method of arrival for these species in the Caribbean and elsewhere (Kraus, 2009). Interestingly, Bomford *et al.* (2009) rated the family Boidae as the least successful colonizing family of reptiles or amphibians. Most records of *Boa constrictor*, presumably from the SA or CA mainland, are of strays that have failed to found populations. The stray found on Terre de Bas (îles de la Petite Terre, Guadeloupe; Barré *et al.*, 1997) might pertain to *Boa nebulosa* (Lorvelec *et al.*, 2011), which is endemic to Dominica. *Epicrates cenchria*, also from SA, is known as a stray on St. Maarten (Powell *et al.*, 2005) and Martinique (Breuil, 2009).

Pythons (family Pythonidae): Pythons, like boas, are frequently encountered in the live animal trade. Four records, *Morelia amethistina* on Guadeloupe (Breuil and Ibéné, 2008; Breuil, 2011), *Python curtus* and *P. regius*, both on St. Maarten (Powell *et al.*, 2005), and *P. regius* on Martinique (Breuil, 2009) document strays. The latter two species also have been found on St.-Barthélemy (Breuil *et al.*, 2010). Establishment of any of these species would be worrisome, as it has been in Florida (e.g., Snow *et al.*, 2007; Reed *et al.*, 2010).

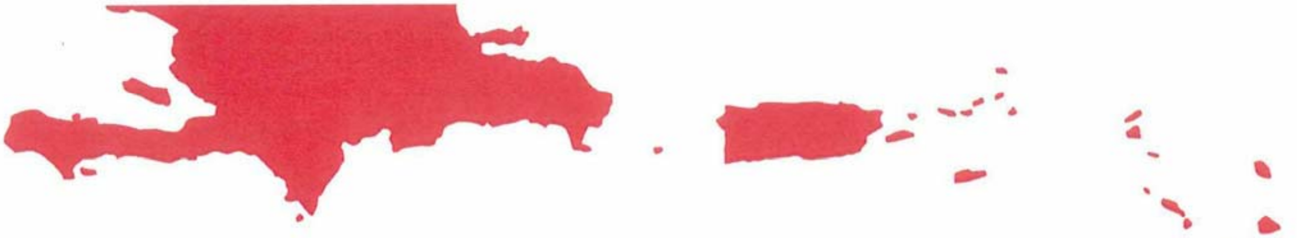
Common snakes (family Colubridae): The pet and nursery trades are the primary vectors for arrival of *Pantherophis guttatus* (formerly *Elaphe guttata*) from NA. All Lesser Antillean records to date of this and another member of the genus (*P. alleghaniensis*; formerly *Elaphe obsoleta*) document only strays. The latter species has been recorded only on Martinique (Breuil and Ibéné, 2008; Breuil *et al.*, 2010). *Tantilla melanocephala*, probably of SA origin, has been found on four islands on the Grenada Bank (Henderson and Powell, 2006; Berg *et al.*, 2009; J. Boone and D. Scantlebury, pers. comm.) and its arrival has been associated with shipments of sand from SA for construction purposes. Its long-term prospects remain unclear. Underwood *et al.* (1999) reported the presence of *Mastigodryas bruesi*, which occurs naturally on the Grenada and St. Vincent banks, on Barbados.

American rear-fanged snakes (family Dipsadidae): *Alsophis rufiventris* from Saba or St. Eustatius was recorded as a stray on St. Maarten (Powell *et al.*, 2005).

Water snakes (family Natricidae): Two stray *Natrix natrix* from Europe have been recorded on Martinique (Breuil, 2009).

Discussion

The number of introductions and the consequent number of established populations in the LA is alarming, even when we consider our uncertainty regarding the origins of some insular populations (particularly some of those of *Eleutherodactylus johnstonei, Rhinella marina, Gymnophthalmus underwoodi, Hemidactylus* spp., *Iguana iguana, Chelonoidis carbonaria*), some of which were almost certainly natural, but others undoubtedly were human-mediated or some combination of the two. Several additional reports arrived as we were working on this review, and the trends shown by both amphibians and reptiles suggest that the rate of arrivals will continue to increase with time. For example, *Scinax* cf. *x-signatus* has been found on five new islands (Grande-Terre, Basse-



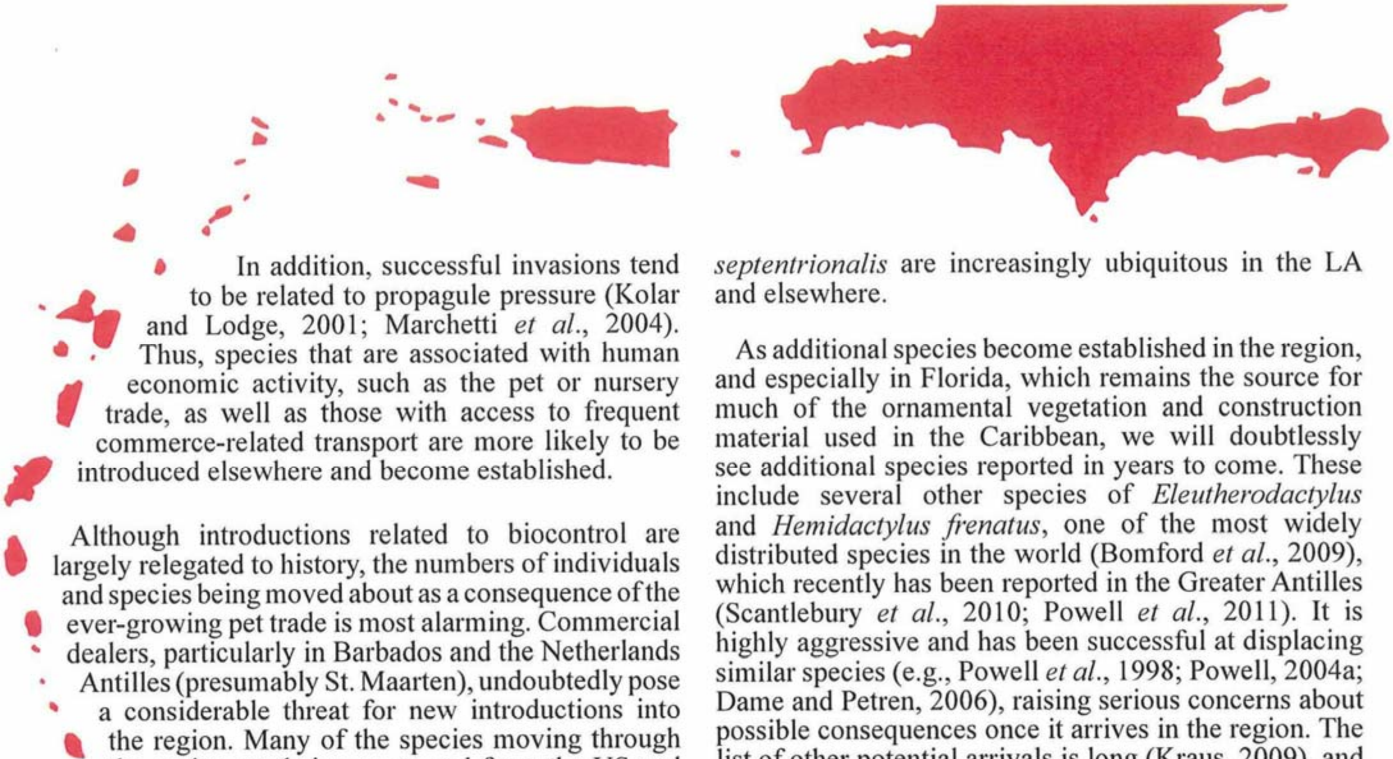
Terre, Désirade, Marie-Galante, Martinique) in the past eight years (Breuil *et al.*, 2010). In some instances, these frogs are phenomenally abundant. Multiple invasions of the same islands are almost certainly responsible, with wooden houses assembled in Brazil and French Guiana apparently serving as the means of introduction (Breuil *et al.*, 2010; Breuil, 2011).

Given the extent of negative ecological and economic effects documented in the region and elsewhere, invasive populations of herpetofauna have become a serious conservation issue. Additional deleterious effects probably go unnoticed or unreported, especially when smaller, less obvious species are introduced and their impact is primarily on smaller invertebrates, which are rarely monitored and the impact on which cannot, at this time, be evaluated. The magnitude of existing problems is almost certainly greater than currently realized, and can only get worse. An integrated policy response is clearly necessary to address what is a regional issue.

Amerindians arrived in the Caribbean islands about 6000 years ago (Wilson, 2001) and Europeans about 500 years ago. The impact of the latter has been felt in the region longer than elsewhere in the Western Hemisphere, and Fosberg (1983) observed that: "The impact of European man on islands made the changes due to aboriginal man seem minor by comparison." Only 5-10% of the West Indian herpetofauna has benefited from human activities (Henderson and Powell, 2001). One of the most substantive and frequently deleterious effects has been the increasing number of introductions of plants and animals to islands where they are not native. Although not covered here, many of those introductions, especially of mammalian herbivores (e.g., goats and cattle) and predators (e.g., mongooses, raccoons, oppossums, dogs, cats, and monkeys, the latter on Grenada and Barbados and, most recently, on St. Maarten; B. Ibéné, pers. comm.), have had varying degrees of deleterious effects on the regional herpetofauna.

The characteristics of amphibian and reptilian species introduced in the region correspond very closely to those outlined for taxa associated with Caribbean urban areas by Powell and Henderson (2008): they (1) are ecologically versatile and capable of tolerating a broad range of sometimes rapidly and dramatically changing conditions; (2) exhibit edificarian tendencies in and outside urban areas (e.g., gekkonids, some sphaerodactyls, many anoles); (3) tend to be edge species or, at least, species that are euryecious, not habitat specialists; (4) are primarily invertebrate predators; (5) are heliotherms if diurnal (e.g., edge-inhabiting anoles); and (6) often are scansorial (e.g., treefrogs, geckos, anoles). These features in turn correlate nicely with those shared by anoles identified by Williams (1969) as successful colonizers, and with the observation that invasive species in general tend to be generalists (Dukes and Mooney, 1999). Our data also support the generalizations that good invaders tend to be small and capable of rapid reproduction (Kolar and Lodge, 2001), have a past record of being invasive elsewhere (Kolar and Lodge, 2001; Marchetti *et al.*, 2004), are highly tolerant of humans (Perry *et al.*, 2008), are related to other documented invaders (Richardson and Pyšek, 2006), and are native to areas with comparable climates (Bomford *et al.*, 2009) and near possible introduction sites (Marchetti *et al.*, 2004). In contrast, our data do not support the view that taxa that are more distantly related to the native biota are more likely to be invasive (Strauss *et al.*, 2006).

The genera *Eleutherodactylus*, *Hemidactylus,* and *Anolis* comprise a substantive fraction of the species tabulated in this review. All are relatively small, capable of high reproductive output, often associated with humans and habitats modified by human activities, are naturally or secondarily found within the region, and have become invasive at multiple locations. Specifically, the species that have successfully colonized the most islands either follow that pattern or have been intentionally introduced for perceived economic benefits. Cane Toads (*Rhinella marina*; 16 islands or island groups, although some populations might have been established by natural over-water dispersal) were introduced widely for biocontrol. E*leutherodactylus johnstonei* (23 islands or island groups), Cuban Treefrogs (*Osteopilus septentrionalis* (7), *Gymnophthalmus underwoodi* (13), and *Ramphotyphlops braminus* (8) are small human commensals easily transported inadvertently with goods and ornamental plants. The latter two are relatively inconspicuous and benefit further by being parthenogenetic, thus requiring but a single individual to establish a population. They probably occur on many more islands than have been documented. In addition, *Hemidactylus mabouia*, introduced populations of which might occur on the majority of LA islands, also functions as a human commensal. *Iguana iguana* (9), *Trachemys scripta* (6), and *Chelonoidis carbonaria* (4) break with the pattern in being large and herbivorous or omnivorous, but all are frequently transported from place to place for food (both historically and recently) or as pets. The situation for *I. iguana*, however, is complicated by the presence of endemic populations that might be subjected to hybridization with more recent arrivals, primarily originating from native Neotropical populations or the introduced populations in Florida and within the region. Two other widely introduced species, *Anolis sagrei* (5) and *Pantherophis guttatus* (5, although no established populations have been documented to date in the LA) are notable because of the potential for severe negative consequences resulting from potential competition (*A. sagrei*) with or predation (*P. guttatus*) on native species.



In addition, successful invasions tend to be related to propagule pressure (Kolar and Lodge, 2001; Marchetti *et al.*, 2004). Thus, species that are associated with human economic activity, such as the pet or nursery trade, as well as those with access to frequent commerce-related transport are more likely to be introduced elsewhere and become established.

Although introductions related to biocontrol are largely relegated to history, the numbers of individuals and species being moved about as a consequence of the ever-growing pet trade is most alarming. Commercial dealers, particularly in Barbados and the Netherlands Antilles (presumably St. Maarten), undoubtedly pose a considerable threat for new introductions into the region. Many of the species moving through the region on their way to and from the US and other markets could easily become established if given the opportunity through escapes or releases. As in Florida (e.g., Meshaka *et al.*, 2004), escapes could be facilitated by hurricanes and releases, especially by dealers seeking to establish local and easily exploitable populations of popular species, and could dramatically change the very nature of the herpetofaunas on a number of islands.

The success rate (66.3%) for establishing new populations was considerably greater than those calculated by Bomford *et al.* (2009) for Britain (12 of 51, 23.5%) or California (13 of 62, 21.0%), comparable to that in Florida (47 of 80, 58.8%), but less than that for the "greater Caribbean" (Powell *et al.*, 2011; 70.2%). Most of the success probably is attributable to the hospitable island climates and high incidence of climate-matching (Bomford *et al.*, 2009) with areas where source populations are native. In addition, with an increasing number of invasions involving alien species established in Florida, the possibility that those species were pre-screened for success as colonizers cannot be discounted.

In general, amphibians are less likely than reptiles to successfully colonize islands, both because of osmotic sensitivity during the dispersal stage and of their more stringent ecological requirements during the establishment phase (Vences *et al.*, 2003). In our sample, however, the number of amphibian populations established via human-aided dispersal is sizeable, although the species diversity of reptiles is considerably greater. The relative abundance of amphibian introductions is largely attributable to four species that are resilient or hardy and have been intentionally introduced or are closely tied to human economic activity. Consequently, species such as *Eleutherodactlylus johnstonei*, among the top five most successful colonizing species of reptiles and amphibians (Bomford *et al.*, 2009), *Rhinella marina*, *Scinax* cf. *x-signatus*, and *Osteopilus septentrionalis* are increasingly ubiquitous in the LA and elsewhere.

As additional species become established in the region, and especially in Florida, which remains the source for much of the ornamental vegetation and construction material used in the Caribbean, we will doubtlessly see additional species reported in years to come. These include several other species of *Eleutherodactylus* and *Hemidactylus frenatus*, one of the most widely distributed species in the world (Bomford *et al.*, 2009), which recently has been reported in the Greater Antilles (Scantlebury *et al.*, 2010; Powell *et al.*, 2011). It is highly aggressive and has been successful at displacing similar species (e.g., Powell *et al.*, 1998; Powell, 2004a; Dame and Petren, 2006), raising serious concerns about possible consequences once it arrives in the region. The list of other potential arrivals is long (Kraus, 2009), and several could become serious ecological or economic pests. In addition, some species already in the region, most notably the increasingly widespread Green Iguana (*I. iguana*; e.g., Sementelli *et al.*, 2008) and the Eastern Corn Snake (*Pantherophis guttatus*) have potential to become considerably more damaging than they have hitherto been. Because of the predominance of Florida as a source for invasive amphibians and reptiles, a concerted effort to sanitize cargo and ornamental plants shipped from there is an urgent need.

Although extended dry periods can preclude many unwanted invasives from becoming established, "garden refugia" are available for some species. Amphibians often cannot survive outside of artificially mesic situations (e.g., gardens, golf courses, hotel and resort grounds) during droughts (e.g., *Eleutherodactylus johnstonei* on Anguilla; Hodge *et al.*, 2011). Even some introduced reptilian populations, such as iguanas, are much more plentiful in inhabited areas than in the bush. For snakes, however, this is rarely an option (diminutive and secretive *Ramphotyphlops braminus* might be an exception). Snakes that cannot survive in relatively natural situations and retreat to "gardens" during dry periods find themselves in a "killing zone," where people and domestic predators (dogs and cats) will see them and kill them (Powell and Henderson, 2008).

Although a few efforts have been made to control or eradicate non-native herpetofauna in the LA, such efforts remain by far the exception — and some that exist are never implemented. For example, in April 2006, the Ministry of Ecology, Energy and Sustainable Development decided to eradicate *Iguana iguana* in Guadeloupe to prevent competition and hybridization with *Iguana delicatissima*, but nothing was done at that time. Thus, we expect that both firmly and newly established species will generally persist in the region unless policy and management efforts change, causing Lesser Antillean islands to become part of international trends toward an enhanced pantropical herpetofauna at the expense of impoverished native herpetofaunas.

The need to advance protection quickly, perhaps well ahead of political support, flows from the very poor evidence that any environmental Kuznets curve affects these outcomes. An environmental Kuznets curve loosely predicts that, as incomes rise and standards of living improve, greater social support often evolves to mitigate social, environmental, and ecological hazards (Arrow *et al.*, 1995). If this phenomenon holds for invasions in the LA, we should be seeing a declining rate of new introductions as GDP rises. That does not seem to be happening at this time. However, economic theory would not predict that invasives would be among the first items corrected as an economy grows. Although growing GDP may have been responsible for declines in emissions of nitrogen oxides, carbon monoxides, sulfur dioxides, and lead in the 1970s and 1980s, the relationship does not seem to hold for aggressive land use conversions to monocultures or impervious surfaces, energy demand, and overall resource consumption. These "high footprint" activities appear to parallel economic development, which would explain why overall atmospheric carbon emissions do not seem to abate with rising GDP (Wagner, 2008). Issues of biodiversity protection in particular have not shown convincing empirical evidence that any abatement turn is emerging on the development horizon (Mills and Waite, 2009). Invasions in the region would arguably be far behind the curve — or the bend in the curve, as invasions seem to correlate with the very activities most directly responsible for economic growth and development on many islands. Without a much more diverse set of economic activities contributing to economic development, the draw of the US economy and the developments in agriculture, tourism, shipping, and resource extractive industries would seem to continue to accelerate these threats at least for the near and intermediate terms. Precautionary approaches in the name of acute economic stress or intrinsic ecological deterioration from regional invasions is arguably the strongest motivation for controlling introduced species.

The benefits of eradicating an invasive species — a single injection of funds and effort and the problem is solved — far outweighs the cost of a perennial control program (Gardener *et al.*, 2010 and references therein). Many regional introductions remain localized, often in anthropogenic situations (e.g., gardens and grounds of hotels and resorts), and are therefore easy targets for cost-effective eradication projects. Consequently, the development of eradication programs should be a high priority for agencies responsible for managing biodiversity.

Nonetheless, prevention remains by far the best — and most economical — approach (Wittenberg and Cock, 2001; Rödder and Weinsheimer, 2010). In that context, increased scrutiny of the transport to and from the islands (whether cargo where inadvertent stowaways may hide, ornamental plants that often carry hitchhikers, or the pet trade that is the source of so many introductions) seems especially desirable. This can help reduce the spread of other problem species, such as agricultural pests, that also are a source of concern for local governments.

To address these concerns, we urge an increased regional and global cooperation on fighting invasive species in general and invasive herpetofauna in particular. Although the LA are highly fragmented both geographically and politically, precedents for such cooperation exist (e.g., the Organization of Eastern Caribbean States [OECS] and the Caribbean Community and Common Market [CARICOM]). We urge the adoption of a similarly integrated approach that incorporates not only governmental controls but also investments in local response capacity. Our combined decades of work in the region show a strong need for considerably more monitoring, education, and research in this area.

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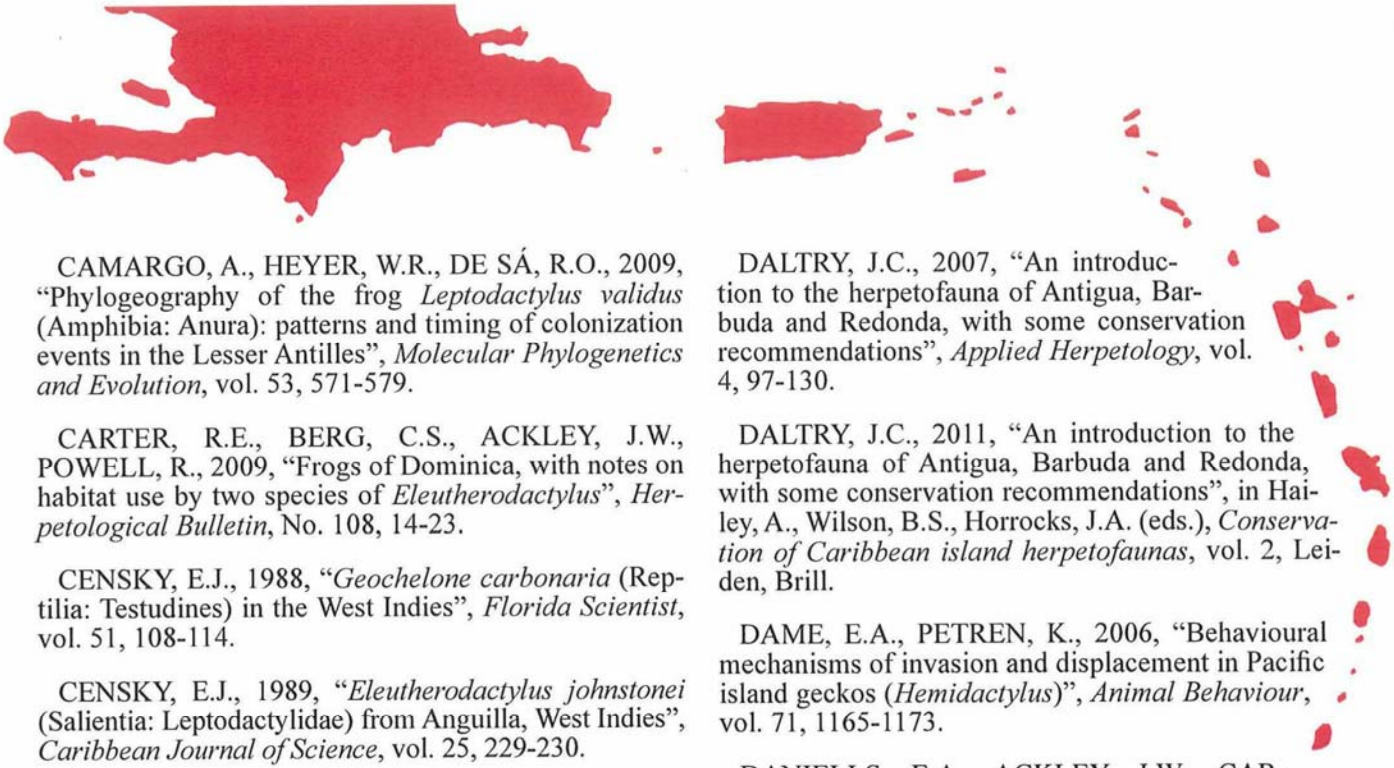

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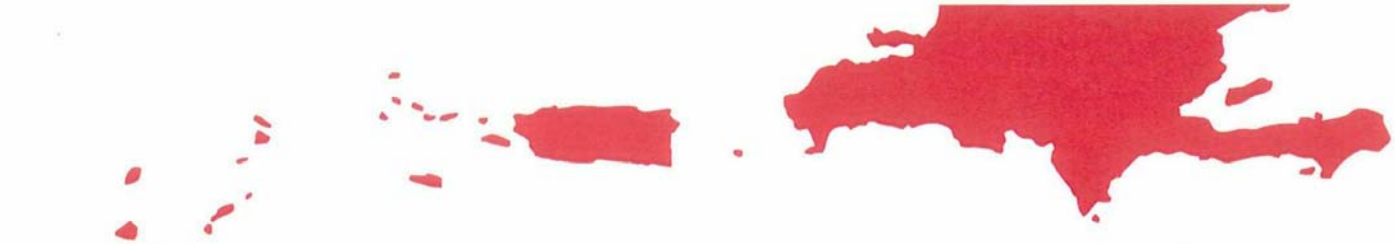

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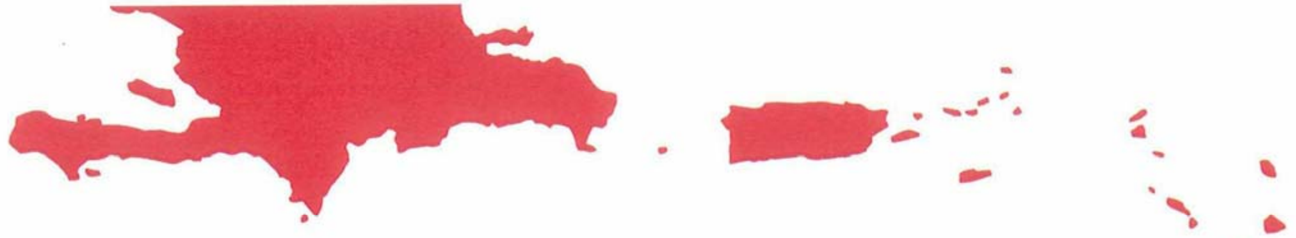

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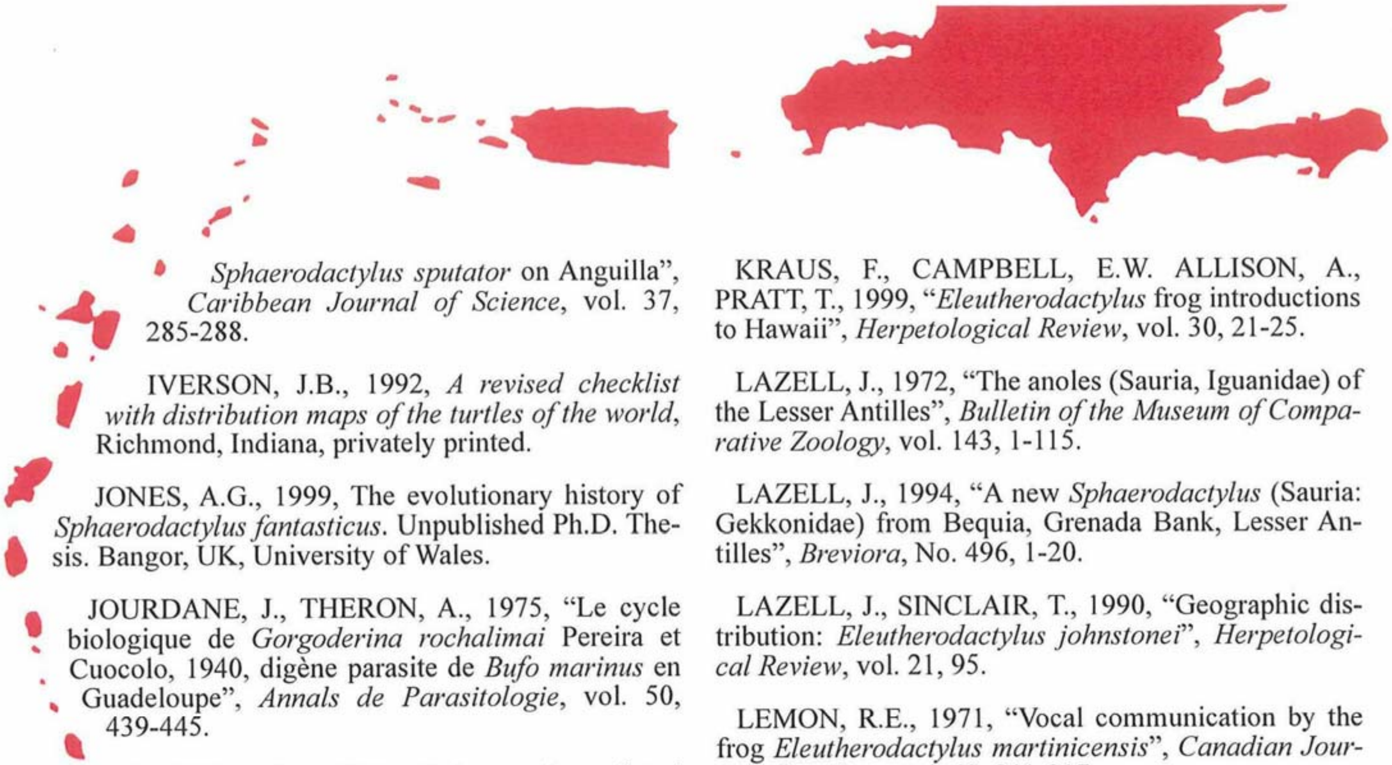

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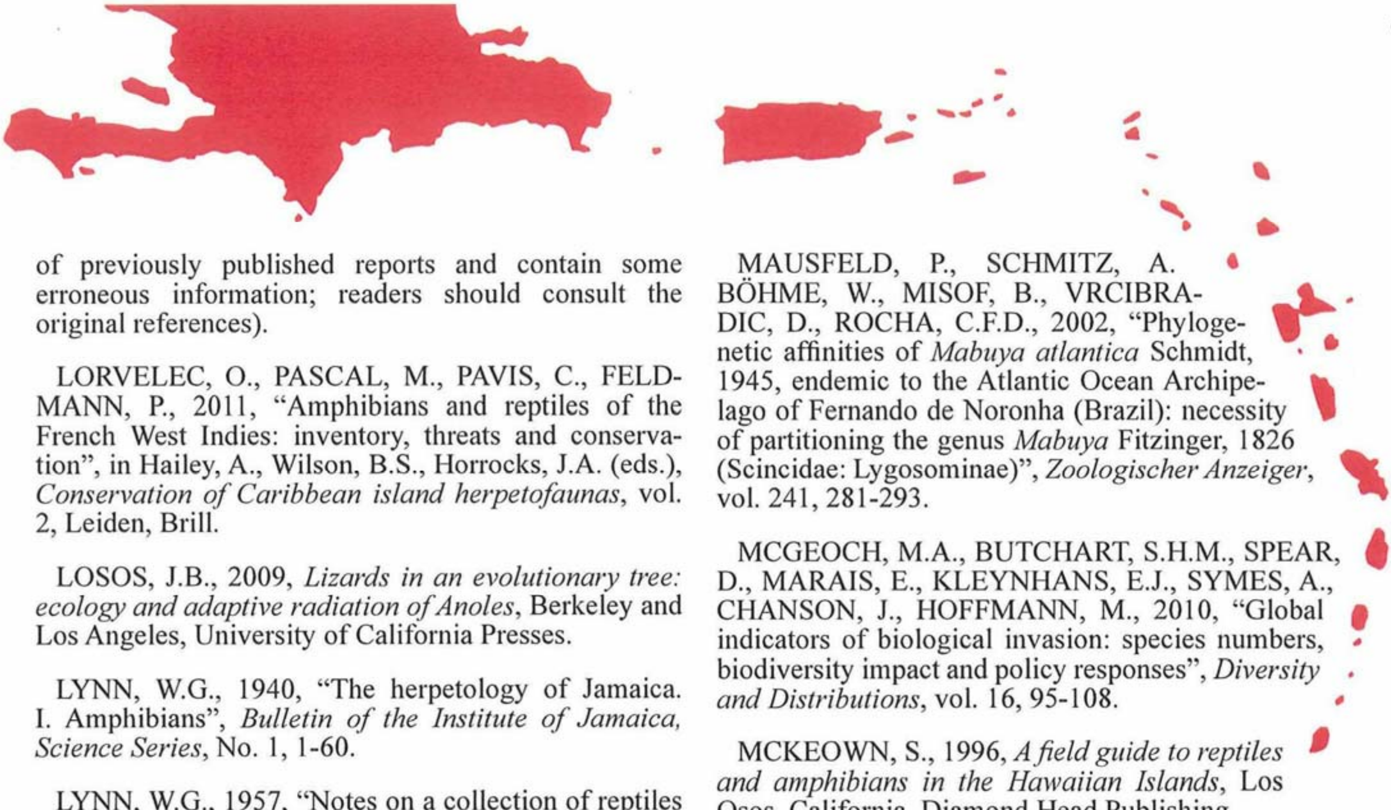

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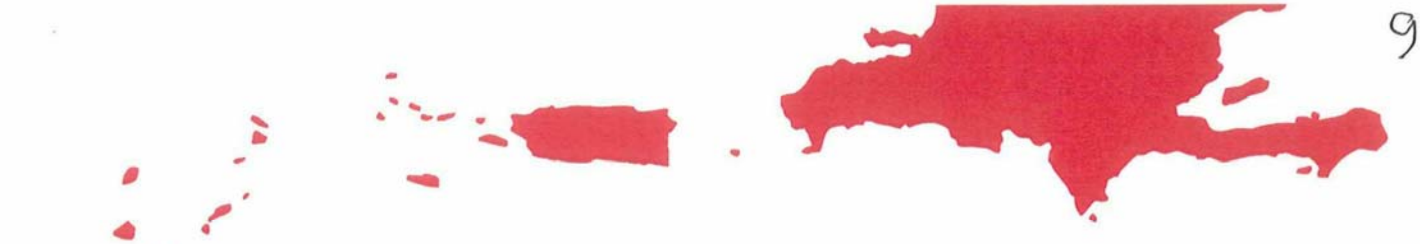

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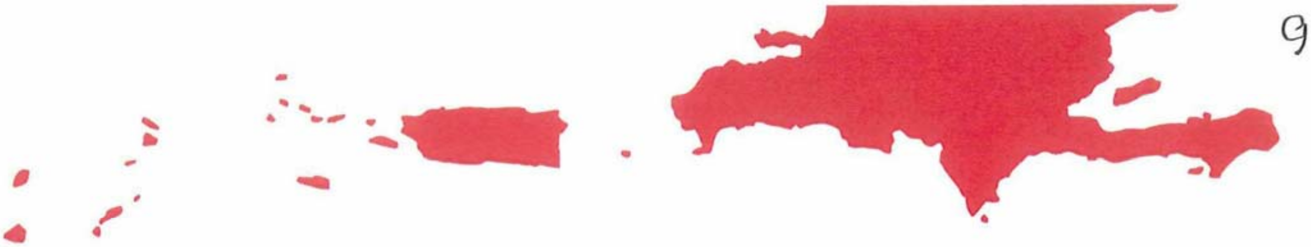

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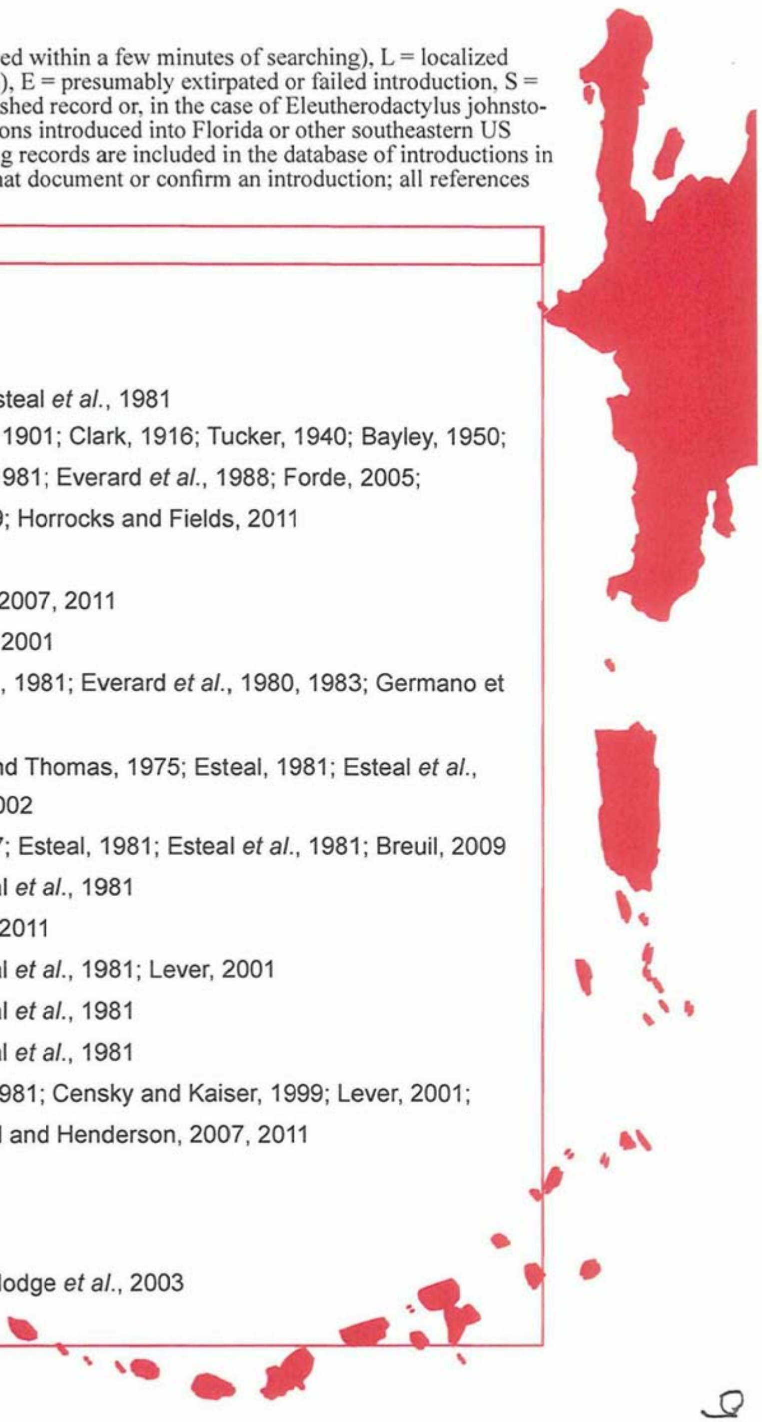
Table 1. Species of amphibians and reptiles introduced in the Lesser Antilles. Status: W = widespread (likely to be encountered within a few minutes of searching), L = localized (likely to be encountered at most sporadically, even in appropriate habitat, although possibly abundant within a few small areas), E = presumably extirpated or failed introduction, S = stray (no indication of a breeding population ever becoming established). Question marks (?) indicate uncertainty about a published record or, in the case of Eleutherodactylus johnstonei, the native range. * = at least some individuals probably introduced intentionally. ** = source almost certainly was populations introduced into Florida or other southeastern US states (although some might be secondary introductions from populations established from Florida stock). Most of the following records are included in the database of introductions in Kraus (2009) and are listed in Schwartz and Henderson (1991) and Henderson and Powell (2009). References cited are those that document or confirm an introduction; all references pertaining to introduced populations are not necessarily listed.

Species (Native Range)	Introduced (Status)	Pertinent Reference(s)
FROGS		
Amphibia: Anura: Bufonidae		
Rhinella marina[1] (Neotropical mainland)	Anguilla (**S**)	Hodge *et al.*, 2003
	Antigua* (**W**)	Clark, 1916; Lynn, 1957; Esteal, 1981; Esteal *et al.*, 1981
	Barbados* (**W**)	Schomburgk, 1848; Gosse, 1851; Waite, 1901; Clark, 1916; Tucker, 1940; Bayley, 1950; Grant, 1959; Esteal, 1981; Esteal *et al.*, 1981; Everard *et al.*, 1988; Forde, 2005; Norville, 2005; Fields and Horrocks, 2009; Horrocks and Fields, 2011
	Canouan (Grenadines) (**S**)	Daudin and de Silva, 2007, 2011
	Carriacou (Grenadines) (**S**)	Lever, 2001, 2003; Daudin and de Silva, 2007, 2011
	Dominica (**E**)	Esteal, 1981; Esteal *et al.*, 1981b; Lever, 2001
	Grenada* (**W**)	Barbour, 1914; Esteal, 1981; Esteal *et al.*, 1981; Everard *et al.*, 1980, 1983; Germano et al., 2003
	Guadeloupe* (**W**)	Jourdane and Theron, 1975; Schwartz and Thomas, 1975; Esteal, 1981; Esteal *et al.*, 1981; Nassi and Dupouy, 1988; Breuil, 2002
	Martinique* (**W**)	Gosse, 1851; Waite, 1901; Barbour, 1937; Esteal, 1981; Esteal *et al.*, 1981; Breuil, 2009
	Montserrat* (**W**)	Barbour, 1914, 1937; Esteal, 1981; Esteal *et al.*, 1981
	Mustique (Grenadines) (**L**)	Paice, 2005; Daudin and de Silva, 2007, 2011
	Nevis* (**W**)	Barbour, 1914, 1937; Esteal, 1981; Esteal *et al.*, 1981; Lever, 2001
	St. Christopher* (**W**)	Barbour, 1914, 1937; Esteal, 1981; Esteal *et al.*, 1981
	St. Lucia* (**W**)	Barbour, 1914, 1937; Esteal, 1981; Esteal *et al.*, 1981
	St. Vincent* (**W**)	Clark, 1916; Esteal, 1981; Esteal *et al.*, 1981; Censky and Kaiser, 1999; Lever, 2001; Treglia, 2006; Mallery *et al.*, 2007; Powell and Henderson, 2007, 2011
	Union (Grenadines) (**S**)	J. Daudin, pers. comm.
Amphibia: Anura: Eleutherodactylidae (formerly assigned to the family Leptodactylidae)		
Eleutherodactylus johnstonei (Antigua Bank?)	Anguilla (**L**)	Censky, 1989; Kaiser and Hardy, 1994; Hodge *et al.*, 2003



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[1] Some insular populations might have become established via natural over-water dispersal.

Species (Native Range)	Introduced (Status)	Pertinent Reference(s)
	Barbados (**W**)[2]	Feilden, 1889, 1903; Bayley, 1950; Grant 1959; Schwartz, 1967; Lemon, 1971; Marsh, 1983; Everard *et al.*, 1990; Ovaska, 1991a, 1991b, 1992; Ovaska and Hunte, 1992; Kaiser and Hardy, 1994; Kaiser, 1997; Fields and Horrocks, 2009; Horrocks and Fields, 2011
	Barbuda (**L**)	Kaiser, 1997
	Bequia (Grenadines)*(**L**)	Lazell and Sinclair, 1990; Kaiser and Hardy, 1994; Lazell, 1994; Daudin and de Silva, 2007, 2011
	Canouan (Grenadines) (**L**)	Daudin and de Silva, 2007, 2011
	Carriacou (Grenadines) (**L**)	Daudin and de Silva, 2007, 2011
	Dominica (**E**[3])	Bullock and Evans, 1990; Corke, 1992; Kaiser, 1992, 1997; Kaiser and Hardy, 1994; Kaiser and Wagenseil, 1995; Daniells *et al.*, 2008
	Grenada (**W**)	Barbour, 1914; Schwartz, 1967; Kaiser and Hardy, 1994; Kaiser and Henderson, 1994; Kaiser, 1997; Goldberg *et al.*, 1998; Williamson *et al.*, 2002; Germano *et al.*, 2003; Sander *et al.*, 2003; Henderson and Berg, 2005, 2006, 2011
	Guadeloupe (**W**)	Schwartz *et al.*, 1978; Hardy and Harris, 1979; Hardy, 1985; Henderson *et al.*, 1992; Kaiser and Hardy, 1994; Kaiser and Henderson, 1994; Kaiser, 1997; Breuil, 2002; Breuil *et al.*, 2009
	Les Îles des Saintes (**W**)	Breuil, 2002
	Marie-Galante (**W**)	Henderson *et al.*, 1992; Kaiser and Hardy, 1994; Breuil, 2002; Breuil *et al.*, 2009
	Martinique (**W**)	Lescure, 1966; Kaiser and Henderson, 1994; Lescure and Marty, 1996; Kaiser, 1997; Breuil, 2009; Breuil *et al.*, 2009
	Montserrat (**?**)	Kaiser and Hardy, 1994
	Mustique (Grenadines) (**L**)	Henderson *et al.*, 1992; Kaiser and Hardy, 1994; Daudin and de Silva, 2007, 2011
	Nevis (**?**)	Kaiser and Hardy, 1994
	Petit St. Vincent (Grenadines) (**L**)	Daudin and de Silva, 2007, 2011
	Saba (**W**)	Kaiser and Hardy, 1994; Powell *et al.*, 2005; Powell, 2006
	St.-Barthélemy (**L**)	Kaiser, 1992; Breuil, 2002; Lorvelec *et al.*, 2007, 2011; Breuil *et al.*, 2009
	St. Christopher (**?**)	Kaiser and Hardy, 1994
	St. Eustatius (**L**)	Kaiser and Hardy, 1994; Powell *et al.*, 2005; Powell, 2006
	St. Lucia (**L**)	Lescure and Marty, 1996; Lescure, 2000
	St.-Martin/St. Maarten (**L**)	Kaiser and Hardy, 1994; Breuil, 2002; Powell *et al.*, 2005; Powell, 2006
	St. Vincent (**W**)	Lescure, 2000; Treglia, 2006; Mallery *et al.*, 2007; Powell and Henderson, 2007, 2011
Eleutherodactylus martinicensis (Antigua, Guadeloupe, Dominica, Martinique)	St.-Barthélemy (**L**)	Kaiser, 1992; Breuil *et al.*, 2009
	St.-Martin/St. Maarten (**L**)	Breuil, 2002; Breuil *et al.*, 2009

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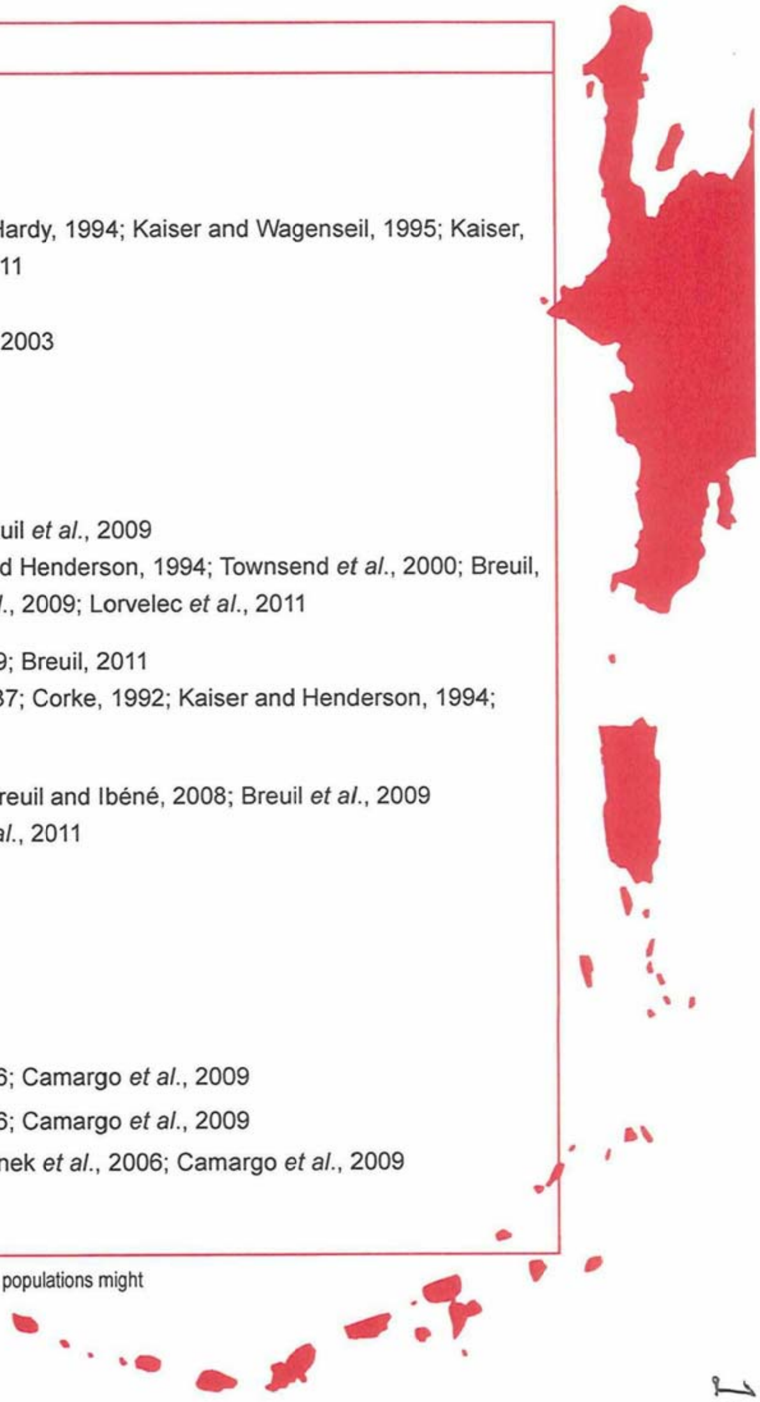
[2] Marsh (1983) indicated that this species was native to Barbados.

[3] See Daniells *et al.* (2008) and Carter *et al.* (2009).

Species (Native Range)	Introduced (Status)	Pertinent Reference(s)
Eleutherodactylus planirostris	Grenada (**S**[4])	Kaiser, 1992; Kraus *et al.*, 1999
(Cuba, Bahamas)		
Eleutherodactylus sp.	Guadeloupe (**S**)	Breuil, 2002
(?)	Union Island (Grenadines) (**L**[5])	Henderson *et al.*, 1992; Kaiser and Hardy, 1994; Kaiser and Wagenseil, 1995; Kaiser, 1997; Daudin and de Silva, 2007, 2011
Amphibia: Anura: Hylidae		
Osteopilus septentrionalis	Anguilla** (**W**)	Townsend *et al.*, 2000; Hodge *et al.*, 2003
(Cuba, Bahamas, Cayman Islands)	Antigua** (**W**)	Daltry, 2007, 2011
	Dominica** (**S**)	Malhotra *et al.*, 2007, 2011
	Nevis** (**S**)	Lever, 2003
	Saba** (**S**)	Powell, 2006, 2007
	St.-Barthélemy** (**W**)	Breuil, 2002; Hodge *et al.*, 2003; Breuil *et al.*, 2009
	St.-Martin/St. Maarten** (**W**)	Powell *et al.*, 1992[6], 2005; Kaiser and Henderson, 1994; Townsend *et al.*, 2000; Breuil, 2002; Hodge *et al.*, 2003; Breuil *et al.*, 2009; Lorvelec *et al.*, 2011
Scinax ruber	Martinique (**W**)	Breuil, 2002, 2009; Breuil *et al.*, 2009; Breuil, 2011
(Neotropical mainland)	St. Lucia (**L**)	Boulenger, 1891; Barbour, 1914, 1937; Corke, 1992; Kaiser and Henderson, 1994; Censky and Kaiser, 1999
Scinax x-signatus	Guadeloupe (**W**)	Breuil, 2004; Lorvelec *et al.*, 2011; Breuil and Ibéné, 2008; Breuil *et al.*, 2009
(Neotropical mainland)	Marie-Galante (**L**)	Breuil and Ibéné, 2008; Lorvelec *et al.*, 2011
	La Désirade (**L**)	Breuil and Ibéné, 2008
	Martinique (**L**)	Breuil *et al.*, 2009; Breuil, 2011
Amphibia: Anura: Leptodactylidae		
Leptodactylus fallax	Grenada* (**E**)	Groome, 1970
(Dominica, Montserrat)	Martinique* (**E**)	Lescure, 1983
Leptodactylus validus[7]	Bequia (Grenadines) (**L**)	Hardy *et al.*, 2004; Yanek *et al.*, 2006; Camargo *et al.*, 2009
(Northern SA)	Grenada (**W**)	Hardy *et al.*, 2004; Yanek *et al.*, 2006; Camargo *et al.*, 2009
	St. Vincent (**W**)	Hardy *et al.*, 2004; Treglia, 2006; Yanek *et al.*, 2006; Camargo *et al.*, 2009
LIZARDS		
Reptilia: Squamata: Gekkonidae		



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[4] Until recently, this species was thought to be native to the Grenada and St. Vincent banks, but Yanek *et al.* (2006) suggested that the Lesser Antillean populations might have arrived with human mediation.

[5] This is almost certainly a spurious record based on an unpublished observation promulgated in the literature.

[6] This frog usually is represented in the literature as *Eleutherodactylus johnstonei*.

[7] Previously listed by Schwartz and Henderson (1991), but misidentified as *Scinax rubra*.

Species (Native Range)	Introduced (Status)	Pertinent Reference(s)
Gekko gecko	Guadeloupe (**L**)	Breuil, 2004, 2009; Breuil and Ibéné, 2008; Breuil *et al.*, 2010; Lorvelec *et al.*, 2011
(Southeastern Asia)	Martinique* (**L**)	Henderson *et al.*, 1993; Breuil, 2009; Breuil *et al.*, 2010
Hemidactylus palaichthus	Maria Island (off St. Lucia) (**L**)	Kluge, 1969; Powell, 1990
(Northeastern SA)		
Reptilia: Squamata: Gymnophthalmidae		
Gymnophthalmus underwoodi[8]	Antigua (**L**)	Powell and Lindsay, 1999; Daltry, 2007, 2011
(Neotropical mainland)	Barbados[9] (**W**)	Grant, 1958; Fields and Horrocks, 2009
	Barbuda (**?**)	Censky and Lindsay, 1997
	Bequia (Grenadines) (**?**)	Lazell and Sinclair, 1990
	Dominica (**L**)	Brooks, 1983 (as "G. pleei"); Daniells *et al.*, 2008
	Grenada (**L**)	Hardy, 1982
	Guadeloupe (**W**)	Schwartz and Thomas, 1975; Breuil, 2002; Breuil *et al.*, 2010
	La Désirade (**W**)	Breuil, 2002
	Marie-Galante (**W**)	Breuil, 2002; Breuil *et al.*, 2010
	Martinique[10] (**L**)	Breuil, 2002, 2009; Breuil *et al.*, 2010
	St.-Martin/St. Maarten (**L**)	van Buel and Powell, 2006; Breuil, 2009; Breuil *et al.*, 2010; Lorvelec *et al.*, 2011 Powell, 2011
	St. Vincent (W)	Schwartz and Thomas, 1975; Treglia, 2006
	Union Island (Grenadines) (L)	RP, RWH, pers. obs.
Reptilia: Squamata: Iguanidae		
Iguana iguana[11]	Anguilla[12] (**L**)	Censky *et al.*, 1998, Hodge *et al.*, 2003, 2011; Powell, 2004b
(Neotropics)	Antigua (**S**)	Powell, 2004b; Powell *et al.*, 2005
	Barbuda (**S**)	Powell, 2004b; Powell *et al.*, 2005
	Guadeloupe[13] (**W**)	Day and Thorpe, 1996; Breuil, 2002; Day *et al.*, 2000; Powell, 2004b; Breuil *et al.*, 2007, 2010
	Les Îles des Saintes[14] (**W**)	Breuil, 2000, 2002; Powell, 2004b; Breuil *et al.*, 2007, 2010
	Marie Galante[15] (**L**)	Breuil, 2002; Powell, 2004b; Breuil *et al.*, 2007, 2010; Lorvelec *et al.*, 2007[16]

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[8] Some insular populations might have become established via natural over-water dispersal.

[9] Horrocks and Fields (2011) implied that the population on Barbados is native.

[10] Also Rocher du Diamant (MB).

[11] Iguanas might have reached many islands via natural over-water dispersal, but populations might also have become established as a consequence of relocations by Amerindians or early European colonists or, more recently, as a result of escaped or released pets. Extant populations might include descendants of individuals that arrived there by all three mechanisms (Powell, 2004).

[12] Anguillian populations include released/escaped pets (Hodge *et al.*, 2003) and descendants of animals that arrived via natural rafting (Censky *et al.*, 1998).

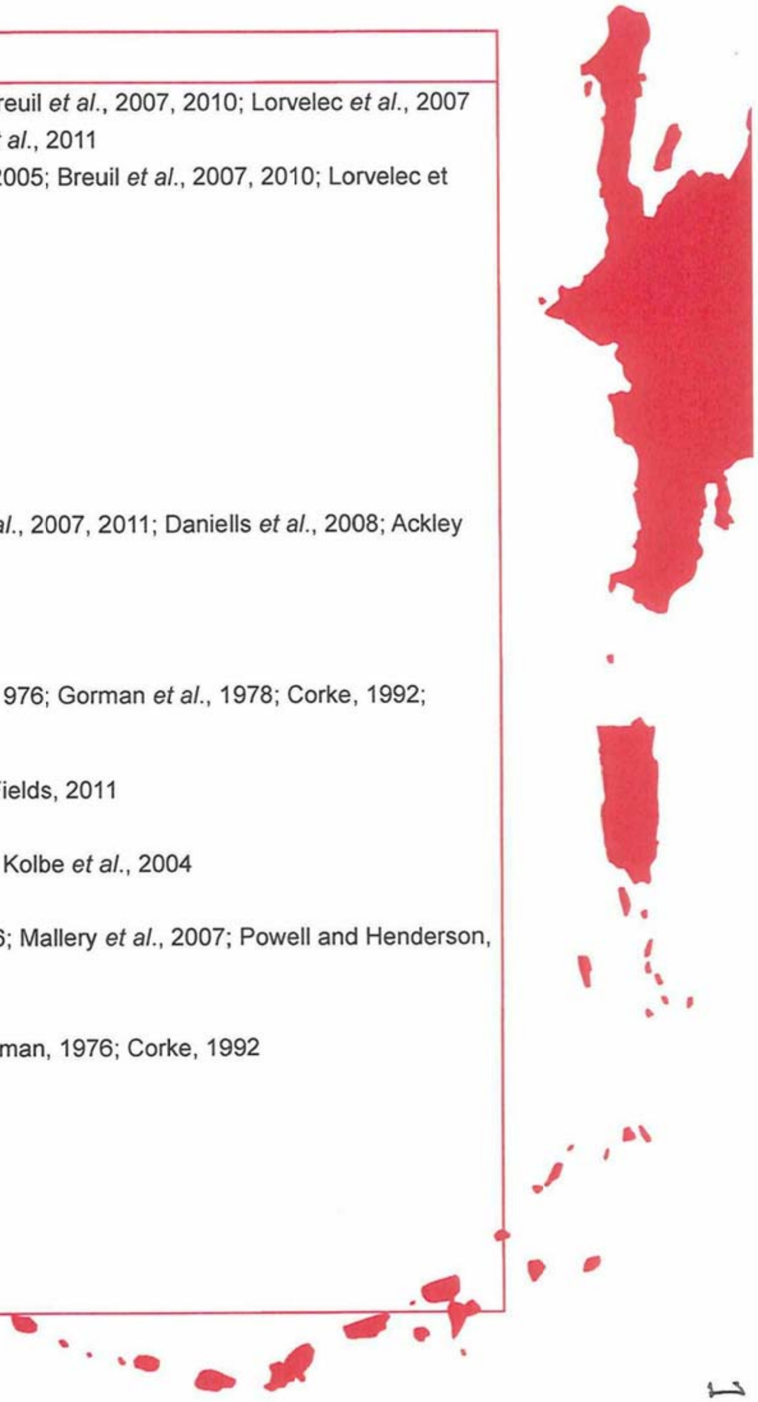
[13] The population might or might not be introduced or may consist of descendants of animals that arrived naturally and of others that were introduced.

[14] The population might or might not be introduced or may consist of descendants of animals that arrived naturally and of others that were introduced.

[15] The population might or might not be introduced or may consist of descendants of animals that arrived naturally and of others that were introduced.

[16] This paper is cited here and elsewhere despite the fact that some of the authors' data are suspect; for example, they indicate that extant populations of *Iguana delicatissima* remain on St.-Martin/St. Maarten, Les Îles de Saintes, and Grande-Terre (Guadeloupe) and they suggest that *I. delicatissima* and invasive *I. iguana* are no longer competing or hybridizing.

Species (Native Range)	Introduced (Status)	Pertinent Reference(s)
	Martinique[17] (**W**)	Breuil, 2000, 2002, 2009; Powell, 2004b; Breuil *et al.*, 2007, 2010; Lorvelec *et al.*, 2007
	St.-Barthélemy (**S**)	Breuil, 2009; Breuil *et al.*, 2010; Lorvelec *et al.*, 2011
	St.-Martin/St. Maarten (**W**)	Breuil, 2002; Powell, 2004b; Powell *et al.*, 2005; Breuil *et al.*, 2007, 2010; Lorvelec et al., 2007; Powell and Henderson, 2008
	St.Lucia (**S**)	Morton, 2008
Reptilia: Squamata: Polychrotidae		
Anolis bimaculatus (St. Christopher Bank)	Dominica (**S**)	A. James, pers. comm.
	St.-Martin/St. Maarten (**E**)	Powell *et al.*, 1992, 2005
Anolis carolinensis (Southeastern US)	Anguilla (**L**)	Eaton *et al.*, 2001; Hodge *et al.*, 2003
Anolis cristatellus (Puerto Rico Bank)	Dominica (**L**)	Powell and Henderson, 2003; Malhotra *et al.*, 2007, 2011; Daniells *et al.*, 2008; Ackley et al., 2009
	St.-Martin/St. Maarten (**L**)	Breuil *et al.*, 2010
Anolis extremus (Barbados)	St. Lucia (**L**)	Underwood, 1962; Lazell, 1972; Gorman, 1976; Gorman *et al.*, 1978; Corke, 1992; Giannasi *et al.*, 1997
Anolis sagrei (Cuba, Bahamas, Lesser Cayman Islands)	Barbados** (**L**)	Fields and Horrocks, 2009; Horrocks and Fields, 2011
	Canouan (Grenadines) (**L**)	M. de Silva, pers. comm.
	Grenada** (L)	Greene *et al.*, 2002; Germano *et al.*, 2003; Kolbe *et al.*, 2004
	St.-Martin/St. Maarten** (**L**)	Fläschendräger, 2010
	St. Vincent** (**L**)	Henderson and Powell, 2005; Treglia, 2006; Mallery *et al.*, 2007; Powell and Henderson, 2007, 2011; Treglia *et al.*, 2008
Anolis wattsi (Antigua)	St. Lucia (**L**)	Underwood, 1959, 1962; Lazell, 1972; Gorman, 1976; Corke, 1992
Reptilia: Squamata: Sphaerodactylidae		
Gonatodes vittatus (Neotropics, Aruba?)	Dominica (**E**)	Malhotra *et al.*, 2007, 2011
Sphaerodactylus microlepis (St. Lucia)	Dominica (**S**)	Evans, 1989; Malhotra and Thorpe, 1999



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[17] The population might or might not be introduced or may consist of descendants of animals that arrived naturally and of others that were introduced.

Species (Native Range)	Introduced (Status)	Pertinent Reference(s)
Reptilia: Squamata: Teiidae		
Ameiva ameiva	Barbados (**L**)	Corrie, 2001; Watson, 2008; Fields and Horrocks, 2009; Horrocks and Fields, 2011
(Trinidad?)		
AMPHISBAENIANS		
Reptilia: Squamata: Amphisbaenidae		
Amphisbaena fuliginosa	Grenada (**S**?)	Murphy *et al.*, 2010
(Neotropics)	St. Lucia (**S**?)	Murphy *et al.*, 2010
SNAKES		
Reptilia: Squamata: Boidae		
Boa constrictor	Guadeloupe*[18] (**S**)	Barré *et al.*, 1997; Breuil, 2002; Breuil *et al.*, 2010
(Neotropics)	Martinique (**S**)	Breuil, 2009; Breuil *et al.*, 2010
	St.-Martin/St. Maarten (**S**)	Powell *et al.*, 2005
Epicrates cenchria	Martinique (**S**)	Breuil and Ibéné, 2008; Breuil, 2009; Breuil *et al.*, 2010
(Neotropics)	St.-Martin/St. Maarten (**S**)	Powell *et al.*, 2005
Reptilia: Squamata: Colubridae		
Mastigodryas bruesi (Grenada or St. Vincent bank)	Barbados (**L**)	Underwood *et al.*, 1999; Greene *et al.*, 2003; Powell and Henderson, 2007, 2011; Fields and Horrocks, 2009; Horrocks and Fields, 2011
Pantherophis alleghaniensis[19] (Eastern US)	Martinique (**S**)	Breuil and Ibéné, 2008; Lorvelec *et al.*, 2011
Pantherophis guttatus	Anguilla (**S**)	Hodge *et al.*, 2003
(Southeastern US)	Antigua (**S**)	Powell and Henderson, 2003
	Martinique (**S**)	Breuil, 2009; Breuil *et al.*, 2010
	St.-Barthélemy (**S**)	Breuil, 2002; Hodge *et al.*, 2003; Breuil *et al.*, 2010
	St.-Martin/St. Maarten (**S**)	Powell *et al.*, 2005; Breuil *et al.*, 2010
Tantilla melanocephala	Carriacou (Grenadines) (**S**)	J. Boone and D. Scantlebury, pers. comm.
(Trinidad, SA)	Grenada (**L**)	Berg *et al.*, 2009; Tolson and Henderson, 2011
	Mustique (Grenadines) (**S**)	Henderson and Powell, 2006; Berg *et al.*, 2009; Tolson and Henderson, 2011
	Union (Grenadines) (**S**)	Berg *et al.*, 2009; Tolson and Henderson, 2011

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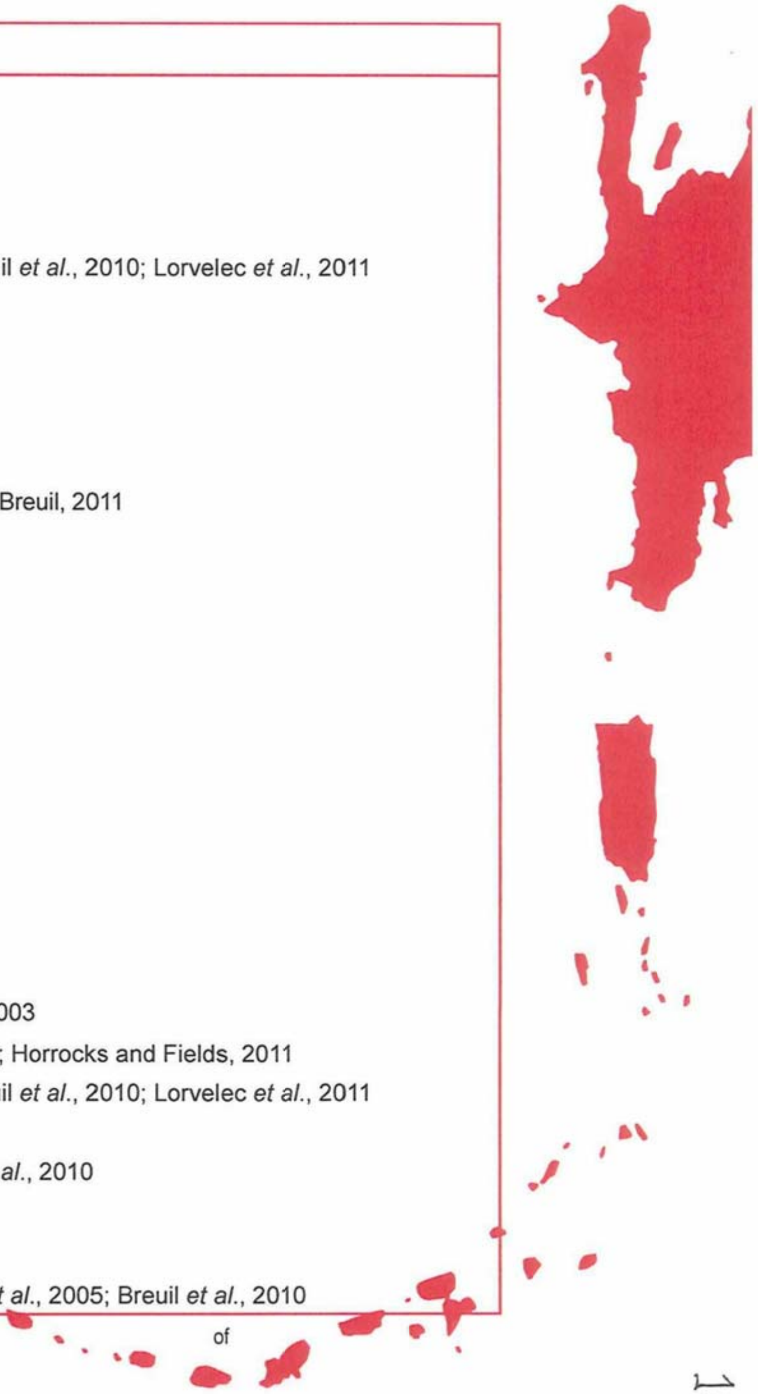
[18] This record might pertain to Boa nebulosa (Lorvelec *et al.*, 2011).

[19] This species also has been assigned to the genus *Scotophis*.

Species (Native Range)	Introduced (Status)	Pertinent Reference(s)
Reptilia: Squamata: Dipsadidae		
Alsophis rufiventris (Saba, St. Eustatius)	St.-Martin/St. Maarten (**S**)	Powell *et al.*, 2005
Reptilia: Squamata: Natricidae		
Natrix natrix (Europe)	Martinique (**S**)	Breuil and Ibéné, 2008; Breuil, 2009; Breuil *et al.*, 2010; Lorvelec *et al.*, 2011
Thamnophis sirtalis (Eastern US)	St.-Barthélemy (**S**)	Breuil *et al.*, 2010
Reptilia: Squamata: Pythonidae		
Morelia amethistina (Indonesia, Papua New Guinea, Australia)	Guadeloupe[20] (**S**)	Breuil and Ibéné, 2008; Breuil *et al.*, 2010; Breuil, 2011
Python bivittatus (Southeastern Asia)	St.-Barthélemy (**S**)	Breuil *et al.*, 2010
Python curtus group (Malaya, Indonesia)	St.-Martin/St. Maarten (**S**)	Powell *et al.*, 2005
Python regius (West-central Africa)	Martinique (S)	Breuil, 2009; Breuil *et al.*, 2010
	St.-Martin/St. Maarten (**S**)	Powell *et al.*, 2005; Breuil *et al.*, 2010
	St. Barthélemy (**S**)	Breuil *et al.*, 2010
Reptilia: Squamata: Typhlopidae		
Ramphotyphlops braminus (Southeastern Asia)	Anguilla** (**L**)	Censky and Hodge, 1997; Hodge *et al.*, 2003
	Barbados** (**W**)	Hedges, 2008; Fields and Horrocks, 2009; Horrocks and Fields, 2011
	Guadeloupe** (**L**)	Breuil and Ibéné, 2008; Breuil, 2009; Breuil *et al.*, 2010; Lorvelec *et al.*, 2011
	Mustique (Grenadines)** (**?**)	M. de Silva, in litt., 2009
	St.-Barthélemy** (**L**)	Breuil, 2002; Hodge *et al.*, 2003; Breuil *et al.*, 2010
	St. Christopher** (**L**)	Orchard, 2010
	St. Eustatius** (**L**)	Powell, 2011
	St.-Martin/St. Maarten** (**L**)	Breuil, 2002; Hodge *et al.*, 2003; Powell *et al.*, 2005; Breuil *et al.*, 2010



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[20] This stray found on Basse-Terre was identified on the basis of a shed skin in February 2008 (Breuil and Ibéné, 2008). It was captured by a agent of the Office National des Forêts (ONF) on 25 March 2010 in the same place. The snake was 3.5 m long and died from injuries the following day (F. Mazeas, in litt., March 2010).

Species (Native Range)	Introduced (Status)	Pertinent Reference(s)
TURTLES		
Reptilia: Testudines: Chelidae		
Phrynops geoffroanus (SA)	Anguilla (**S**)	Hodge *et al.*, 2011
Reptilia: Testudines: Emydidae		
Graptemys pseudogeographica (Central US)	Martinique (**S**)	Breuil, 2009; Breuil *et al.*, 2010
Terrapene carolina (Eastern US)	Martinique (**S**)	Breuil, 2009; Breuil *et al.*, 2010
Trachemys scripta (Eastern US)	Barbados (**S**)	Horrocks and Fields, 2011
	Guadeloupe (**S**)	Schwartz and Thomas, 1975; Lescure, 1979; Schwartz and Henderson, 1988, 1991; Breuil, 2002; Breuil *et al.*, 2010
	Marie-Galante (**S**)	Breuil, 2002
	Martinique (**S**)	Servan and Arvy, 1997; Breuil, 2002
	St. Eustatius (**S**)	Powell *et al.*, 2005
	St.-Martin/St. Maarten (**W**)	Powell *et al.*, 2005
Trachemys stejnegeri (Turks & Caicos, Hispaniola, Puerto Rico)	Dominica (**E**)	Fritz, 1991; Seidel, 1996
	Guadeloupe (**S**)	Breuil, 2002, 2003; Breuil *et al.*, 2010
	Les Îles des Saintes* (**L**)	Breuil, 2002
	Marie-Galante (**L**)	Seidel and Adkins, 1987; Seidel, 1988; Ernst and Barbour, 1989; Breuil, 2002, 2003; Breuil *et al.*, 2010
	Martinique (**S**)	Breuil, 2011
Reptilia: Testudines: Pelomedusidae		
*Pelusios castaneus**[21] (Western Africa)	Guadeloupe (**L**)	Pinchon, 1967; Lescure, 1979, 1983; Schwartz and Henderson, 1991; Iverson, 1992; Breuil, 2002, 2003; Breuil *et al.*, 2010
Reptilia: Testudines: Testudinidae		
Centrochelys sulcata (Northern Africa)	Martinique (**S**)	Breuil, 2009; Breuil *et al.*, 2010

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[21] Previously misidentified as Pelusios subniger.

Species (Native Range)	Introduced (Status)	Pertinent Reference(s)
Chelonoidis carbonaria[22] (Neotropics)	Barbados (**L**)	Fields and Horrocks, 2009; Horrocks and Fields, 2011
	Saba (**S**)	Powell *et al.*, 2005
	St.-Barthélemy* (**W**)	Breuil, 2004; Devaux, 2010
	St. Eustatius* (**S**)	Powell *et al.*, 2005
Chelonoidis denticulata (Neotropical mainland)	Guadeloupe (L)	Pritchard and Trebbau, 1984; Breuil, 2002; Breuil *et al.*, 2010
*Kinixys erosa** (Western Africa)	Guadeloupe (**E**)	Breuil, 2002, 2003
*Kinixys homeana** (Western Africa)	Guadeloupe (**E**)	Breuil, 2002, 2003
CROCODILIANS		
Reptilia: Crocodilia: Alligatoridae		
Caiman crocodilus (Neotropics)	Carriacou (Grenadines) (**S**)	Devas, 1964; Groome, 1970
Reptilia: Crocodilia: Crocodylidae		
Crocodylus intermedius (SA)	Grenada (**S**)	Groome, 1970

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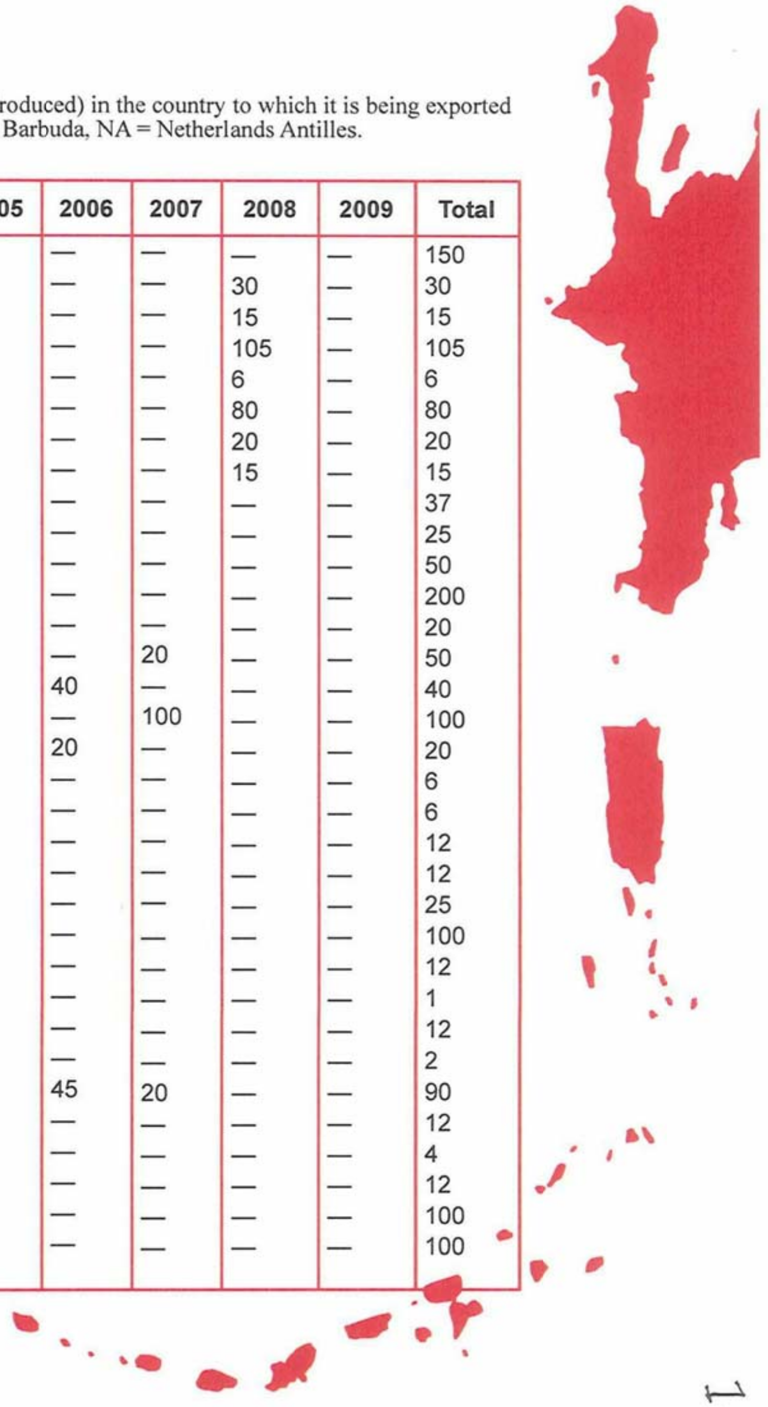
[22] These tortoises might have reached many islands via natural over-water dispersal, but populations may also have become established as a consequence of relocations by Amerindians or early European colonists or, more recently, as a result of escaped or released pets (Censky, 1988). Extant populations may include descendants of individuals that arrived there by all three mechanisms (Powell and Henderson, 2005; Powell *et al.*, 2005).

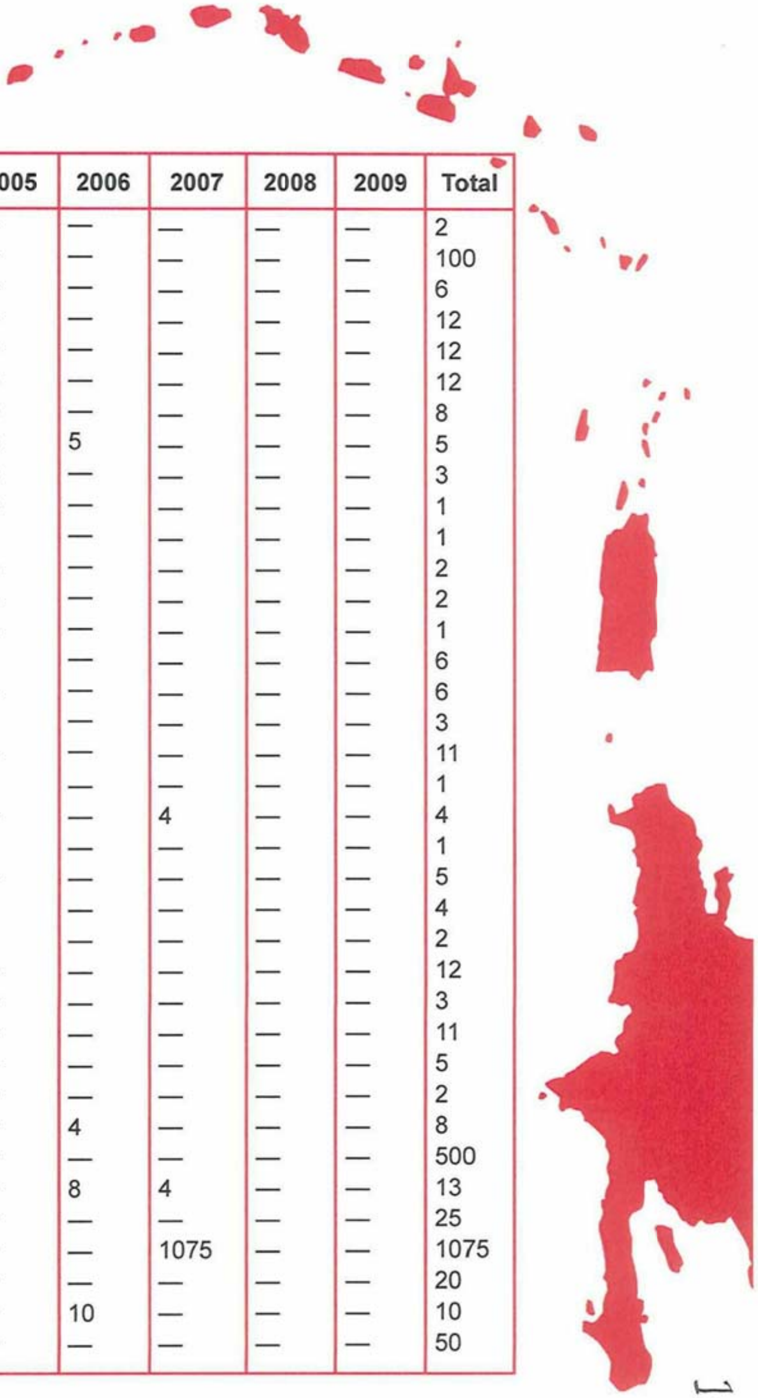
Table 2. Species of amphibians and reptiles introduced in the Lesser Antilles for research or conservation (including restorations). Status: W = widespread (likely to be encountered within a few minutes of searching), L = localized (likely to be encountered at most sporadically, even in appropriate habitat, although possibly abundant within a few small areas), E = presumably extirpated or failed introduction. Most of the following records are included in the database of introductions in Kraus (2009) and listed in Henderson and Powell (2009). References cited are those that document or confirm an introduction; all references pertaining to introduced populations are not necessarily listed.

Species (Native Range)	Introduced (Status)	Pertinent Reference(s)
LIZARDS		
Reptilia: Squamata: Iguanidae		
Iguana delicatissima (Îlet Chancel, Martinique)	Îlet à Ramiers (Martinique) (**L**)	Breuil, 2009
Reptilia: Squamata: Polychrotidae		
Anolis pogus (Anguilla Bank)	Anguillita (E)	Roughgarden *et al.*, 1984
Reptilia: Squamata: Teiidae		
Cnemidophorus vanzoi (Maria Major, St. Lucia)	Praslin Island (W)	Dickinson and Fa, 2000
SNAKES		
Reptilia: Squamata: Dipsadidae		
Alsophis sajdaki (Great Bird Island, Antigua)	Green and Rabbit islands (L)	Daltry, 2007, 2011

Table 3. Species exported from the US to the countries indicated. Those marked with an asterisk (*) do not occur (native or introduced) in the country to which it is being exported (USFWS LEMIS database). Those marked with a double-asterisk (**) do not occur in the Lesser Antilles. A&B = Antigua and Barbuda, NA = Netherlands Antilles.

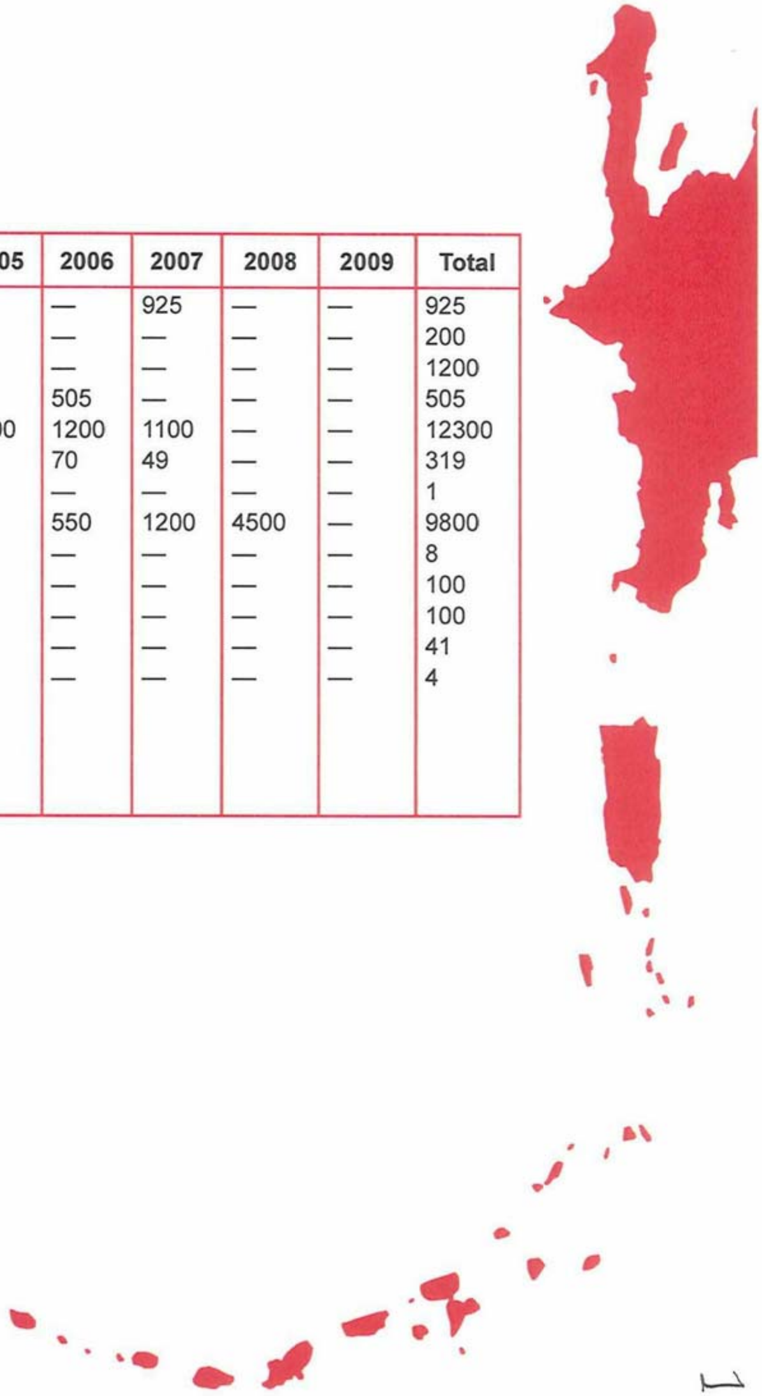
Species	Country	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	Total
*Bombina orientalis***	NA	—	—	—	—	150	—	—	—	—	—	—	—	150
*Cryptophyllobates azureiventris***	NA	—	—	—	—	—	—	—	—	—	—	30	—	30
*Dendrobates auratus***	NA	—	—	—	—	—	—	—	—	—	—	15	—	15
*Dendrobates azureus***	NA	—	—	—	—	—	—	—	—	—	—	105	—	105
*Dendrobates imitator***	NA	—	—	—	—	—	—	—	—	—	—	6	—	6
*Dendrobates tinctorius***	NA	—	—	—	—	—	—	—	—	—	—	80	—	80
*Dendrobates ventrimaculatus***	NA	—	—	—	—	—	—	—	—	—	—	20	—	20
*Phyllobates terribilis***	NA	—	—	—	—	—	—	—	—	—	—	15	—	15
*Hyla cinerea***	NA	12	—	—	—	25	—	—	—	—	—	—	—	37
*Ceratophrys cranwelli***	NA	—	—	—	—	25	—	—	—	—	—	—	—	25
*Hymenochirus curtipes***	Barbados	—	—	—	—	—	—	—	50	—	—	—	—	50
*Xenopus laevis***	Barbados	—	—	—	—	200	—	—	—	—	—	—	—	200
*Necturus maculosus***	Barbados	—	—	—	—	—	—	—	20	—	—	—	—	20
*Cynops pyrrhogaster***	Barbados	—	—	—	—	—	30	—	—	—	20	—	—	50
*Cynops sp.***	Barbados	—	—	—	—	—	—	—	—	40	—	—	—	40
*Paramesotriton hongkongensis***	Barbados	—	—	—	—	—	—	—	—	—	100	—	—	100
*Taricha torosa***	Barbados	—	—	—	—	—	—	—	—	20	—	—	—	20
*Furcifer pardalis***	Dominica	—	—	—	—	—	—	6	—	—	—	—	—	6
*Coleonyx mitratus***	NA	—	—	—	—	6	—	—	—	—	—	—	—	6
*Eublepharis macularius***	Barbados	—	—	—	—	—	—	—	12	—	—	—	—	12
*Gekko gecko**	NA	—	—	—	—	12	—	—	—	—	—	—	—	12
*Gekko sp.***	Barbados	—	—	—	—	—	1	—	24	—	—	—	—	25
Hemidactylus sp.	NA	—	—	—	—	100	—	—	—	—	—	—	—	100
*Ptychozoon sp.***	NA	—	—	—	—	12	—	—	—	—	—	—	—	12
*Basiliscus plumifrons***	NA	1	—	—	—	—	—	—	—	—	—	—	—	1
*Basiliscus vittatus***	NA	—	—	—	—	12	—	—	—	—	—	—	—	12
*Corytophanes cristatus***	NA	2	—	—	—	—	—	—	—	—	—	—	—	2
Iguana iguana	NA	—	—	—	—	25	—	—	—	45	20	—	—	90
*Sceloporus malachiticus***	NA	—	—	—	—	12	—	—	—	—	—	—	—	12
*Sceloporus olivaceus***	NA	—	—	—	—	4	—	—	—	—	—	—	—	4
*Sceloporus variabilis***	NA	—	—	—	—	12	—	—	—	—	—	—	—	12
*Takydromus sp.***	NA	—	—	—	—	100	—	—	—	—	—	—	—	100
*Anolis carolinensis**	NA	—	—	—	—	100	—	—	—	—	—	—	—	100





Species	Country	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	Total
*Anolis equestris***	NA	2	—	—	—	—	—	—	—	—	—	—	—	2
Anolis sagrei	NA	—	—	—	—	100	—	—	—	—	—	—	—	100
Anolis sp.	NA	—	—	—	—	6	—	—	—	—	—	—	—	6
*Novoeumeces (= Eumeces) schneideri***	NA	—	—	—	—	12	—	—	—	—	—	—	—	12
	NA	—	—	—	—	12	—	—	—	—	—	—	—	12
*Ameiva ameiva**	NA	—	—	—	—	12	—	—	—	—	—	—	—	12
*Cnemidophorus lemniscatus***	Dominica	—	—	—	—	—	8	—	—	—	—	—	—	8
*Boa constrictor**	NA	—	—	—	—	—	—	—	—	5	—	—	—	5
*Corallus caninus***	Barbados	—	—	—	3	—	—	—	—	—	—	—	—	3
*Corallus hortulanus***	Barbados	—	—	—	1	—	—	—	—	—	—	—	—	1
*Elaphe quadrivirgata***	Barbados	—	—	—	—	—	—	—	1	—	—	—	—	1
*Epicrates cenchria**	A&B	2	—	—	—	—	—	—	—	—	—	—	—	2
*Eunectes murinus***	Barbados	—	—	—	2	—	—	—	—	—	—	—	—	2
*Pantherophis guttatus**	Barbados	—	—	—	1	—	—	—	—	—	—	—	—	1
*Pantherophis obsoletus**	Barbados	—	—	—	—	—	—	—	6	—	—	—	—	6
*Pantherophis vulpinus***	NA	—	—	—	—	6	—	—	—	—	—	—	—	6
*Lampropeltis calligaster***	Barbados	—	—	—	—	—	—	—	3	—	—	—	—	3
*Lampropeltis getula***	NA	—	—	—	—	11	—	—	—	—	—	—	—	11
*Lampropeltis sp.***	Barbados	—	—	—	—	—	—	—	1	—	—	—	—	1
*Lampropeltis triangulum***	NA	—	—	—	—	—	—	—	—	—	4	—	—	4
*Lamprophis fuliginosus***	Barbados	—	—	—	—	—	—	—	1	—	—	—	—	1
*Opheodrys aestivus***	NA	—	5	—	—	—	—	—	—	—	—	—	—	5
*Spilotes pullatus***	Barbados	—	—	—	—	—	—	—	4	—	—	—	—	4
*Thamnophis sirtalis**	Barbados	—	—	—	—	—	—	—	2	—	—	—	—	2
*Morelia spilota***	NA	—	—	—	—	12	—	—	—	—	—	—	—	12
*Python molurus (probably P. bivittatus)***	Barbados	—	—	—	—	3	—	—	—	—	—	—	—	3
	NA	—	—	—	—	11	—	—	—	—	—	—	—	11
*Python regius**	A&B	5	—	—	—	—	—	—	—	—	—	—	—	5
*Chrysemys sp.***	Barbados	—	—	—	1	1	—	—	—	—	—	—	—	2
*Cuora amboinensis***	NA	—	2	—	—	2	—	—	—	4	—	—	—	8
*Graptemys geographica***	A&B	500	—	—	—	—	—	—	—	—	—	—	—	500
*Graptemys nigrinoda***	NA	—	—	—	—	1	—	—	—	8	4	—	—	13
	Barbados	—	—	—	—	—	—	25	—	—	—	—	—	25
	NA	—	—	—	—	—	—	—	—	—	1075	—	—	1075
	NA	—	—	—	—	20	—	—	—	—	—	—	—	20
	Barbados	—	—	—	—	—	—	—	—	10	—	—	—	10
	NA	50	—	—	—	—	—	—	—	—	—	—	—	50

Species	Country	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	Total
*Graptemys pseudogeographica***	NA	—	—	—	—	—	—	—	—	—	925	—	—	925
*Pseudemys floridana***	NA	100	—	—	—	—	100	—	—	—	—	—	—	200
*Pseudemys nelsoni***	NA	200	—	—	—	—	1000	—	—	—	—	—	—	1200
*Pseudemys sp.***	Barbados	—	—	—	—	—	—	—	—	505	—	—	—	505
Trachemys scripta	NA	5000	—	1000	1500	—	500	1000	1000	1200	1100	—	—	12300
Trachemys sp.	Barbados	—	—	—	—	—	100	100	—	70	49	—	—	319
*Apalone ferox***	Grenada	—	—	—	—	—	1	—	—	—	—	—	—	1
Chelonoidis carbonaria	NA	850	500	—	—	200	2000	—	—	550	1200	4500	—	9800
Non-CITES entry (reptiles)	Dominica	8	—	—	—	—	—	—	—	—	—	—	—	8
	Grenada	—	—	—	—	100	—	—	—	—	—	—	—	100
	NA	100	—	—	—	—	—	—	—	—	—	—	—	100
	Barbados	—	—	41	—	—	—	—	—	—	—	—	—	41
	NA	—	—	—	—	4	—	—	—	—	—	—	—	4



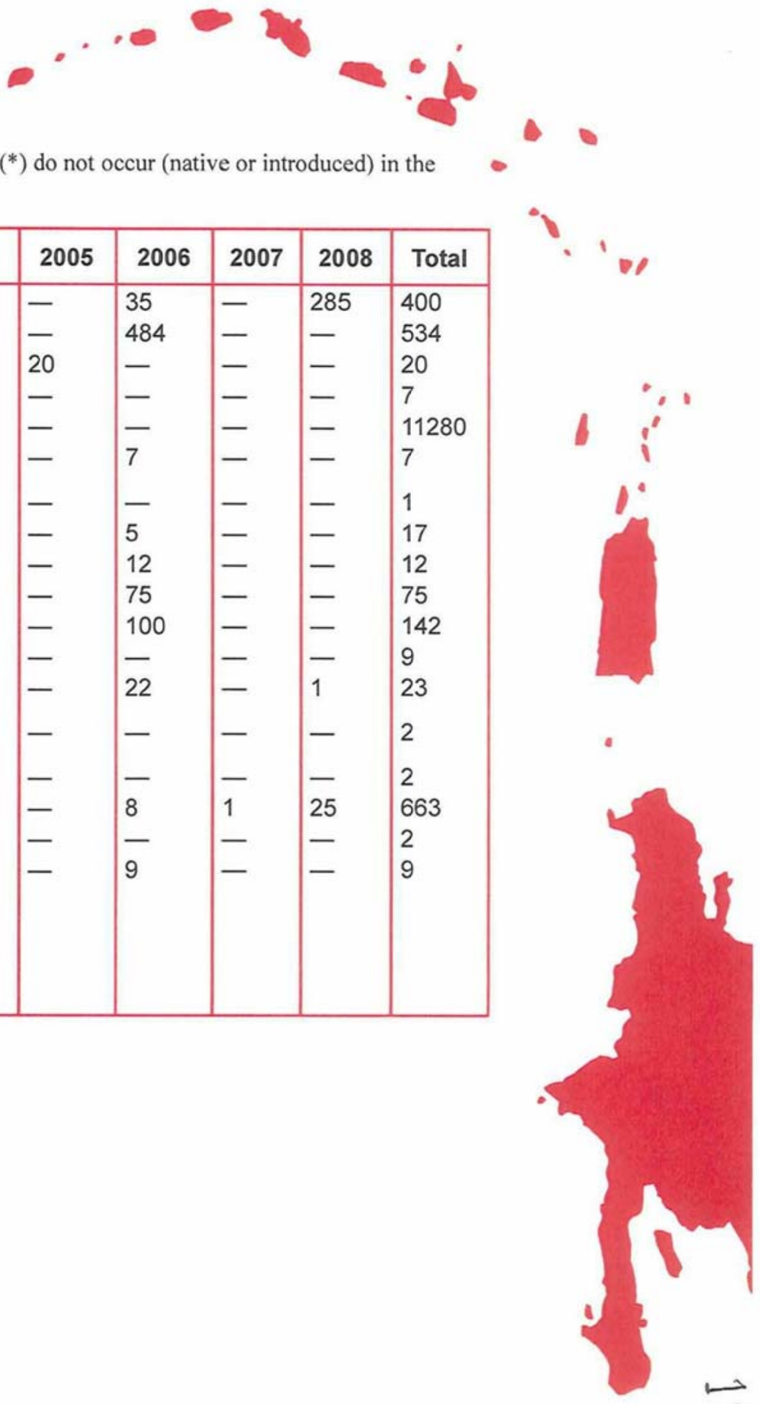
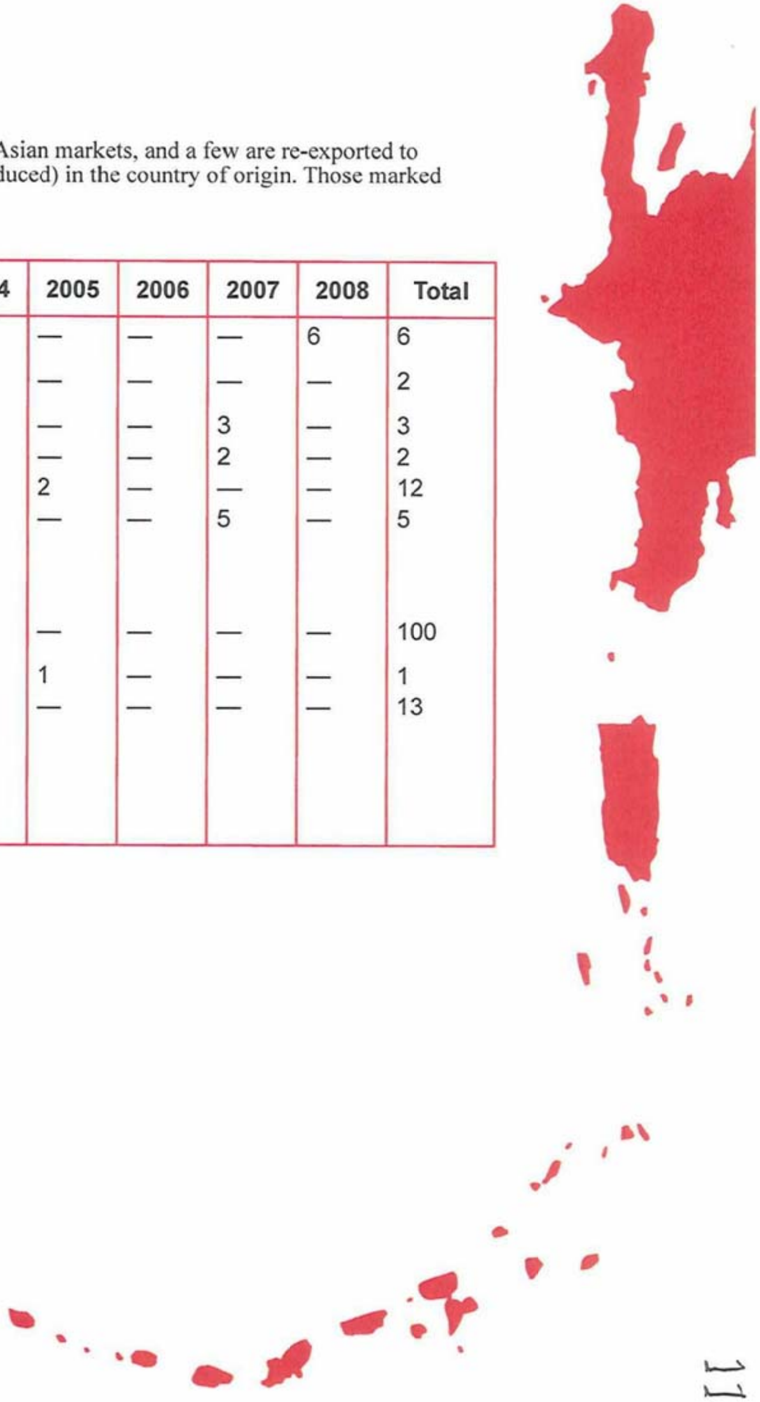


Table 4. Species imported into the US from the countries indicated (USFWS LEMIS database). Those marked with an asterisk (*) do not occur (native or introduced) in the country of origin. Those marked with a double-asterisk (**) do not occur in the Lesser Antilles. NA = Netherlands Antilles.

Species	Country	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	Total
Rhinella marina	Barbados	—	—	—	—	—	80	—	—	35	—	285	400
Eleutherodactylus sp.	Barbados	—	—	—	—	50	—	—	—	484	—	—	534
	Grenada	—	—	—	—	—	—	—	20	—	—	—	20
Leptodactylus fallax	Dominica	—	—	—	7	—	—	—	—	—	—	—	7
*Lithobates catesbeianus***	Dominica	—	6280	—	—	5000	—	—	—	—	—	—	11280
Non-CITES entry (amphibian)	Barbados	—	—	—	—	—	—	—	—	7	—	—	7
*Gekko sp.**	Barbados	—	—	—	—	—	1	—	—	—	—	—	1
Hemidactylus mabouia	Barbados	—	—	—	—	12	—	—	—	5	—	—	17
Hemidactylus sp.	Barbados	—	—	—	—	—	—	—	—	12	—	—	12
*Anolis equestris***	Barbados	—	—	—	—	—	—	—	—	75	—	—	75
Anolis sp.	Barbados	—	—	—	—	20	22	—	—	100	—	—	142
*Lacerta sp.***	NA	—	9	—	—	—	—	—	—	—	—	—	9
Ameiva ameiva	Barbados	—	—	—	—	—	—	—	—	22	—	1	23
Bothrops sp.	St. Lucia	—	—	—	2	—	—	—	—	—	—	—	2
*Terrapene sp.***	NA	—	2	—	—	—	—	—	—	—	—	—	2
Chelonoidis carbonaria	Barbados	98	—	20	451	20	40	—	—	8	1	25	663
*Pyxis arachnoides***	Martinique	—	—	—	—	—	—	2	—	—	—	—	2
Non-CITES entry (reptile)	Barbados	—	—	—	—	—	—	—	—	9	—	—	9

Table 5. Species exported from the shown country, imported to the US, then re-exported mostly to European, Canadian, some Asian markets, and a few are re-exported to countries in the Greater Caribbean (USFWS LEMIS database). Those marked with an asterisk (*) do not occur (native or introduced) in the country of origin. Those marked with a double-asterisk (**) do not occur in the Lesser Antilles. NA = Netherlands Antilles.

Species Exported to the US	Country	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	Total
Rhinella marina	Barbados	—	—	—	—	—	—	—	—	—	6	6
*Pseustes poecilonotus***	NA	—	—	—	—	—	2	—	—	—	—	2
*Terrapene carolina**	Montserrat	—	—	—	—	—	—	—	—	3	—	3
*Terrapene ornata***	Montserrat	—	—	—	—	—	—	—	—	2	—	2
Chelonoidis carbonaria	Barbados	—	—	10	—	—	—	2	—	—	—	12
*Testudo horsfieldii***	Montserrat	—	—	—	—	—	—	—	—	5	—	5
Species Re-exported to the Greater Caribbean												
*Cynops orientalis***	St. Lucia	—	—	100	—	—	—	—	—	—	—	100
Chelonoidis carbonaria	Barbados	—	—	—	—	—	—	1	—	—	—	1
Non-CITES entry (reptile?)	NA	—	—	—	—	13	—	—	—	—	—	13



113

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December 1, 2013

Re: 2013 Research Summary Report
Guana Island – Red imported fire ants impact and management
Personnel: Dr. Tracy Langkilde and Dr. Katriona Shea

To whom it may concern,

Please find below a summary of the research conducted by the Langkilde lab on Guana Island in 2013.

Motivation

The Red Imported Fire Ant, *Solenopsis invicta*, is an invasive ant of ecological concern (Figure 1a). It has been introduced to over 7 countries, including the British Virgin Islands, and is predicted to spread globally. This invader outcompetes native ants within their introduced range in the USA, leading to changes in the ant fauna following invasion that can have important flow-on effects throughout the community. These invasive Fire Ants also prey on native vertebrates and their eggs, including native lizards and turtles. And they readily attack people; the consequences range from the formation of itchy and unsightly pustules to anaphylactic shock and death (~10% of people are allergic to Fire Ant venom). Red Imported Fire Ants have been documented on Guana Island, but little is known about the impact of this invader on the island's unique fauna. Of particular concern are species which nest on beaches, including sea birds and the endangered Stout Iguana, *Cyclura pinguis*.

There is another fire ant found on Guana Island - the Tropical Fire Ant, *Solenopsis geminata* (Figure 1b). This species has had a longer period of establishment in the Caribbean, and it is possible that it is native to the British Virgin Islands. Unlike the Red Imported Fire Ant, the Tropical Fire Ant is not known to detrimentally impact wildlife, and does not attack people. Furthermore, our research is suggesting that this species is slowing the spread of the voracious Red Imported Fire Ant.

Our research had 2 main aims:

1) To continue monitoring the distribution of the two species of fire ants: *Solenopsis invicta* and *S. geminata,* to track the invasion and determine how these species interact on Guana island.
2) To start work on a model to predict the impact of the Red Imported Fire Ant on the Stout Iguana, and inform management of this invader.

Figure 1. Comparison of the mounds and workers of the two Fire Ant species found on Guana Island. a) *S. invicta* mounds are convex and rounded. Ants immediately boil out of the mounds at the slightest disturbance and begin stinging anything they crawl upon. b) *S. geminata* mounds are ring-shaped and concave, often with pitted entrance holes. Soldier ants have obviously enlarged heads. Instead of pouring out to defend the mound when disturbed, they ignore their attacker and instead quickly disappear into the mound.

Research and Results

1. Monitoring Red Imported Fire Ant invasion

Approach

We continued surveys that have been conducted over the past several years to monitor the spread of Red Imported Fire Ant (*S. invicta*), and its impact on the Tropical Fire Ant (*S. geminata*). We walked transects across the west side of Guana Island, marking the location of all Fire Ant mounds, using a GPS. We also set up experimental bait stations in four habitat types on the island: the flats, the forest adjacent the sand dunes, the sand dunes at the main swimming beach (White Bay Beach), and the area immediately surrounding the bar and lounge area at White Bay Beach (see Fig. 2, 3). We monitored these for ant presence to determine the numbers and identity of ants present. An identical study was conducted in 2010, and 2012, and we intend to continue this protocol during each return trip for long-term comparisons. Together, these data allow us to determine if the Red Imported Fire Ant is spreading to new areas of the island, and what their impact is on the Tropical Fire Ant.

Figure 2. Bait station used to detect the presence and abundance of ants, including fire ants.

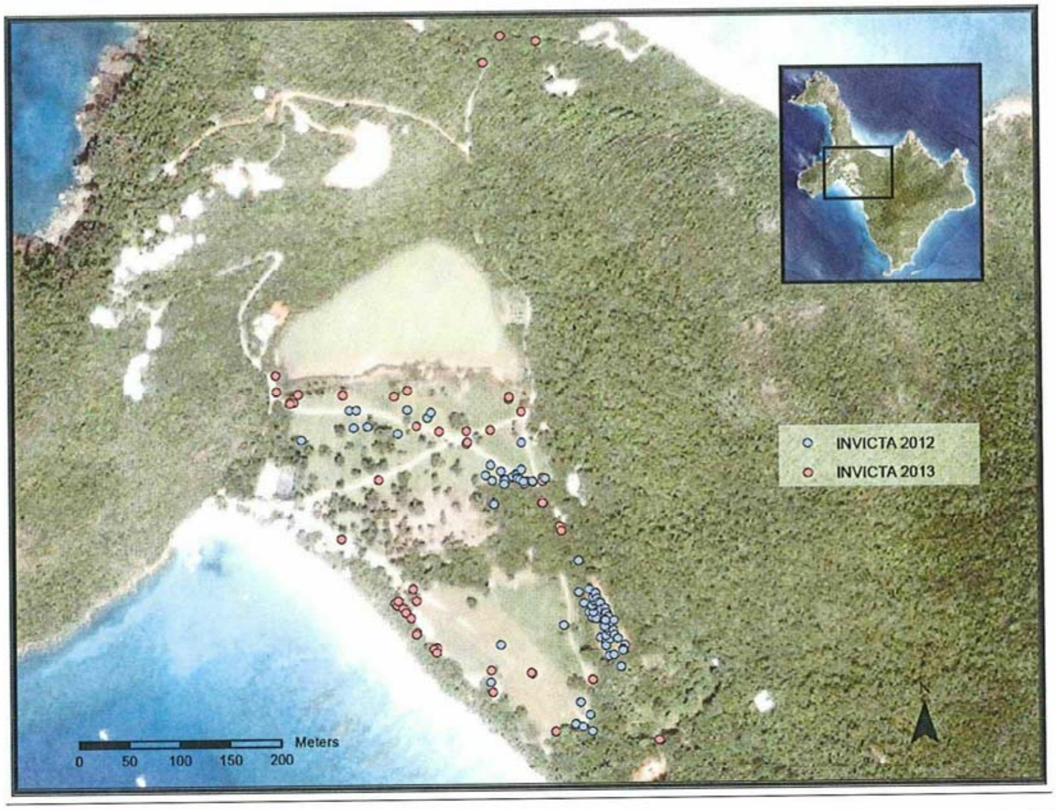

Figure 3. Results from GPS survey showing the Red Imported Fire Ant (*S. invicta*) spreading to the forest adjacent the beach dunes on White Beach, and towards North Beach.

Results and Implications

Our bait sampling shows that numbers of Red Imported Fire Ants increased dramatically from 2010 to 2013 (Fig. 4). By 2013, the Red Imported Fire Ant outnumbers the Tropical Fire Ant on the flats and native Fire Ants disappeared from our samples, suggesting that these invaders are starting to outcompete the native ants. These venomous aggressive invaders spread to the main swimming beach in 2012, and to the area surrounding the beach bar in 2013 (Fig. 3 and 4). We found Red Imported Fire Ants actively foraging on the beach including in known nesting locations of the Stout Iguana (Fig. 5), and found foraging trails across the beach chairs put out for tourists. We also found Red Imported Fire Ant mounds on the "Honeymoon beach" for the first time in 2013 (Fig. 3). Together, these data suggest that encounters between Fire Ants and humans might become increasingly common on the island.

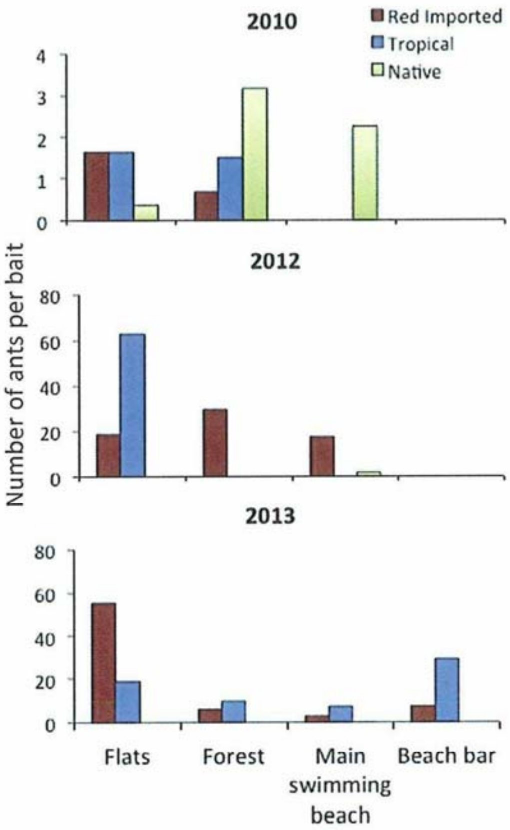

Figure 4. Results from bait sampling of ants in the grass flats, forest adjacent the beach, the dunes of the main swimming beach (White Bay Beach), and the area surrounding the beach bar. Note the difference in scale from 2010 to 2012 and 2013.

2. Predicting the impact of Red Imported Fire Ants on the Stout Iguana
We had planned to construct artificial nests to measure the potential impact of Red Imported Fire Ants on this fragile life history stage. Flight cancellations on the way to Guana Island in 2013 unfortunately meant that we lost 1 of our 4 days of research and we were unable to carry out this study. We were able to consult with other scientists on the island and determine what data is available for use in the model we are developing to predict the impact of the invasive predatory Fire Ants on this endangered Iguana. We hope to pursue this project in 2014, if invited back.

Executive Summary and Management Recommendations

The Tropical Fire Ant, *Solenopsis geminata*, does not attack people or wildlife, and helps to prevent the spread of the Red Imported Fire Ant, *Solenopsis invicta*, which is a major pest. Red Imported Fire Ants readily attack people, even far away from their mounds, and can cause fatal anaphylaxis (allergic reactions). Our findings that these **invasive Fire Ants have spread to the main swimming beach and the area surrounding the beach bar** at White Bay Beach caution that Fire Ants and humans may come into increasing contact; Red Imported Fire Ants were found foraging across the beach chairs and can get into beach towels. These invasive ants were also found at North Beach for the first time this year, immediately adjacent Stout Iguana nests (Fig. 5). This is a concern, as Red Imported Fire Ants are known to attack sea turtle nests on beaches within their invasive range within the USA.

We recommend eradicating Red Imported Fire Ant mounds to reduce their densities and hamper their spread. This is commonly achieved by poisoning, however this can easily be mis-managed. Poisons that kill Red Imported Fire Ants also kill other species; this can actually promote the spread of these invaders by freeing them from competition. **Poisoning of both species will actually exacerbate the problem: targeted poisoning of ONLY Red Imported Fire Ants is essential.** Fast acting bait products (hydramethylnon, indoxacarb, spinosad) that treat individual Red Imported Fire Ant mounds help to avoid this (Red Imported Fire Ant mound workers are distinct from native species – see Fig. 1. If in doubt, it may be better to avoid poisoning the mound). Ants are killed only if the insecticide contacts them, so proper application is essential. These treatments are most effective when ants are nesting close to the mound surface (as they do when the temperature is mild). Mounds should not be disturbed during treatment. It may be most beneficial to poison the mounds at the front of the invasion – particularly those around White Bay Beach and North Beach, where they are most likely to impact tourists and nesting seabirds and Iguanas (Fig. 5). Management of these vulnerable species will require understanding the likely impact of these Fire Ants on different life history stages (e.g. is it more important to protect nests or hatchlings?).

Continued monitoring of Red Imported Fire Ant Spread is strongly recommended. This will determine whether these invaders are spreading across the island, or are restricted to open, disturbed areas (as they are in the USA). Although these disturbed areas are also the places most used by people, if these Fire Ants spread into the forest they will by much more difficult to manage as they can easily recolonize long distances making localized eradication efforts fruitless. Red Imported Fire Ants can spread rapidly, so detecting spread early can help prevent this issue, and save time and money involved in island-wide eradication efforts.

Figure 5. A large adult of the endangered Stout Iguana, *Cyclura pinguis* (left); a juvenile being used in a long term mark-recapture study to monitor this fragile population (middle); and a recently hatched nest showing an egg in the foreground (right), next to which we located a Red Imported Fire Ant Mound.

Proposal for Continued Research in 2014

If invited back for 2014, we plan to continue our monitoring of the spread of Red Imported Fire Ants, and assessing their impact on the native species of Guana Island. Native ant species are known to slow the spread of this aggressive invasive ant through increased competition for resources. Continued monitoring of both this invader and the native ants species is critical to inform management. Our data show that the Red Imported Fire Ant is spreading and starting to eliminate native species; follow-up monitoring will inform whether this is a pattern to be concerned about, or if 2013 was an anomalous year.

These additional data on the distribution and spread of Red Imported Fire Ants will allow us to provide more informed management recommendations. We can use this information to explore baiting scenarios in order to rank options in order to get the greatest impact for the least investment of time, effort, and money. Continued monitoring may allow us to implement an adaptive management approach – modifying management as we become more informed or as the situation changes (e.g. Red Imported Fire Ants start spreading into the forest).

We also plan to experimentally determine effect of Red Imported Fire Ants on the eggs of the endangered Stout Iguana, *Cyclura pinguis*. We will construct artificial nests, with camera access, at different depths and distances from vegetative cover. We will monitor these daily to determine how long it takes for Red Imported Fire Ants (or other predators) to find and attack the simulated nests. We will use these data, in combination with long-term data collected by Guana Island researchers on clutch size, sex ratio, growth rates, population size, survival rates, to parameterize integral projection models to determine the net effect of Fire Ants on the population of these Iguanas as a whole. We can model perturbations to different parts of the life cycle and hence predict their impact; for example, we can assess how important it is to protect Iguana nests from threats including invasive Fire Ants and sheep trampling, versus increasing numbers of sexually mature adults to the population. This model can therefore be used to determine the best management practices for this important and highly threatened species.

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CYMAPAMPHANTUS VALENTINEORUM, A NEW GENUS AND SPECIES OF PAMPHANTINAE (HETEROPTERA: LYGAEOIDEA: GEOCORIDAE) FROM THE BRITISH VIRGIN ISLANDS, WITH A CHECKLIST OF THE SPECIES AND KEYS TO THE TRIBES AND GENERA OF THE SUBFAMILY

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Abstract.—The **new genus and new species *Cymapamphantus valentineorum***, belonging to the geocorid subfamily Pamphantinae, is described from one brachypterous male and six brachypterous females taken on Guana Island, British Virgin Islands. A dorsal habitus illustration, dorsal and lateral photographs of the male and female, diagnosis, and description of *C. valentineorum* are provided to help distinguish this new Caribbean bug from other New World pamphantines. A checklist of the species, keys to the three tribes and eight genera, and a color photograph of a representative species of each genus of the New World Pamphantinae are provided.

Key Words: Insecta, Hemiptera, Heteroptera, Geocoridae, Pamphantinae, new genus, new species, British Virgin Islands, Guana Island, keys, checklist

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The family Geocoridae contains the four subfamilies Australocorinae Malipatil, Geocorinae Stål, Henestarinae Douglas and Scott, and Pamphantinae Barber and Bruner (Henry 1995, Malipatil 2012). The Geocorinae are a worldwide group, the Henestarinae are restricted to the Old World, the Pamphantinae are found only in the Western Hemisphere (Slater 1964), except one genus and species described from Queensland, Australia (Slater 1981a), and the Australocorinae are known only from Queensland (Malipatil 2012). Slater (1999) reviewed the systematic position of the Pamphantinae and recognized the tribes Cattarini Slater, Epipolopini Slater, and the nominate Pamphantini. Slater and Henry (1999) reviewed the cattarine genus *Cattarus* and described a remarkable new mimetic genus and species from Ecuador, Brailovsky (1989) provided a key to the genera of the New World Pamphantinae, Baranowski and Slater (2005) gave a key to the genera and species of the West Indies, and Henry (2006) revised *Epipolops* Herrich-Schaeffer and discussed its position within the Pamphantinae.

While sorting undetermined specimens in the collection of Dr. Barry Valentine (Emeritus Professor, Ohio State University, Columbus) in preparation for a synopsis of the Heteroptera of Guana Island

(Lazell 2005) in the British Virgin Islands, I discovered four specimens of an unusual brachypterous pamphantine geocorid, which represent a new genus and new species. In 2012, the first known male and two additional females were taken in Malaise trap samples on Guana Island.

In this paper, I describe, diagnose, and provide an illustration and color photographs of *Cymapamphantus valentineorum*. A checklist of the species, keys to the three tribes and eight genera, and color photographs of representative species of each genus of the New World Pamphantinae are provided to facilitate recognition.

METHODS

Color adult habitus images were captured using an EntoVision Imaging Suite that included a JAI Technologies (AT-200GE) digital camera mounted to a Leica Z16 zoom lens via a Leica z-step microscope stand. Multiple focal planes were merged using Cartograph 8.0.6 (Microvision Instruments, France) software. Final illustrations were rendered using Adobe Photoshop CS4 and the plates were prepared using Adobe Illustrator CS4. The digital illustration of the adult female was created using Adobe Photoshop CS4.

All specimens are deposited in the National Museum of Natural History (USNM), Smithsonian Institution, Washington, D.C.

Cymapamphantus Henry, new genus

Type species: *Cymapamphanus valentineorum* Henry, new species.

Diagnosis.—This new genus is distinguished from all other Pamphantini by the presence of a small fore femoral spine; the lack of ocelli; the quadrate pronotum with the anterior lobe slightly broader and 2.5 times longer than the posterior lobe; the staphylinoid condition of the hemelytra (sensu Slater 1975) in both sexes, lacking any trace of a membrane; and the presence of a stridulitrum on each side of abdominal segment III and a plectron across the base of each hind femur.

Description.—Length to apex of abdomen 2.93–3.14; length to apex of hemelytra 1.73–1.86 mm. *Head*: Nearly quadrate, slightly wider than long; eyes relatively small, coarsely faceted; ocelli absent; antenniferous tubercles prominent; vertex, frons, and clypeus alutaceous to finely punctate, with a few large deep punctures between clypeus and antenniferous tubercles; undersurface densely and deeply punctate; buccula short, enclosing only base of labial segment I. *Labium*: Extending to bases of hind coxae; length of segments I, II, and IV subequal; ratios 14: 14: 11: 14. *Antenna*: Segment I elongate barrel-shaped, extending beyond apex of clypeus; segment II longest, segment I shortest, segment IV longer than III; ratios 9: 20: 14: 19. *Pronotum*: Bilobed; anterior lobe broader and 2.5 times as long as posterior lobe, deeply and densely punctate except for smooth or impunctate area around calli, lateral margins rounded or convex with a narrow lateral carina; posterior lobe shorter and narrower than anterior lobe, deeply and densely punctate. *Ventral surface of thorax*: Deeply and densely punctate. *Scutellum*: Equilateral; deeply and densely punctate. *Hemelytron*: Staphylinoid, clavus and corium fused without a suture between, each hemelytron meeting evenly along midline, truncate posteriorly, apex extending nearly to abdominal tergum III, membrane absent. *Abdomen*: Dorsum impunctate, with scent gland scars between terga 4 and 5 and 5 and 6 exposed; sutures 4 and 5 U-shaped through middle, strongly curving posteriorly; hypandrium impunctate, extending posteriorly slightly beyond genital capsule; ventrally impunctate, smooth, shiny, segments II and III fused, segment II swollen posteriorly with a distinct curving stridulitrum on each side; spiracles II–IV dorsal on connexiva, spiracles V–VII ventral. *Ostiolar evaporative area*: Reduced, covering slightly protruding auricle and narrow surrounding margin. *Legs*: Femora moderately swollen, fore femur with a small subapical spine, hind femur with a transverse plectron across base; tibiae slender basally, gradually thickening distally; tarsi three-segmented; claws strongly curving, with large fleshy pulvilli.

Etymology.—The prefix of the name of this new genus is taken from the superficially similar but distantly related cymid genus *Cymus* [Cymidae] and is combined with the pamphantine genus *Pamphantus* with which this new genus shares the most characters. The gender is masculine.

Discussion.—Unlike members of the Cattarini (*Cattarus* and *Cephalocattarus*), which have a distinct stridulitrum on the side of the head below the eyes and a plectron on the fore femur in both sexes, only males of *Cymapamphantus valentineorum* possess a stridulitrum on the side of the abdomen and a plectron on the hind femur. I have examined males of other pamphantine genera, including all species of *Epipolops*, *Neopamphantus maculatus* Barber and Brunner, *Pamphantus elegantulus* Stål, *Parapamphantus erikae* Brailovsky, and *Tropicoparapamphantus amazonicus* Brailovsky and have not found any stridulatory structures among them. Males are unknown for *Adpamphantus gibbosus* Barber, so it is not certain if this species has such sound-producing mechanisms.

Cymapamphantus valentineorum Henry, new species

(Figs. 1–5)

Diagnosis.—This species is distinguished by the combination of generic characters, including the presence of a small fore femoral spine, the lack of ocelli, the quadrate pronotum, and the short quadrate hemelytral pads lacking any remnants of a membrane, as well as the uniformly yellowish-brown color and the evenly and deeply punctate pronotum and hemelytral pads.

Description.—*Holotype male* (Figs. 2, 3): Length to apex of abdomen 2.90 mm, length to apex of hemelytra 1.73 mm, width across hemelytra 0.64 mm; width across abdomen 0.77 mm. *Head*: Length 0.51 mm; width across eyes 0.64 mm, interocular width 0.40 mm. *Labium*: Length 1.25 mm, extending to the bases of the hind coxae. *Antenna*: Segment I length 0.24 mm, II 0.50 mm, III 0.42 mm, IV 0.51 mm. *Pronotum*: Anterior lobe length 0.38 mm, posterior lobe length 0.18 mm; anterior lobe width 0.69 mm, posterior lobe width 0.64 mm.

COLORATION: Uniformly yellowish brown; labium and legs more pale yellow

STRUCTURE, TEXTURE, AND VESTITURE: *Head*: Quadrate, dorsal surface mostly alutaceous or finely punctate, either side of clypeus with several large, deep punctures, ventral surface evenly and deeply punctate; vertex with a short central carina at middle, each side bordering eyes with a shallow ridge or carina. *Pronotum*: Anterior lobe 2.5 times as long as posterior lobe, lateral margins convex and narrowly carinate, surface punctate, except for shiny, impuncate calli; posterior lobe much wider than long, narrower than anterior lobe, lateral margins weakly rounded and ecarinate. *Scutellum*: Equilateral, evenly and deeply punctate. *Hemelytron*: Micropterous or staphylinoid, quadrate, evenly and deeply punctate; truncate apically, membrane absent. *Abdomen*: Dorsum impunctate, segments II and III fused; ventral surface shiny, impunctate, segment III

122

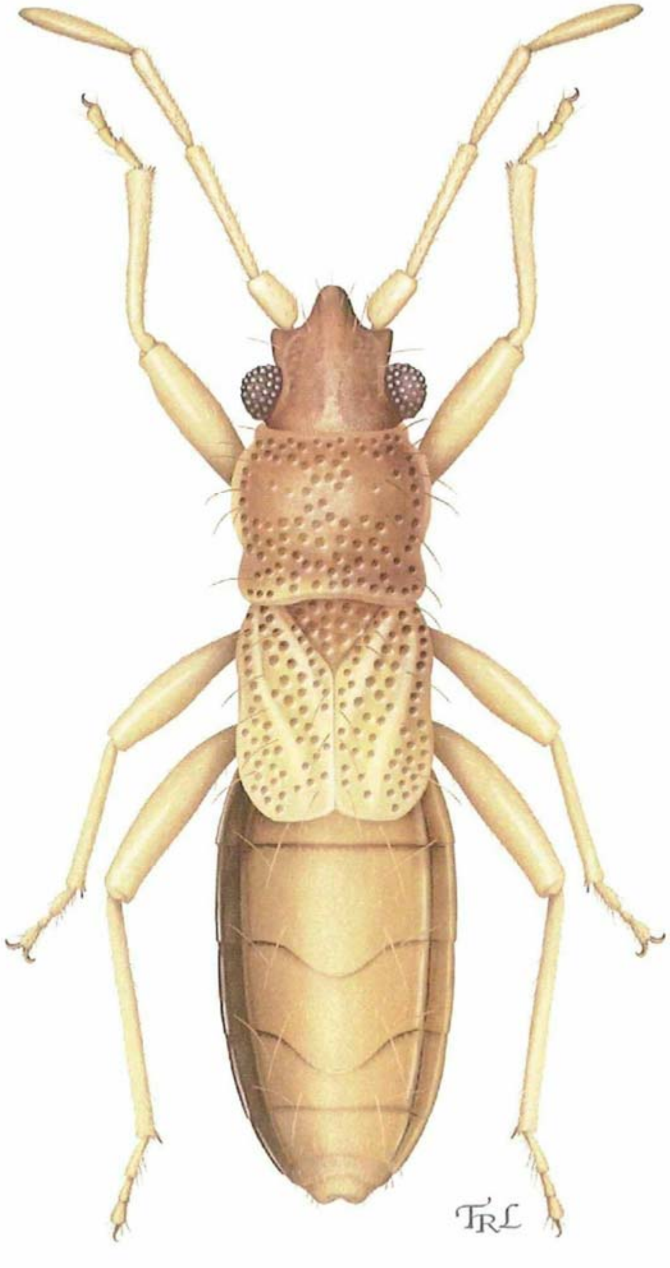
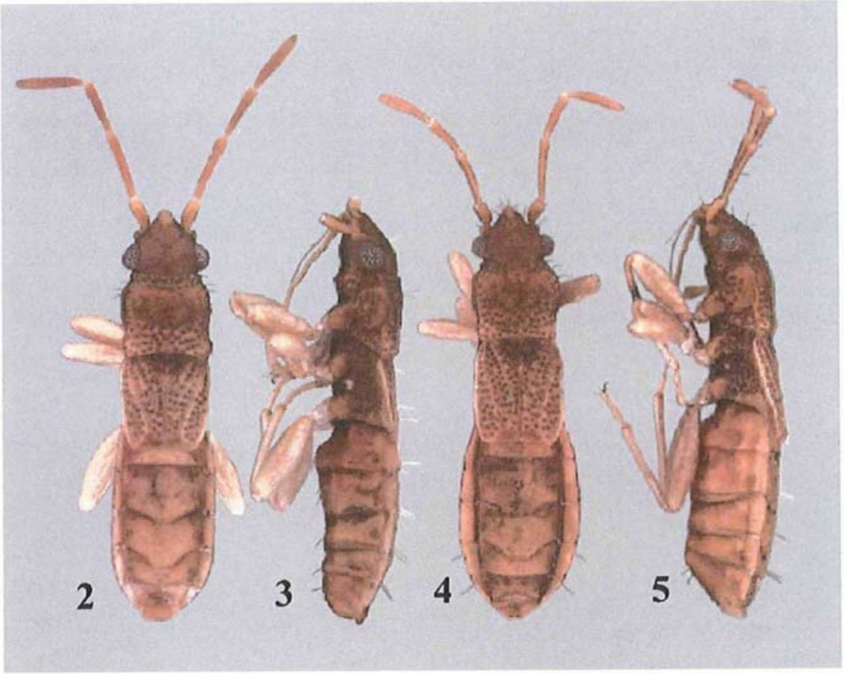


Fig. 1. Dorsal habitus illustration of adult female *Cymapamphantus valentineorum*.

swollen posteriorly (Fig. 3) with a distinct stridulitrum on each side. *Dorsal setae*: Head, pronotum, scutellum, and hemelytra with a few scattered, long, erect setae; abdominal segment III with four long, erect trichobothria across middle, segment IV with three, and segments V–VI with two.

Male genitalia: Unique male holotype not dissected until more material becomes available.

Female (Figs. 1, 4, 5) (n = 4): Length to apex of abdomen 2.93–3.14 mm, length to apex of hemelytra 1.73–1.86 mm, width across hemelytra 0.69–0.74 mm. *Head*: Length 0.53–0.58 mm, width across



Figs. 2–5. Photographs of the adult male and female of *Cymapamphantus valentineorum*. 2, adult male (holotype), dorsal aspect. 3, adult male (holotype), lateral aspect. 4, adult female, dorsal aspect. 5, adult female, lateral aspect.

eyes 0.61–0.65 mm, interocular width 0.38–0.42 mm. *Labium*: Length 1.30–1.57 mm, extending to bases of hind coxae. *Antenna*: Segment I length 0.22–0.26 mm, II 0.50–0.54 mm, III 0.38–0.40 mm, IV 0.48–0.53 mm. *Pronotum*: Length 0.53–0.58 mm, anterior lobe width 0.69–0.70 mm, posterior lobe width 0.61–0.64 mm.

Etymology.—I am pleased to name this new brachypterous pamphantine in honor of Dr. Barry D. and Mrs. Buena Valentine, and their daughter Susan Valentine-Cooper for their efforts to inventory the insect fauna of Guana Island, including their collections of the first four known specimens of this new species.

Discussion.—This peculiar new species is known from only seven adults, all of which are short winged and flightless (hind wings absent). Nevertheless, three adults and one third-instar nymph were taken in a Malaise trap and one was taken on a sheet at ultraviolet light, indicating that these bugs are wide roaming and crawled into the traps. The three remaining specimens were either beaten or swept from foliage. Nothing is known of the feedings habits or biology of this bug or any other Pamphantinae.

The male genitalia have been illustrated for only a few species of Pamphantinae (Slater 1981a, 1999), primarily because of the lack of males or adequately long series. I too refrain from dissecting the unique male of *C. valentineorum* until additional comparative material becomes available.

Type material.—Holotype ♂, British Virgin Islands, Guana Island, North Beach, nr gravel pit, 18°28′47.33″N, 64°34′26.78″W, Sept. 2012, W. P. Liao, Malaise trap. Paratypes: 1 ♀, British Virgin Is[lands]., Guana I[sland], 11/20-x-2002,

R. R. Snelling, E end of White Beach; 1 ♀, British Virgin Islands, Guana Island, 1/7-x-03, B[arry]. & B[uena]. Valentine, sweeping & beating; 1 ♀, British Virgin Islands, Guana Is[land], Upper Camanoe, u/v [light], 26 Oct. 2008, B. D. and S [usan]. C. Valentine; 1 ♀, British Virgin Islands, Guana Is[land], Monkey Point Trail, 27-x-2009, S. Valentine-Cooper; 2 ♀♀, same data as for holotype (and one 3rd instar, May 2012), with dates Dec. 2011 & June 2012.

KEY TO THE NEW WORLD TRIBES OF PAMPHANTINAE

1. Males and females with a distinct lunate stridulitrum on side of head below eyes and a plectron on inner face of fore femur; male abdomen with a distinct tubercle on each side of segment III; anterior and posterior pronotal lobes separated by a deep transverse impression (Figs. 6, 7) . . . . Cattarini
– Male and females without a stridulitrum on head or a plectron on fore femur; male abdominal segment III without tubercle, though sometimes slightly swollen; pronotal lobes usually not separated by a deep transverse impression 2
2. Eyes strongly stylate, extending laterally well beyond outer margin of head; pronotum usually with lobes and/or spines along lateral margins (Fig. 8); includes only *Epipolops* . . . . Epipolopini
– Eyes not stylate, never extending beyond outer margin of head; pronotum entire, without lateral lobes or spines (Figs. 9–13) . . . . Pamphantini

KEY TO THE GENERA OF CATTARINI

1. Lateral margins of pronotal lobes unarmed (Fig. 6) . . . . *Cattarus* Stål
– Lateral margin of anterior pronotal lobe with a broad winglike process and each humeral angle of posterior lobe with a spinelike projection (Fig. 7) . . . . *Cephalocattarus* Slater and Henry

KEY TO THE GENERA OF PAMPHANTINI

– Anterior femur without a distinct subapical spine 2
– Anterior femur with one or two distinct subapical spines 3
2. Anterior and posterior lobes of pronotum little separated, without a deep transverse impression; posterior lobe of pronotum almost flat, without swellings (Fig. 12) . . . . *Parapamphantus* Barber
– Anterior and posterior lobe of pronotum separated by a deep transverse impression; posterior lobe with a distinct swelling or blunt tubercle on each side (Fig. 13) . . . . *Tropicoparapamphantus* Brailovsky
3. Head lacking ocelli 4
– Head with distinct ocelli between eyes . . . 5
4. Anterior pronotal lobe greatly swollen or globose; narrow posterior lobe with a long, slender, curving spine arising at each humeral angle (Fig. 9) . . . . *Abpamphantus* Barber
– Anterior pronotal lobe not greatly swollen, two and half times as long and only slightly wider than posterior lobe; humeral angles unarmed (Figs. 2–5) . . . . *Cymapamphantus*, new genus
5. Eyes large and substylate, inner margin of eye extending laterally past anterior angle of pronotum; distance between ocelli less than to subequal to the distance from an ocellus to an eye; posterior half of hemelytra convex or rounded; profemur with two spines (apical spine broken on three specimens examined) (Fig. 10) . . . . *Neopamphantus* Barber & Bruner
– Eyes prominent, but not substylate, inner margin of eye not extending laterally past anterior angle of pronotum; each ocellus closer to eye than to each other; hemelytra subparallel throughout; profemur with only one spine (Fig. 11) . . . . *Pamphantus* Stål

CHECKLIST OF THE PAMPHANTINAE

Tribe Cattarini

Cattarus balteatus (Distant), 1893: 413 [Brazil, Panama]

Cattarus erwini Slater and Henry, 1999: 308 [Peru]

Cattarus formicarius (Distant), 1893: 413 [Panama]

Cattarus insignis Stål, 1860: 42 [Brazil]

Cattarus nigritus Slater and Henry, 1999: 312 [Ecuador]

Cattarus pallidus Slater and Henry, 1999: 315 [Ecuador] (Fig. 6)

Cattarus pseudoculatus Slater and Henry, 1999: 316 [Ecuador]

Cattarus stysi Slater, 1999: 204 [Brazil]

Cephalocattarus waorani Slater and Henry, 1999: 326 [Ecuador] (Fig. 7)

Tribe Epipolopini

Epipolops acuminatus (Distant), 1893: 389 [Bolivia, Costa Rica, Panama]

Epipolops angelae Henry, 2006: 507 [Brazil] (Fig. 8)

Epipolops arboricolus Brailovsky, 1989: 126 [Brazil]

Epipolops bellus Brailovsky, 1990:127 [Venezuela]

Epipolops frondosus Herrich-Schaeffer, 1850: 202 [Argentina, Bolivia, Brazil, Paraguay]

Epipolops kathrynae Henry, 2006: 514 [Ecuador]

Epipolops lenkoi Canter, 1964: 64 [Brazil, Ecuador]

Epipolops mucronatus (Distant), 1893: 389 [Panama]

Epipolops oculuscanri (De Geer), 1773: 343 [Brazil, Colombia, Costa Rica, Guyana, Mexico, Panama, Suriname]

Epipolops quadrispinus Stål, 1874: 134 [Colombia]

Epipolops rettenmeyeri Slater, 1998: 64 [Ecuador, Peru]

Epipolops scudderi Henry, 2006: 522 [Panama]

Epipolops slateri Henry, 2006: 525 [Ecuador]

Epipolops thomasi Henry, 2006: 528 [Bolivia]

Tribe Pamphantini

Abpamphantus gibbosus Barber, 1954a: 351 [Cuba] (Fig. 9)

Austropamphantus woodwardi Slater, 1981a:111 [Queensland, Australia].

Cymapamphantus valentineorum Henry, 2013 (this paper) [Guana Island, British Virgin Islands] (Figs. 2–5)

Neopamphantus calvinoi Barber and Bruner, 1933: 535 [Cuba]

Neopamphantus hispaniolus Slater, 1965: 188 [Haiti]

Neopamphantus maculatus Barber and Bruner, 1933: 533 [Cuba] (Fig. 10)

Pamphantus atrohumeralis atrohumeralis Barber and Bruner, 1933: 537 [Haiti]

Pamphantus atrohumeralis dominicanus Slater, 1981b: 83 [Dominican Republic]

Pamphantus barberi Slater (in Baranowski and Slater), 2005: 76 [Dominican Republic]

Pamphantus binotatus Slater, 1981b: 86 [Venezuela]

Pamphantus elegantulus Stål, 1874:157 [Cuba]

Pamphantus mimeticus Barber, 1926: 434 [Cuba]

Pamphantus pallidoides Slater, 1981b: 83 [Dominican Republic]

Pamphantus pallidus Barber and Bruner, 1933: 536 [Cuba] (Fig. 11)

Pamphantus pellucidus Slater, 1956: 50 [Puerto Rico]

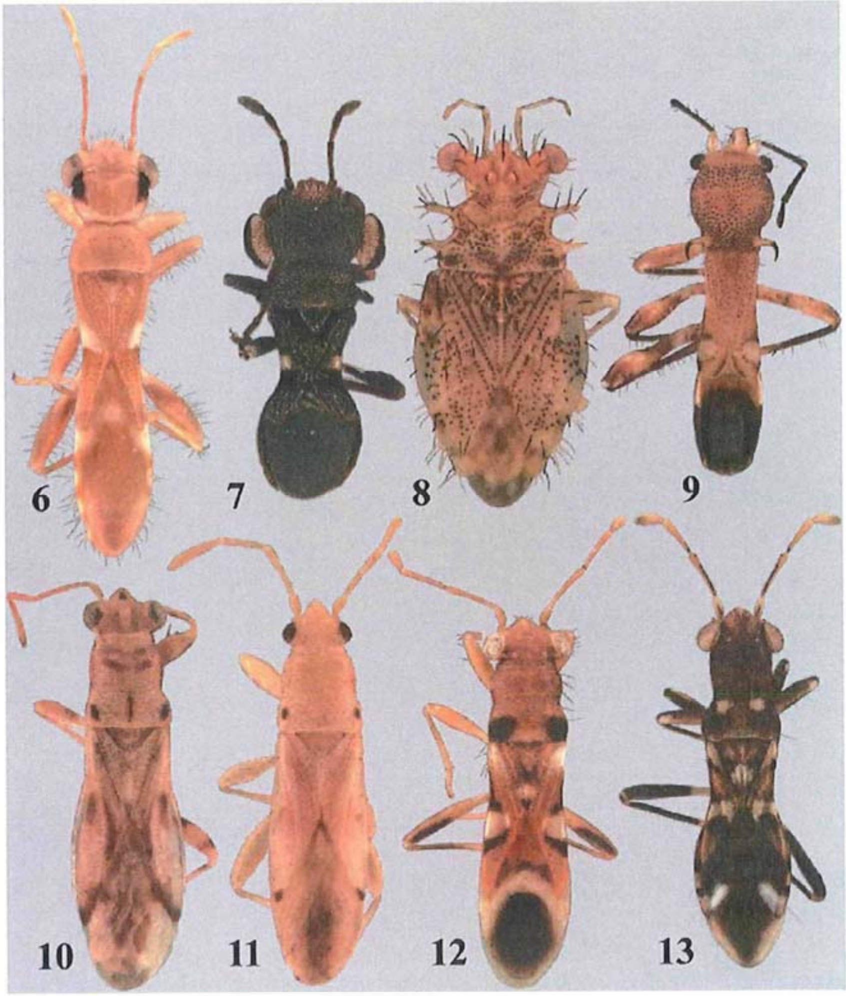
Pamphantus stenoides Guérin-Méneville, 1857: 400 [Cuba]

Pamphantus trimaculatus Slater, 1981b: 83 [Dominican Republic]

Pamphantus vittatus Bruner, 1932: 141 [Cuba]

Parapamphantus braziliensis Barber, 1954b: 216 [Brazil]

Parapamphantus elongatus Slater, 1981b: 83 [Brazil]



Figs. 6–13. Photographs of Neotropical Pamphantinae. 6, 7, Cattarini. 6, *Cattarus pallidus* Slater and Henry (holotype ♂, Orellana Prov., Ecuador). 7, *Cephalocattarus waorani* Slater and Henry (paratype ♂, Orellana Prov., Ecuador). 8, Epipolopini. 8, *Epipolops angelae* Henry (holotype ♂, Federal District, Brazil). 9–13, Pamphantini. 9, *Abpamphantus gibbosus* Barber (holotype ♀, Jarahueca, Cuba), dorsal aspect. 10, *Neopamphantus maculatus* Barber & Bruner (holotype ♀, Pico Turquino, Cuba). 11, *Pamphantus pallidus* Barber & Bruner (holotype ♂, Sierra Maestra, Cuba), dorsal aspect. 12, *Parapamphantus erikae* Brailovsky (♂, Loja Prov., Ecuador). 13, *Tropicoparapamphantus amazonicus* Brailovsky (♂, Orellana Prov., Ecuador).

Parapamphantus erikae Brailovsky, 1989: 197 [Brazil, Ecuador, Venezuela] (Fig. 12)

Tropicoparapamphantus amazonicus Brailovsky, 1989: 195 [Brazil, Ecuador, Peru] (Fig. 13)

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129

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Ecology and Diversity of Cockroaches (Dictyoptera: Blattaria) from the Virgin Islands

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Ecology and Diversity of Cockroaches (Dictyoptera: Blattaria) from the Virgin Islands

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Abstract. The Virgin Islands (except St. Croix) are geologically part of the Puerto Rico Bank and biologically related to Puerto Rico, but their cockroaches (Dictyoptera: Blattaria) were not yet as well studied as those on Puerto Rico. To elucidate the number of species, life history, range distribution, and seasonal abundance of these cockroaches, we have conducted a quantitative study since June 2000 using a Malaise trap on Guana Island, British Virgin Islands, in addition to other conventional collecting methods. We found 21 species: *Blattella germanica* (Linnaeus), *Cariblatta antiguensis* (Saussure and Zehntner), *Cariblatta* sp. 2, *Cariblatta* sp. 3, *Colapteroblatta* sp. 1, *Eurycotis improcera* Rehn, *Eurycotis* sp. 2, *Euthlastoblatta facies* (Walker), *Hemiblabera brunneri* (Saussure), *Nyctibora lutzi* Rehn and Hebard, *Panchlora sagax* Rehn and Hebard, *Periplaneta americana* (Linnaeus), *P. australasiae* (Fabricius), *Plectoptera infulata* Rehn and Hebard, *P. rhabdota* Rehn and Hebard, *Plectoptera* sp. 3, *Pycnoscelus surinamensis* (Linnaeus), *Symploce pararuficollis* Roth, *S. ruficollis* (Fabricius), polyphagid sp. 1 (*Compsodes* sp. 1), and polyphagid sp. 2. Among them, nine are new records for the Virgin Islands and five for Guana Island. In addition, *Euthlastoblatta diaphana* (Fabricius), *Nyctibora noctivaga* Rehn, *Panchlora nivea* (Linnaeus), *P. viridis* (Fabricius), and *Rhyparobia maderae* (Fabricius) were recorded historically but were not rediscovered. As a result, the number of species is increased from 17 to 26 for the Virgin Islands, and from 10 to 15 for Guana Island. Overall, only five species are edificarian and likely introduced. Nymphs of polyphagid sp. 2 and *Euthlastoblatta facies* are reported for the first time as dwellers in termite runways. Only eight species came to the Malaise trap; their phenology illustrates close but not necessarily synchronic relationship with both the timing and amount of rainfall. Monthly abundance showed spring and fall highs and summer and winter lows. Yearly abundance reached lows when annual rainfall decreased below a threshold average of 2.0 mm per day. Seasonality and response to drought varied among species. This paper lays a foundation for further research on diversity of cockroaches from the Virgin Islands and their relationships with those from Puerto Rico.

Keywords. Blaberidae, Blattellidae, Blattidae, Polyphagidae, seasonality, termite, phenology, Guana

Introduction

Geologically and biologically the Virgin Islands (except St. Croix) are part of the Greater Puerto Rico Bank, which united these islands until about 10,000 years ago as continuous land. Thus their floras and faunas are expected to have much affinity with those of Puerto Rico (Heatwole et al. 1981). Politically these islands are divided into the British Virgin Islands (BVI) and U. S. Virgin Islands (USVI). There are two annual rainfall peaks in the Virgin Islands (Lazell 2005). Guana Island is a small, privately owned, BVI island located off the northeast end of Tortola at 18°28'N by 64°35'W (Fig. 1). Its rugged topography of 297 hectares features exceptionally well-preserved subtropical dry forest that covers most of the island from sea level to its highest elevation (Sugarloaf Peak at 246 m). Since 2000 we have been studying the ecology and diversity of Virgin Island cockroaches (Dictyoptera: Blattaria), using Guana Island as our base and research station. Our overall goals are to build a data matrix for further diversity study among an array of the Virgin Islands, to understand the biogeographic relationships of the cockroaches from these islands with those from Puerto Rico, and to provide a reference point for future studies on the impacts of climatic changes.

A synoptic study provides a list of cockroach species of Puerto Rico (Gutiérrez and Fisk 1998). In contrast, there is little information about the cockroaches of the Virgin Islands other than taxonomic species accounts scattered over >235 years. Fabricius (1787) described *Blatta ruficollis*, now in *Symploce*, from St. Thomas, which is the first species originally described from the Virgin Islands on the Greater Puerto Rico Bank. Shelford (1910) reported eight USVI species and others now synonyms: *Euthlastoblatta diaphana* (Fabricius), *Hemiblabera brunneri* (Saussure), *Periplaneta americana* (Linnaeus), *P. australasiae* (Fabricius), *Pycnoscelus surinamensis* (Linnaeus), *Panchlora nivea* (Linnaeus), and *Rhyparobia maderae* (Fabricius), but his *Nyctibora noctivaga* from Loango (now Lovango) Island near St. Thomas is dubious because the identification was based on an immature male (Rehn and Hebard 1927). Rehn (1930) described *Eurycotis improcera* from St. Croix, the second species originally from the Virgin Islands. Princis (1964) recorded *Panchlora viridis* (Fabricius) from St. John and St. Croix of USVI. Roth (1985) recorded *Blattella germanica* (Linnaeus) from "British West Indies." This pest species is presumably present on the Virgin Islands because of its edificarian status: being found around human constructions. Miller (1994) recorded *P. surinamensis* as a "quarantine" pest on a shipment of potted plants being unloaded at Guana Island. Roth (1994) studied specimens taken by various collectors on Guana Island. Based on that material he described the third species originally from the Virgin Islands, *Symploce pararuficollis*, and added *Cariblatta antiguensis* (Saussure and Zehntner), *Euthlastoblatta facies* (Walker), *Panchlora sagax* Rehn and Hebard, and *Plectoptera rhabdota* Rehn and Hebard to the Virgin Islands list. As the result, there are three names of *Panchlora* green cockroaches recorded from the Virgin Islands. Seven of the eight species recorded by Roth were from Guana Island; *Hemiblabera brunneri* was from the island of Virgin Gorda. Recently Lazell (2005) provided a list of 10 cockroach species, adding the names *Eurycotis decipiens* (Kirby) and *Hemiblabera brunneri* (Saussure) to the fauna of Guana Island. However, the identification of *Eurycotis decipiens,* a cockroach species originally described from Trinidad (Kirby 1903), is now for the first time corrected to *E. improcera*, a species originally described from St. Croix (Rehn 1930). In all, 17 species were previously recorded from the Virgin Islands and 10 of these from Guana Island.

In this paper we report for the first time the increase of species diversity to 26 for the Virgin Islands and 15 for Guana Island. Changes in cockroach abundance and the impact of rainfall on abundance were studied with monthly samples from a Malaise trap over a period >12 years from June 2000 to October 2011. Our hypothesis was that the abundance changed not only among species, but also among years and different months of a year in response to rainfall. Habitats, multiple new island records, behaviors, life histories, and nymphal morphology of several species are provided for the first time. This study contributes new information on the ecology and fine mapping of cockroach distributions in the West Indies.

Materials and Methods

We collected cockroach specimens on Guana Island since 2000 every October, using a variety of collection methods such as sweeping or beating vegetation with an entomological net, looking under

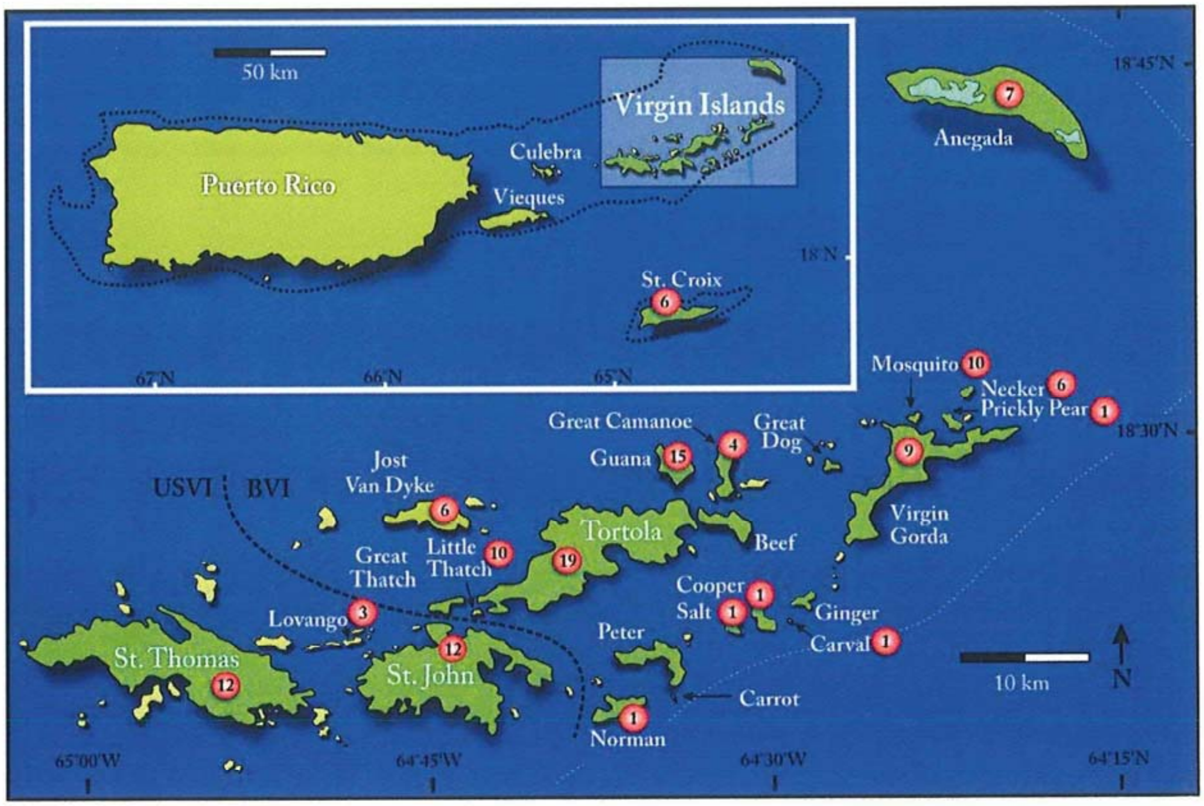


Figure 1. Maps of the Greater Puerto Rico Bank and the Virgin Islands with numbers of cockroaches recorded from the Virgin Islands historically and presently indicated for each sampled island.

detritus, logs, and rocks, at white (incandescent) or black (ultraviolet) lights, and at night with a headlamp, and covering the entire diversity of geography and habitats, in diurnal and nocturnal forays. Whenever possible, we also collected on other islands of BVI and USVI. In addition, a Malaise trap was set up in Quail Dove Ghut on Guana Island behind an orchard within a forest edge, at about 5 m above sea level on the leeward side. It provided monthly samples starting in June 2000. We sorted and counted the total number of individuals (nymphs and adults combined) by species, month, and year, and presented the average results of abundance changes across months or years. Four (VII/IX.2004, IV.2005, VII.2007) monthly samples were incomplete and replaced by respective monthly averages across years for computational ease. A resident scientist, Professor Liao Wei-Ping, and his assistants, maintained this trap and collected samples once a month except every October when we were present.

Specimens are deposited in the museum of Guana Island Wildlife Sanctuary (**GIWS**), the entomological collection of the University of Delaware, Newark, DE (**UDCC**), the Virgin Islands Insect Survey, Virgin Islands National Park, St. John, USVI (**VIIS**), the Entomological Museum of Montana State University, Bozeman, MT (**MAIC**), the U. S. National Museum of Natural History, Smithsonian Institution, Washington, DC (**NMNH**), and the American Museum of Natural History, New York, NY (**AMNH**), where specimens in VIIS collected on 18-27.VII.1972 from St. John at Lameshur Bay were collected at the Virgin Islands Environmental Resource Station by junior members of the New York Entomological Society under the direction of Alice Gray. A complete synoptic set of 700 specimens is in the private collection of B. D. Valentine (**BDVC**) and will be deposited in the Florida State Collection of Arthropods, Gainesville, FL. Specimens from St. John, USVI, at MAIC are a loan from BDVC. In the section for specimens examined, specimen labels for collectors are corrected as follows: Valentine-C = S. Valentine-Cooper, and Y.-P. Liao = W.-P. Liao. When a species is common on Guana Island, we did not save many hundreds of specimens; for those saved, we provide the number of specimens by sex or stage, sample months, collection methods, but often omit collection dates, years, or collectors.

Beating, sweeping, white light, or black (ultraviolet) light is shortened to beat, sweep, at light, or at UV, respectively, and only the first letter of directions is used in upper case, if given on the specimen labels. Some islands do not include the word "island" in their names (e.g., Anegada); for clarity, we have added "Is." to these in our specimen records (e.g., Anegada Is.). This will avoid confusion with localities on islands. We followed Roth (1968, 1971) for terminology and McKittrick (1964) and Roth (2003) for higher taxonomic categories; an oothecum is the egg case of cockroaches; the forewing is termed tegmen (plural tegmina); the last visible tergite is the supra-anal plate; and the last visible sternite is the subgenital plate. Because synonyms for each taxon are completely treated in Princis (1963–1967, 1969), Roth (2003), and Beccaloni (2007), we only include references for original descriptions and for relevant geographical distributions. Most of the species descriptions were brief, reflecting trends of historic times; we provided additional detailed characteristics concurrent with modern taxonomy.

We obtained daily rainfall data from colleagues at the National Oceanic and Atmospheric Administration (NOAA) and the National Aeronautic and Space Administration (NASA). The NOAA Climate Prediction Center (CPC) (http://www.cpc.ncep.noaa.gov/) makes a "unified gauge" data product of global land precipitation (0.1 mm) in a spatial resolution of 0.5-degree latitude by longitude grid and a 1-day temporal resolution. Precipitation amounts and gauge counts for the pixel in the grid corresponding to the Virgin Islands (grid 18.0–18.5°N latitude by 64.5–65.0°W longitude) were extracted from each grid file. The dataset is based on precipitation gauges, but values represent an average over a large area rather than a point measurement. When there are multiple gauges, the rainfall amount should be essentially the average over those gauges located within the grid. Over the years the gauge count varies from 0 to 11 as old gauges fail or are taken offline or new gauges are installed. At least one gauge was periodically stationed on Beef Island, just southeast of Guana Island. We used daily rainfall from June 2000 to October 2011 averaged per month or averaged per year to look for correlation of rainfall with monthly and yearly fluctuations of cockroach abundance, respectively.

Results

Among >5,000 cockroach specimens taken we found 12 of the 17 species previously recorded. The five names known historically, but missing currently, are *Euthlastoblatta diaphana*, *Nyctibora noctivaga*, *Panchlora nivea*, *P. viridis*, and *Rhyparobia maderae*. In addition, we recorded nine species new to the Virgin Islands and five new to Guana Island (Table 1). The overall number of species recorded was thus increased from 17 to 26 in 14 genera and four families (Blaberidae 7 species, Blattellidae 13, Blattidae 4, and Polyphagidae 2) for the Virgin Islands; for Guana Island, the number of species was increased from 10 to 15. Only eight species were caught by the year-round Malaise trap on Guana Island: *Cariblatta antiguensis*, *Eurycotis improcera*, *Euthlastoblatta facies*, *Nyctibora lutzi*, *Panchlora sagax*, *Plectoptera rhabdota*, *Symploce pararuficollis*, and *S. ruficollis*. Among these, *E. improcera*, *N. lutzi*, and *P. sagax* were caught at very low frequency (<20 specimens over 12 years); *S. pararuficollis* was the most abundant (2,655), followed by *C. antiguensis* (1,366), *S. ruficollis* (190), *E. facies* (177), and *P. rhabdota* (83).

When compared among months, total Malaise trap captures of all species closely followed the timing of the spring rainfall (Fig. 2A, 3). The average number of individuals reached its spring high in June after the rainfall peak in April-May, then slid to its summer low, but regained a slow and steady fall-winter increase often until January after the rainfall peak in September-November, and finally decreased to its winter low from February to April. However, this monthly pattern of abundance synchrony with each rainy peak was species dependent. Only two species frequently captured in the Malaise trap showed the monthly pattern; *Euthlastoblatta facies*, *Plectoptera rhabdota*, and *Symploce ruficollis* showed only one abundance peak, in the summer (Table 2). Also, four species showed a delayed burst of abundance 1–2 months after the spring rainy peak; only *S. ruficollis* demonstrated tight synchrony with the spring rainfall peak (Table 2). Furthermore, four species reached their maxima in late spring or early summer (Table 2) when the rainfall amount was much less than the fall rainy peak (Fig. 2A); only *S. pararuficollis* showed close correlation with the amount of rainfall; its abundance reached maximum in the fall. Overall, the spring rainfall peak induced a delayed burst of abundance in late spring, and the fall rainfall peak only sustained a small increase of individuals from the summer low.

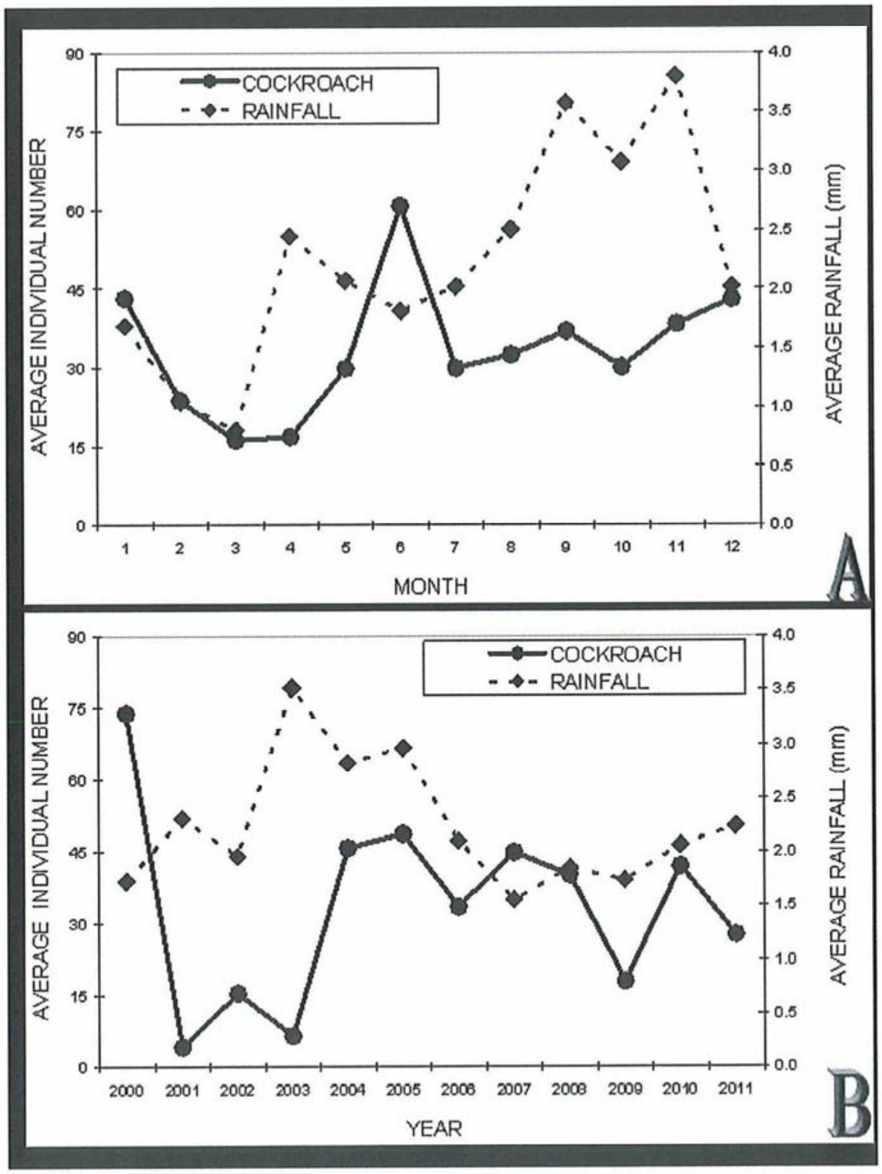


Figure 2. Relationship of rainfall (mm) with abundance of all cockroaches captured in a Malaise trap within a forest edge from June 2000 through October 2011 on Guana Island, British Virgin Islands (missing 4 samples of VII/IX.2004, IV.2005, and VII.2007; A: numbers of individuals per month averaged across years; B: numbers of individuals per year averaged across months).

When compared among years, total Malaise trap captures of all species closely followed the amount of annual rainfall (Fig. 2B, 3). There was a crash in the average number of individuals in 2001, 2003, and 2009, corresponding to decreased rainfall during each of the previous year(s): 2000, 2002, and 2007–2009 had a rainfall averages below 2.0 mm per day. This yearly pattern of low abundance in response to drought applied to all five species frequently captured in the Malaise trap (Table 3). However, high abundance occurred differently among species; *Euthlastoblatta facies* and *Plectoptera rhabdota* both reached maxima in 2010 after the 3-year period of low rainfall below 2.0 mm, while the other three species had high numbers in 2000 (Table 3), when annual rainfall of prior three years before our study was above 2.5 mm and averaged 3.1 mm. Overall, high annual rainfall coincided with high abundance, but a threshold below a daily average of 2.0 mm triggered abundance plunges in some and leaps in others.

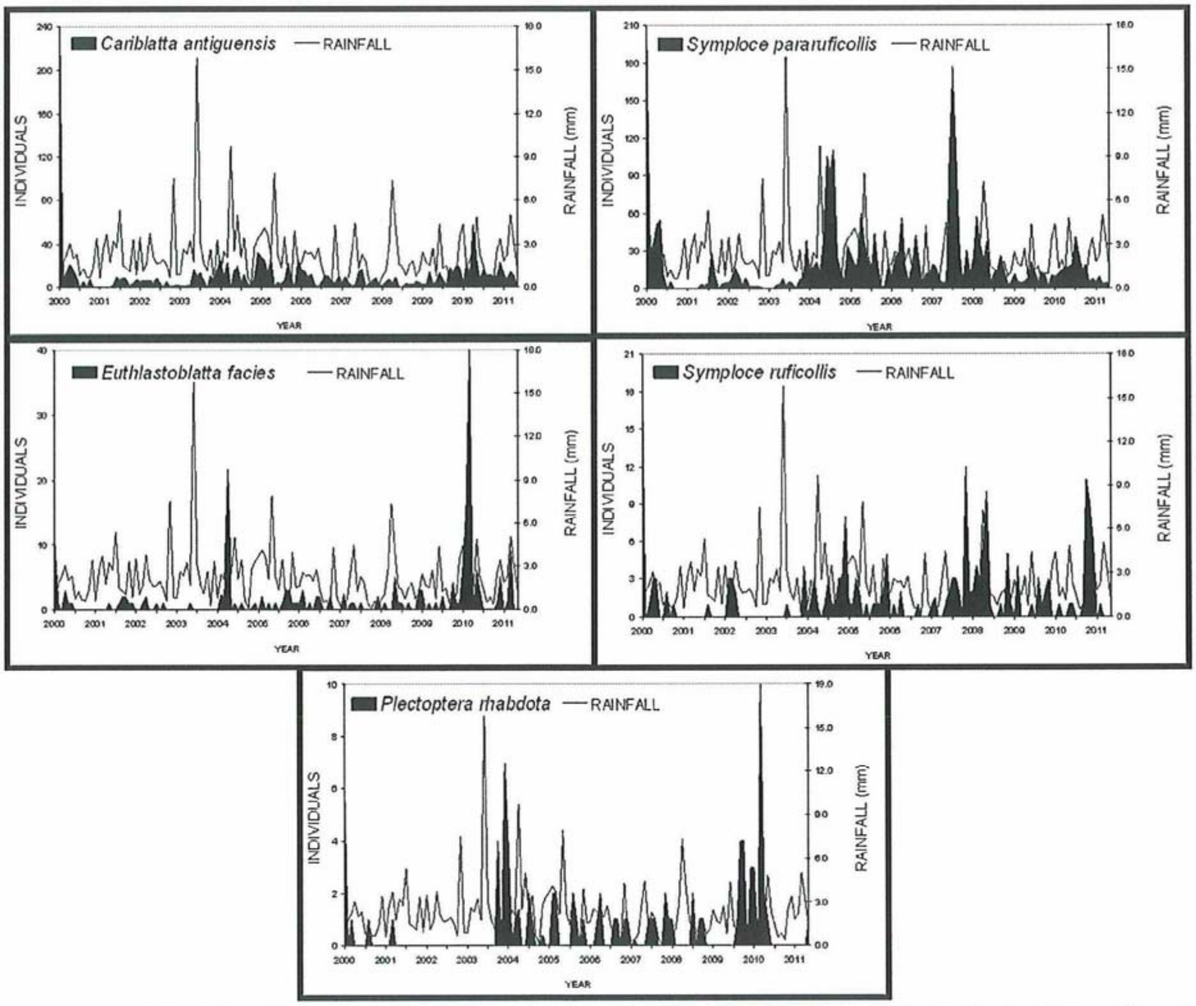


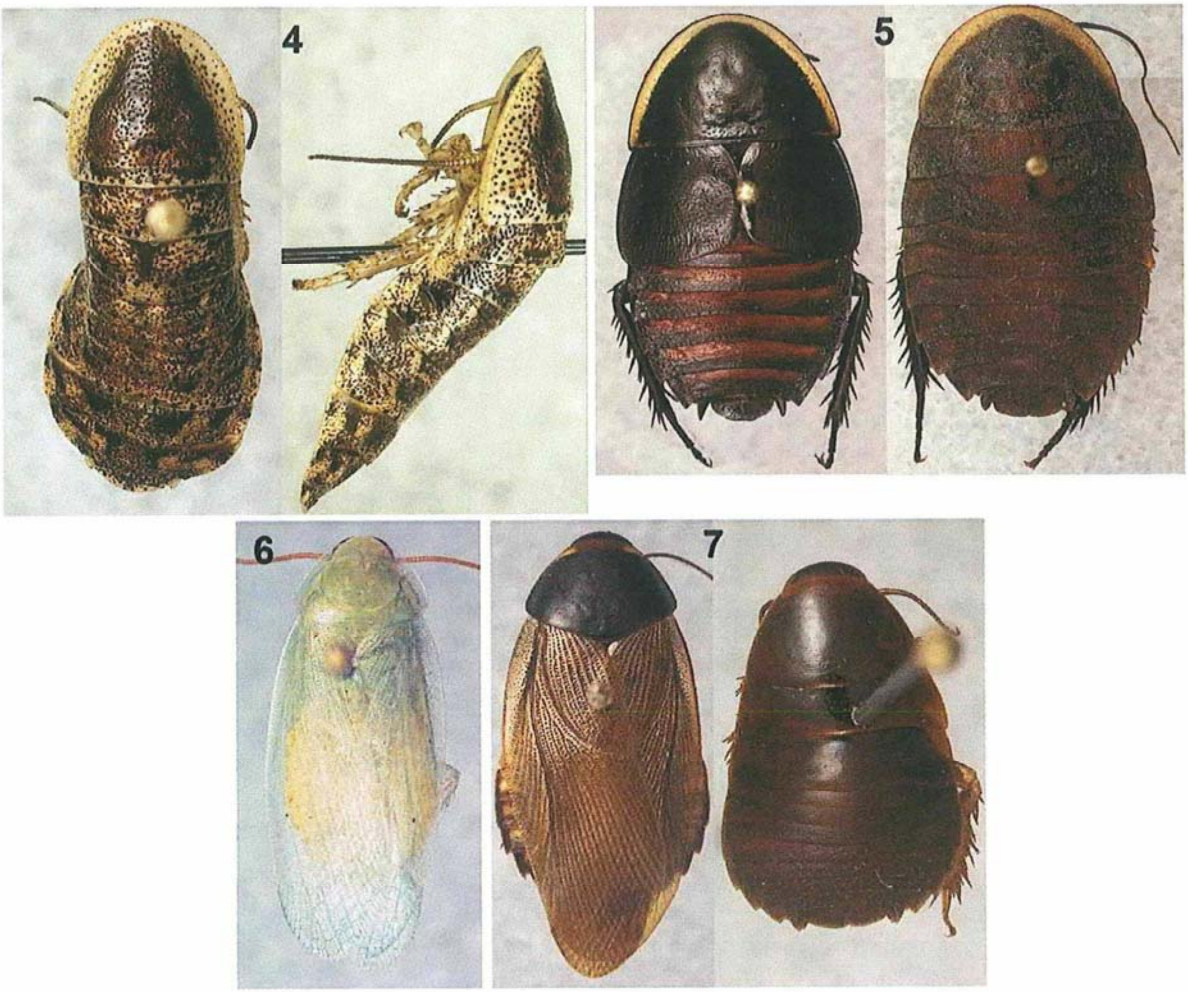
Figure 3. Relationship of average rainfall (mm) with monthly abundance in number of individuals of five cockroach species frequently captured in a Malaise trap within a forest edge from June 2000 through October 2011 on Guana Island, British Virgin Islands (missing 4 samples of VII/IX.2004, IV.2005, and VII.2007).

The distributions of these 26 cockroach species are summarized from 17 islands (Table 4): 19 on Tortola, 15 on Guana, 12 on St. John and St. Thomas, 10 on Little Thatch and Moskito, and <10 on each of the other islands. *Hemiblabera brunneri* is most widespread (13 islands), followed by *Symploce ruficollis* (11), *Cariblatta antiguensis*, *Euthlastoblatta facies*, and *Pycnoscelus surinamensis* (10 each). These figures reflect present collecting success, not final diversity. The morphological diagnosis, habitat, behavior, new island records, and phenology for each species are given below.

Family Blaberidae

1. *Colapteroblatta* sp. 1 (Fig. 4), NEW RECORD

Diagnosis. Nymph 17 mm, relatively convex and elongate, pale yellowish brown and mottled dark brown; dorsum with dense, dark punctures, plus 5 very irregular longitudinal fields of brown markings, leaving margins of pronotum pale yellow-brown. Frons mostly dark ferruginous, vertex slightly darker with 3 pale, narrow, interocular stripes; antennomeres basally straw-colored, then progressively darker; pronotum disc convex, margin thickened and flared upward, with a large, irregular, mottled brown central area, and sides yellow with dark punctures; rest of dorsum irregularly spotted with dark brown,



Figures 4–7. Blaberidae. **4)** *Colapteroblatta* sp. 1 nymph from Tortola Island. **5)** *Hemiblabera brunneri* male adult from Guana Island and nymph from Little Thatch Island. **6)** *Panchlora sagax* from Guana Island. **7)** *Pycnoscelus surinamensis* from Guana Island (all specimens in BDVC).

forming 5 longitudinal series, of which the middle series is the least developed; venter pale straw and dark brown, with 2 darker mottled lateral fields that are wider posteriorly and connected across the last sternite; pale lateral margins continuous to cerci, then abruptly narrowed to a thin line; cerci very short, 1 segmented, straw-colored; legs pale with dark-tipped spines and scattered dark spots; posterior ridges of femora narrowly edged with dark brown.

Comments. In the most recent revision of the Antillean species of the genus *Colapteroblatta*, there is no mention of Virgin Islands (Gutiérrez 2012a). This only specimen was found in the wet zone of Sage Mountain on Tortola. Our species may be related with *C. portoricense* described from a tropical wet forest on Puerto Rico by Gutiérrez and Roth (1999), but we need adults for confirming the taxonomic status.

Specimen examined. **BDVC**—1 female nymph, BVI, Tortola Is., Sage Mt., 1600–1700 ft., 6.X.2001, B. & B. Valentine.

2. *Hemiblabera brunneri* (Saussure) (Fig. 5)

Blabera brunneri Saussure 1869: 113; Brazil.

Table 1. Species and capture methods as indicator of habitat and behavior of cockroaches recorded from the Virgin Islands and their presence on Guana Island and Puerto Rico, with GD for ground cover such as detritus, rocks, or logs, MT for Malaise trap, PT for pitfall traps, SB for sweeping or beating vegetation, UV for ultraviolet light trap, WL for white lights, - for requiring further study, * and ° for records new to the Virgin Islands and Guana, respectively.

Family		Species	Capture methods	Presence	
				Guana	Puerto Rico
Blaberidae	1*	*Colapteroblatta* sp. 1	SB	no	-
	2	*Hemiblabera brunneri*	GD, MT, PT, SB, WL	yes	yes
	3	*Panchlora nivea*		no	yes
	4	*Panchlora sagax*	MT, SB, UV, WL	yes	yes
	5	*Panchlora viridis*		no	no
	6	*Rhyparobia maderae*		no	yes
	7	*Pycnoscelus surinamensis*	GD, SB, UV, WL	yes	yes
Blattellidae	8	*Blattella germanica*		no	yes
	9	*Cariblatta antiguensis*	MT, SB, UV, WL	yes	-
	10*	*Cariblatta* sp. 2	WL	no	-
	11*	*Cariblatta* sp. 3	SB	no	-
	12	*Euthlastoblatta diaphana*		no	yes
	13	*Euthlastoblatta facies*	MT, SB, UV, termite runway	yes	yes
	14*	*Nyctibora lutzi*	GD, MT, UV, WL	°	yes
	15	*Nyctibora noctivaga*		no	no
	16*	*Plectoptera infulata*	SB, WL	°	yes
	17	*Plectoptera rhabdota*	MT, SB, UV, WL	yes	yes
	18*	*Plectoptera* sp. 3	SB	no	-
	19	*Symploce pararuficollis*	MT, SB, UV, WL	yes	yes
	20	*Symploce ruficollis*	MT, SB, UV, WL	yes	yes
Blattidae	21	*Eurycotis improcera*	MT, PT, SB, UV, WL	yes	no
	22*	*Eurycotis* sp. 2	GD, SB	no	-
	23	*Periplaneta americana*	GD, UV, WL	yes	yes
	24	*Periplaneta australasiae*	GD, UV, WL	°	yes
Polyphagidae	25*	Polyphagid sp. 1 (*Compsodes* sp. 1)	MT, UV, WL	°	-
	26*	Polyphagid sp. 2	termite runway	°	-

Diagnosis. Brachypterous adults 21–37 mm, oval, with quadrate tegmina in both sexes; dorsum shiny, dark brown, with prominent yellowish pronotal margin reaching basal angles; head dark with 2 small, pale spots (ocelli) between antennal insertions and a larger reddish area on frons above clypeus; pronotum broader than long; tegmina unicolor or faintly paler laterally, with small punctures and vague wrinkles, without transverse discal grooves; anteroventral margin of fore femur with a row of stout proximal spines, followed by a row of short uniform spinules, and one larger terminal spine (Type B_1); supra-anal plate rectangular, with rounded angles and slight apical emargination in both sexes; tarsi almost black, variably 4 or 5 hind tarsomeres; abdominal segments dark red anteriorly, dark brown posteriorly; cerci short, flat, and rounded at tip.

Wingless adults and nymphs are very unlike the brachypterous adults; yellow pronotal margin narrow, dull, sometimes extending to meso- and metanotal margins; pronotum dull and rough with many small, flattened tubercles, which are progressively smaller and more acute on the rest of dorsum; head dark but genae and frons sometimes lighter, abdominal tergites transversely banded with light and dark brown, sometimes with a vague yellowish spot on each side. There are 10 instars based on anterior pronotal width corresponding to head width categories of 1.5, 3.0, 3.5, 4.0, 5.5, 6.0, 7.5, 9–10, 11.0–12.0, and 12.5–13.0 mm. We could not sex instars 1–3; the sex ratio of male and female adults and older nymphs is about 1:1. In addition, the posterior lateral margin of tegmina is longer than the sutural margin in females compared to males.

Table 2. Abundance changes across months of five cockroach species frequently captured in a Malaise trap within a forest edge on Guana Island, British Virgin Islands (missing 4 samples of VII/IX.2004, IV.2005, and VII.2007), with N = number of sample years from June 2000 through October 2011.

	Average numbers of cockroach individuals per month					
Month	*Cariblatta antiguensis*	*Euthlastoblatta facies*	*Plectoptera rhabdota*	*Symploce pararuficollis*	*Symploce ruficollis*	N
1	6.0	0.3	0.6	35.2	1.0	11
2	7.3	0.6	0.6	14.5	0.7	11
3	6.1	1.0	0.8	6.6	1.6	11
4	6.4	0.4	0.4	6.5	3.1	10
5	12.9	1.3	1.1	12.1	2.4	11
6	27.9	1.8	1.2	27.8	2.0	12
7	9.1	2.4	0.2	16.7	1.5	10
8	10.0	4.4	1.3	15.6	1.1	12
9	12.1	2.4	0.5	20.5	1.3	11
10	8.2	1.3	0.2	19.1	1.3	12
11	8.6	0.8	0.1	28.1	0.6	11
12	6.7	0.6	0.5	34.5	0.6	11

Comments. *Hemiblabera brunneri* is ovoviparous; a 27 mm female collected on Guana on 22 October 2004 gave live birth to 17 nymphs overnight, each about 7 mm long. It is a dimorphic species with both brachypterous and wingless adults. We found all sizes of individuals except the brachypterous form under rocks on Carval Rock, a very small island between Cooper and Ginger Islands with only herb-stage vegetation except for a few *Coccoloba uvifera* L. (Polygonaceae) shrubs (Lazell 2005), suggesting that it reproduces without winged adults. Furthermore, many wingless individuals are larger than brachypterous males. In early October 2008, nymphs and more than 20 both brachypterous and wingless adults were found coexisting in daytime under a coral rock in a low, sandy, wooded area next to the White Bay beach on Guana Island; that night they all disappeared, but many were found under the same rock the next day. This suggests it may be aggregative socially or nuptially. In daylight when disturbed, most dove into the sand and "swam" away. It is nocturnal and usually stays close to the ground, but was once found on branches >2 m above the ground. It can be found abundantly in suitable habitats on Guana Island (Table 1), from almost sea level to near the highest point.

Shelford (1910) first recorded this species from St. Thomas, Roth (1994) from Virgin Gorda, and Lazell (2005) from Guana Island; it is herein recorded for the first time on Anegada, Carval Rock, Little Thatch, Moskito, Necker, Norman, Prickly Pear, Salt, and Tortola of BVI, in addition to other previous records on St. John and St. Thomas of USVI, Culebra Island, Puerto Rico, and St. Vincent (Rehn and Hebard 1927, Princis 1963, Gutiérrez and Fisk 1998).

Specimens examined. BDVC—1 male, BVI, Anegada Is., airport vicinity, 22.X.2004, Valentines & Sibleys; 2 females/1 male, BVI, Anegada Is., SW coast, 20-21.X.2004, Valentines & Sibleys, at UV; 1 female, BVI, Guana Is., Grand Ghut, 13.X.2006, B. D. Valentine family, sweep; 2 females, BVI, Guana Is., 22-28.X.2001, 23-30.X.2002, B. & B. Valentine, at UV; 1 female/2 males, BVI, Guana Is., White Beach, 15.X.2007, W. Lu; 1 female/17 hatchlings, BVI, Guana Is., 22.X.2004, B. D. Valentine & S. C. Valentine-Cooper; 1 male, BVI, Guana Is., 22.X.2007, B. D. Valentine family; 2 females, BVI, Little Thatch Is., 25.X.2008, Valentine-Cooper & Lu; 3 adults, BVI, Little Thatch Is., 11.X.2010, E. Wright; 1 male, BVI, Moskito Is., 25.X.2007, W. Lu, sweep; 1 male/2 females, BVI, Moskito Is., 23.X.2008, Valentine-Cooper & Lu; 1 male/1 female, BVI, Moskito Is., 26.X.2009, W. Lu & S. Valentine-Cooper; 1 male, BVI, Prickly Pear Is., 23.X.2011, [K. Street, in Agave]; 1 female, BVI, Necker Is., 2-5.VI.2005, W. Lu; 1 female, BVI, Norman Is., 25.X.2002, T. Willard; 1 female/1 male, BVI, Salt Is., 12.X.2007, W. Lu, sweep; 1 female, BVI, Virgin Gorda Is., Oil Nut Bay, 12.X.2008, [B. S. Barker, mango tree litter]. **NMNH**—1 female, BVI, Tortola, Sopers Hole, 31.III.1958, J.F.G. Clarke. Wingless adults and nymphs examined: **BDVC**—3

Table 3. Abundance changes across years of five cockroach frequently captured in a Malaise trap within a forest edge on Guana Island, British Virgin Islands (missing 4 samples of VII/IX.2004, IV.2005, and VII.2007), with N = number of sample months from June 2000 through October 2011.

	Average numbers of cockroach individuals per year					
Year	*Cariblatta antiguensis*	*Euthlastoblatta facies*	*Plectoptera rhabdota*	*Symploce pararuficollis*	*Symploce ruficollis*	N
2000	29.2	1.6	0.9	39.1	3.0	7
2001	2.4	0.1	0.2	1.2	0.3	12
2002	5.6	0.9	0.0	8.2	0.8	12
2003	4.4	0.2	0.0	1.8	0.1	12
2004	11.4	2.2	1.6	29.5	1.1	10
2005	13.3	0.5	0.5	32.4	2.0	11
2006	10.2	1.5	0.6	20.1	1.1	12
2007	7.4	0.6	0.5	35.6	0.8	11
2008	3.8	0.8	0.6	31.2	3.8	12
2009	5.1	0.9	0.2	10.8	1.0	12
2010	18.1	6.5	2.3	14.1	1.0	12
2011	10.5	1.5	0.1	13.2	2.4	10

male/1 female nymphs, BVI, Anegada Is., airport vicinity, 22.X.2004, Valentines & Sibleys; 1 female/9 nymphs, BVI, Carval Rock Is., between Cooper & Ginger Is., 6.X.1999, W. Lu; 1 female nymph, BVI, Guana Is., 8-14.X.2001, B. & B. Valentine; 1 female nymph, BVI, Guana Is., 14.X.2007, W. Lu, sweep; 1 female nymph, BVI, Guana Is., 21.X.2007, B. D. Valentine family; 1 nymph, BVI, Guana Is., 24.IX.2005, B. D. Valentine & S. C. Valentine-Cooper; 3 male nymphs, BVI, Little Thatch Is., 18.X.2004, S. C. Valentine-Cooper, at light; 3 females/2 nymphs, BVI, Little Thatch Is., 25.X.2008, Valentine-Cooper & Lu; 1 male/1 nymph, BVI, Moskito Is., 23.X.2008, Valentine-Cooper & Lu; 2 nymphs, BVI, Moskito Is., 26.X.2009, W. Lu & S. Valentine-Cooper; 1 female, BVI, Virgin Gorda Is., Oil Nut Bay, 12.X.2008, [B. S. Barker, mango tree litter]. **MCZ**—9 nymphs, BVI, Carval Rock Is., between Cooper & Ginger Is., 6.X.1999, W. Lu. **NMNH**—1 male, BVI, Guana Is., 9-30.X.2000, W. Lu, Malaise trap; 1 female, BVI, Guana Is., nr Sugarloaf Mt. top, 806 ft., 7.X.2001, D. Perez. **VIIS**—1 female, USVI, St. John Is., 1970; 1 female, USVI, St. John Is., Lameshur Ranger Station, 23.XI.1958, C. F. Adams.

3. *Panchlora nivea* (Linnaeus)

Blatta nivea Linnaeus 1758: 423; Neotropical.

Comments. Among 49 known species in *Panchlora*, the major speciation occurred in Central and South America, with only two African and three West Indian species (Beccaloni 2007). The West Indian species are all likely adventives from Central and South America because of their establishment near edificarian environments (Gutiérrez 2013, pers. comm.). Shelford (1910) first reported this species from Loango (now Lovango) Island near St. Thomas, USVI; it is listed from Puerto Rico (Wolcott 1948), Antilles, West Indies, Central and South Americas (Princis 1964). It is one of the three green species in the genus recorded from the Virgin Islands; we have not yet found it and are not certain of its identity.

4. *Panchlora sagax* Rehn and Hebard (Fig. 6)

Panchlora sagax Rehn and Hebard 1927: 251; Dominica; Puerto Rico, Culebra Island.

Diagnosis. Adults 14–19 mm, flat, oval, with full tegmina in both sexes; when alive dorsum mostly pale green, with lateral submarginal borders of pronotum and costal cells of tegmina pale yellow; head with a reddish brown interocular band; venter and legs greenish yellow; ventro-posterior of hind femora without a minute spur; cerci tapering.

Table 4. Current (+) and historical (-) records of 26 cockroach names from the Virgin Islands. **1)** *Colapteroblatta* sp. 1. **2)** *Hemiblabera brunneri*. **3)** *Panchlora nivea*. **4)** *P. sagax*, 5: *P. viridis*. **6)** *Pycnoscelus surinamensis*. **7)** *Rhyparobia maderae*. **8)** *Blattella germanica*. **9)** *Cariblatta antiguensis*. **10)** *Cariblatta* sp. 2. **11)** *Cariblatta* sp. 3. **12)** *Euthlastoblatta diaphana*. **13)** *E. facies*. **14)** *Nyctibora lutzi*. **15)** *N. noctivaga*. **16)** *Plectoptera infulata*. **17)** *P. rhabdota*. **18)** *Plectoptera* sp. 3. **19)** *Symploce pararuficollis*. **20)** *S. ruficollis*. **21)** *Eurycotis improcera*. **22)** *Eurycotis* sp. 2. **23)** *Periplaneta americana*. **24)** *P. australasiae*. **25)** Polyphagid sp. 1 (*Compsodes* sp. 1). **26)** Polyphagid sp. 2.

	Cockroach species																									
Island	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26
Anegada		+				+			+										+	+			+	+		
Carval Rock		+																								
Cooper						+																				
Great Camanoe													+						+	+	+					
Guana		+		+		+			+				+	+		+	+		+	+	+		+	+	+	+
Jost van Dyke						+			+				+							+	+			+		
Little Thatch		+		+		+			+				+	+					+	+	+		+			
Moskito		+		+		+			+				+				+		+	+	+			+		
Necker		+		+					+				+				+			+						
Norman		+																								
Prickly Pear		+																								
Salt		+																								
St. Croix					-	+		-	+												+		-			
St. John		+		+	-			-	+				+	+			+		+	+	+		+			
St. Thomas		+	-			+	-	-				-	+		-		+			+			-	+		
Tortola	+	+		+		+		-	+	+	+		+	+		+	+	+	+	+	+	+	-	+		
Virgin Gorda		+		+		+		-	+				+							+	+		-			

Comments. *Panchlora sagax* is delicate, rather flat, and one of the three green species recorded from the Virgin Islands. Many specimens turn pale brown after death, especially if killed with alcohol or ethyl acetate. Males are generally shorter and narrower than females. We have not found the nymphs, which are reported to be brown (Gurney and Fisk 1987). Specimens from St John at VIIS were labeled as *P. nivea* but examination and comparison with Guana Island specimens indicate that they are all *P. sagax*, which differs from *P. nivea* in lacking the minute spur near the middle of the ventro-posterior margin of the hind femur.

This species is ovoviparous; a now faded brown female collected on 23.X.2008 from Moskito Island carries unborn nymphs, two of which are visible at the abdominal apex, and a green female collected on 26-28.X.2000 from Guana Island has an accidentally extruded brown egg mass. Nuptial aggregation may be normal in this species. In October 2001, approximately 30 individuals were attracted to a UV light; they formed a tight group on the trap sheet, all bodies in contact, and in simultaneous action when one moved. This aggregation phenomenon was observed for three consecutive days. Both sexes were present with males outnumbering females.

This is a common species on Guana Island, arboreal, and diurnal; we never found them under rocks or logs or active at night other than perching on vegetation or coming to lights (Table 1). We could only find individuals in the forest edge Malaise trap in July 2000, March 2003, May 2005, and September 2006 during the 12-year period.

Roth (1994) first recorded this species from Guana Island and checked identity for some of our specimens. It is herein recorded for the first time from St. John of USVI, Little Thatch, Moskito, Necker, Tortola, and Virgin Gorda of BVI, in addition to a previous record from Colombia (Princis 1964). It is probably of South American origin despite its Antillean type localities (Rehn and Hebard 1927).

Specimens examined. BDVC—3 females, BVI, Guana Is., Quail Dove Ghut, 9.V.-9.VI.2000, W.-P. Liao, Malaise trap; 6 females, BVI, Guana Is., 26-28/30.X.2000, 1-7/8-14.X.2001, 13.X.2005, B. & B. Valentine, at UV; 2 females, BVI, Guana Is., 23.IX./5.X.2005, B. D. Valentine & S. C. Valentine-Cooper, at UV; 1 female, BVI, Guana Is., 26.IX/1.X.2006, J. Cokendolpher, at UV; 3 males, BVI, Guana Is., 23.X.2004, 22.IX.2005, B. D. Valentine & S. C. Valentine-Cooper, at UV; 1 male, BVI, Guana Is., 9.X.2007, W. Lu; 3 males, BVI, Guana Is., 16.X.2006, 29.X.2007, B. D. Valentine family, at UV; 8 males, BVI, Guana Is., 26-29.X.2000, 1-7.X.2001, B. & B. Valentine, at UV; 1 adult, Jost Van Dyke, 8.X.2010, Lu & Valentine-Cooper; 1 male, Little Thatch Is., 18.X.2004, S. Valentine-Cooper, at light; 2 females [1 with young nymphs], BVI, Moskito Is., 23.X.2008, Valentine-Cooper & Lu; 1 female, BVI, Moskito

Is., 25X.2007, W. Lu, sweep; 1 male, BVI, Necker Is., 2-5.VI.2005, W. Lu; 2 females, BVI, Tortola Is., Paraquita Bay, 28.X.2001, Chalwell, VII-VIII.2003, both C. Petrovic, at light; 2 females, BVI, Virgin Gorda Is., SW coast, 14.X.2004, B. & S. Valentine, at UV. **MCZ**—11 adults, BVI, Guana Is. **UDCC**—1 female/7 males, BVI, Guana Is., 7.X.1994, 11.VIII.1997, 23.X.1997, C. R. Bartlett, beat/sweep/at UV; 1 male, BVI, Guana Is., 16.X.1993, C. Bartlett & J. Cryan; 10 adults, BVI, Guana Is., 21.X.1997, C. R. Bartlett. **VIIS**—1 adult (missing abdomen), USVI, St. John Is., Lameshur Bay, 18-27.VII.1968, A. Gray; 1 female, USVI, St. John Is., Lameshur Bay, 13.VII.1970, J. B. Hanzely; 2 females, USVI, St. John Is., Cruz Bay, A. E. Dammann; 1 male, USVI, St. John Is., VIII.1968, A. E. Dammann; 1 male/1 female, USVI, St. John Is., Chocolate Hole, 25.X.1968, A. E. Dammann.

5. *Panchlora viridis* (Fabricius)

Blatta viridis Fabricius 1775: 272; America.

Comments. This species is recorded from St. John and St. Croix of USVI, and is distributed from Trinidad to Cuba (Princis 1964, Bonfils 1969). It is one of the three green species in the genus recorded from the Virgin Islands; we have not yet found it and are not certain of its identity.

6. *Pycnoscelus surinamensis* (Linnaeus) (Fig. 7)

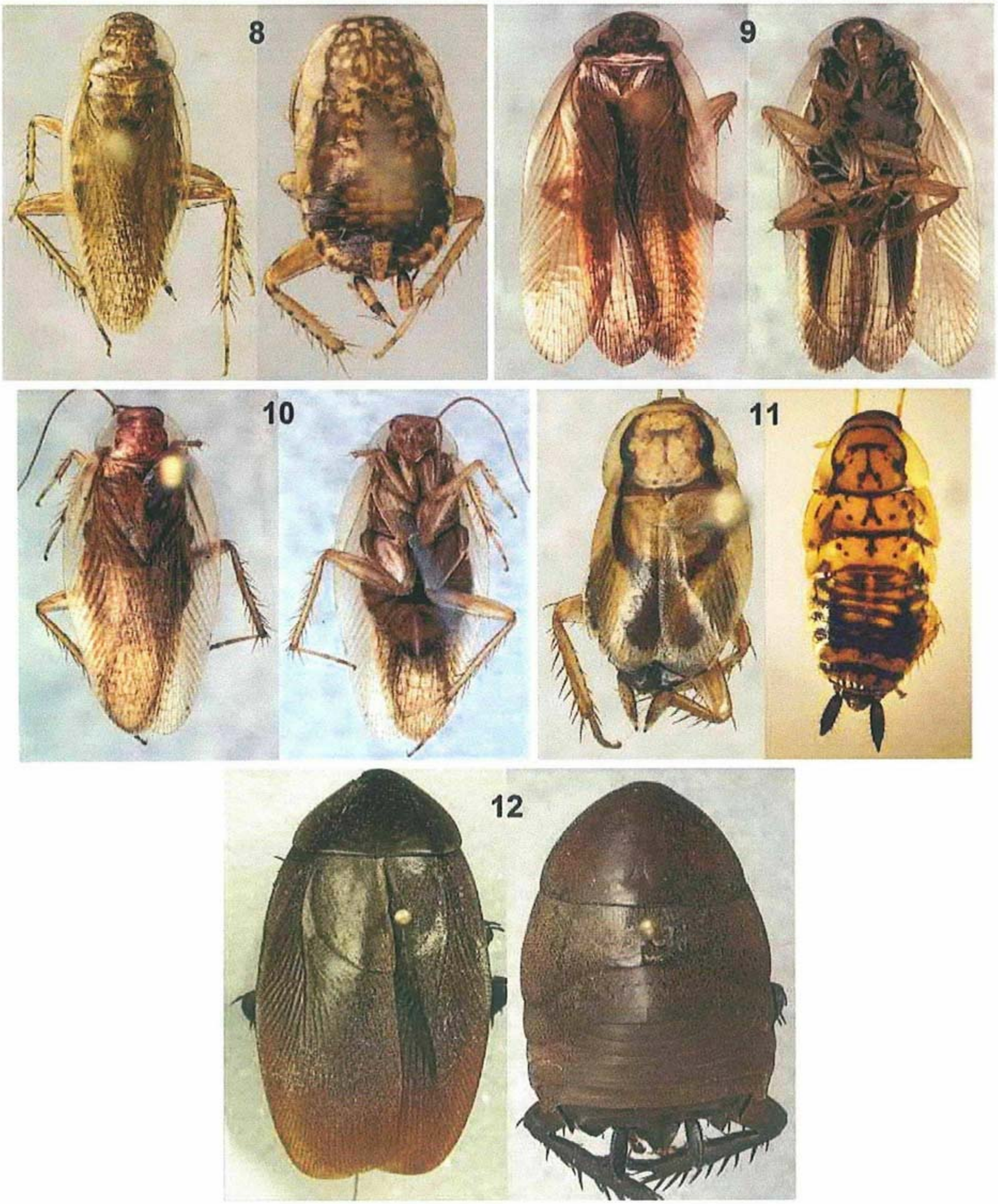
Blatta surinamensis Linnaeus 1758: 424; Surinam; circumtropical, of Asian origin.

Diagnosis. Adults 15–22 mm, oval, with full tegmina in both sexes, bicolored with black and pale brown; head dark brown; pronotum dark brown to almost black, with narrow yellowish (pale brown) anterior and lateral margins that are sometimes interrupted anteriorly; tegmina pale brown, contrasting with pronotum, with many basal punctures usually in double rows; abdominal apex not covered fully by tegmina in some. Nymphs reddish to dark brown to almost black, thorax and first 3 visible abdominal tergites smooth and shining, but segments 4–8 dull and very finely tuberculate, less evident in some very small individuals.

Comments. *Pycnoscelus surinamensis* adults appear to be all female, which is consistent with being parthenogenetic. It is common on Guana under debris, and a nocturnal ground-dweller (Table 1). Individuals are active and abundant at night in the pasture area, perhaps as scavengers on the donkey dung there. It is known throughout the Greater Antilles and tropical America (Princis 1964, 1967). It has more than 10 synonyms probably due to its edificarian circumtropical distribution.

Shelford (1910) first recorded this species from St. Thomas and Trinidad; Miller (1994) reported it in a shipment of plants being unloaded on Guana Island. It is herein recorded for the first time on Anegada, Cooper, Jost Van Dyke, Little Thatch, Moskito, Tortola, and Virgin Gorda of BVI, in addition to other previous records on St. Croix of USVI (Rehn and Hebard 1927), Puerto Rico (Gutiérrez and Fisk 1998), and Hispaniola (Gutiérrez and Perez-Gelabert 2000).

Specimens examined. BDVC—1 nymph, BVI, Anegada Is., airport vicinity, 22.X.2004, Valentines & Sibleys; 4 nymphs, BVI, Cooper Is., 12.X.2007, W. Lu; 2 females, BVI, Guana Is., 22.IX/10.X.2005, B. D. Valentine & S. C. Valentine-Cooper, at UV; 5 females, BVI, Guana Is., 19/21.X.2006, 9/20.X.2007, B. D. Valentine family, at UV; 2 females, BVI, Guana Is., 15.X.2007, W. Lu; 1 female, BVI, Guana Is., 5-19.X.2005, B. D. & B. S. Valentine; 2 nymphs, BVI, Guana Is., 8/14.X.2001, B. D. Valentine family, at UV; 8 nymphs, BVI, Guana Is., 4/10-11.X.2005, B. D. Valentine & S. C. Valentine-Cooper; 1 nymph, BVI, Guana Is., 20.X.2007, B. D. Valentine family, at UV; 1 nymph, BVI, Guana Is., White Beach, 15.X.2007, W. Lu; 1 adult, Jost Van Dyke, 18-19.X.2010, W. Lu & S. C. Valentine-Cooper; 1 female, BVI, Little Thatch Is., 23.X.2005, W. Lu, sweep; 2 females, BVI, Moskito Is., 23.X.2012, E. Hill; 1 female, BVI, Tortola Is., Chalwell, II.2003, C. Petrovic, at light; 2 females, BVI, Virgin Gorda Is., The Valley, 27.X.2003, J. Egelhoff; 1 female, BVI, Virgin Gorda Is., Oil Nut Bay, 12.X.2008, S. C. Valentine-Cooper [mango tree litter]. **NMNH**—1 female, BVI, Virgin Gorda Is., The Valley, 27.X.2003, J. Egelhoff.



Figures 8–12. Blattellidae. **8)** *Cariblatta antiguensis* female adult from Tortola Island and nymph from Guana Island. **9)** *Cariblatta* sp. 2 from Tortola Island. **10)** *Cariblatta* sp. 3 from Tortola Island. **11)** *Euthlastoblatta facies* adult and nymph from Guana Island. **12)** *Nyctibora lutzi* adult and nymph from Guana Island (all specimens in BDVC).

7. *Rhyparobia maderae* (Fabricius)

Blatta maderae Fabricius 1781: 341–342; circumtropical, probably of African origin.

Comments. This species is reported from Loango (now Lovango) Island near St. Thomas of USVI (Shelford 1910), Puerto Rico (Wolcott 1948), West Indies, Central and South Americas (Princis 1964). It is large and usually associated with animal husbandry. We have not yet found it in the Virgin Islands.

Family Blattellidae

8. *Blattella germanica* (Linnaeus)

Blatta germanica Linnaeus 1767: 688; cosmopolitan.

Comments. Princis (1969) believes this species is probably of East Asian origin, and Roth (1985) agrees. Although no specimens collected, it is most likely a result of our target bias for natural habitats. In addition to these previous records on St. Croix, St. John, and St. Thomas, a local BVI pest control agent has also confirmed its presence in major edificarian habitats on Virgin Gorda and Tortola (J. Egelhoff 24.X.2011, pers. comm.).

9. *Cariblatta antiguensis* (Saussure and Zehntner) (Fig. 8)

Theganopteryx antiguensis Saussure and Zehntner 1893: 17; Antigua Island.

Diagnosis. Adults 9–11 mm, elongate and narrow, with full tegmina in both sexes; pale brown with light antennae; vertex with interocular pairs of brown spots, frons with an irregular brown area below these dark spots; pronotal disc with complex, symmetrical, dark markings plus a cluster of 5 small dark spots at base; legs pale, tibiae with a small black spot at base of each spine; costal cell of tegmina without a creamy-white stripe; 7–8 costal veins thickened, clubbed radiate dark gray; underside light with lateral black markings on each segment; basal and apical articles of cerci darker than intermediate; legs, especially tibiae, with a black spot at base of each spine.

Nymphs complexly mottled; tarsi yellow with tarsomeres 2–3 usually darker, cerci darker at base and apex. Oothecae dark brown, 3–3.5 mm long, kidney-shaped, with crowded, fine, longitudinal ridges that curve towards the hinge at both ends; egg chambers not visible externally; surface with sparse, short, truncate projections that become less numerous near the hinge; open edge with about 18–20 larger marginal tubercles. Older nymphs can be sorted according to head width categories of 0.5–0.6, 0.7–0.8, 0.9–1.0, 1.2–1.3, and 1.4–1.5 mm, suggesting more than five instars (adult 1.5–1.6 mm). The sex ratio is about 2 females to 1 male.

Comments. *Cariblatta antiguensis* is probably arboreal and nocturnal; individuals were active at night or perching on vegetation but never under ground cover such as detritus, rocks, or logs (Table 1). Oothecae were found in October with four adults from Guana Island and one adult from Moskito Island. Nymphs were found in the forest edge Malaise trap in all months, suggesting multiple generations per year. The abundance pattern showed two highs; the fall increase was low in number as compared with the spring increase (Table 2). Abundance was particularly high in 2000 (237 individuals in June) (Fig. 3, Table 3), when annual rainfall of prior three years averaged above 3.1 mm. A spike of 15.8 mm heavy rainfall in November 2003 did not induce a striking abundance increase like that in 2000 (Fig. 3).

Roth (1994) first recorded this species from Guana Island where it is abundant. It is herein recorded for the first time on St. John of USVI, Anegada, Jost Van Dyke, Little Thatch, Moskito, Necker, Tortola, and Virgin Gorda of BVI, in addition to other previous records on St. Croix of USVI, St. Barts, Antigua, and Trinidad (Rehn and Hebard 1927, Princis 1969), Dominica and St. Martin (Bonfils 1969), and Cuba (Gutiérrez 1995). It is not yet recorded from Hispaniola, but ranges from east and south of Puerto Rico, all the way to Trinidad; Puerto Rico should also have this species.

Specimens examined. BDVC—2 males, BVI, Anegada Is., 26-27.X.2009, W. Lu & S. Valentine-Cooper; 47 females/25 males/12 nymphs, BVI, Guana Is.; 5 adults/1 nymph, Jost Van Dyke, 18-19.X.2010, W. Lu & S. C. Valentine-Cooper; 1 nymph, BVI, Little Thatch Is., 13.X.2007, W. Lu, sweep; 1 adult, BVI, Little Thatch Is., 25.X.2008, Valentine-Cooper & Lu; 1 adult, BVI, Little Thatch Is., 11.X.2010, E. Wright; 2 females, BVI, Moskito Is., 25.X.2007, S. C. Valentine-Cooper, sweep; 1 male, BVI, Necker Is., 2-5.VI.2005, W. Lu; 3 adults/1 nymph (1st instar), BVI, Necker Is., 16.X.2010, W. Lu; 2 females, BVI, Tortola Is., Sage Mt., 11.X.2007, W. Lu; 1 female, BVI, Tortola Is., Sage Mt., 1600-1700 ft., 6.X.2001, B. & B. Valentine; 2 males, BVI, Tortola Is., Chalwell, 1500 ft., 25-27.X.2001, C. Petrovic, at light; 1 male, BVI, Tortola Is., Sage Mt., 1600-1700 ft., 6.X.2001, B. & B. Valentine; 2 nymphs, BVI, Virgin Gorda, 23.X.2011, S. C. Valentine-Cooper. **MAIC**—5 adults, USVI, St. John Is., Great Cruz Bay, 15-23.VI.1996, B. & B. Valentine. **MCZ**—24 adults, BVI, Guana Is., B. & B. Valentine; 5 adults, USVI, St. John, Great Cruz Bay, 15-23.VI.1996, B. & B. Valentine. **UDCC**—6 females/2 males, BVI, Guana Is., 11.VIII.1997, 9.V-4.VI.2000, 27.X.1997, C. R. Bartlett, sweep/Malaise trap; 1 male, BVI, Little Thatch Is., 9.X.1994, C. R. Bartlett, sweep. **VIIS**—1 female, USVI, St. John Is., nr Lameshur Bay, 30.III.1970, L. Curry.

10. *Cariblatta* sp. 2, NEW RECORD (Fig. 9)

Diagnosis. Female adult 11 mm, elongate and narrow, with full tegmina; pale brown with dark antennae (in contrast to Species 9, *C. antiguensis*); frons and vertex ferruginous, without prominent spots; pronotal central area variegate, brown, lacking dark spots as in *C. antiguensis*, but with a short, subbasal, curved, dark, transverse bar; legs all pale, tibiae without black spots at base of spines; costal cell of tegmina with a strongly contrasting creamy-white stripe along its inner margin; 7–8 costal veins thickened, clubbed radiate white; underside mostly black, but lateral and posterior margins of each segment creamy white; cerci with base dark, tip pale, and a black, tapering, dorsal stripe on intervening articles; venter and legs without black spots.

Comments. This species is less spotted than *C. antiguensis*. It may be one of the six species known from Puerto Rico (Gutiérrez and Fisk 1998). A single female is known; new collecting efforts, especially for males, will better define its taxonomic status.

Specimen examined. BDVC—1 female, BVI, Tortola Is., Chalwell, X.2007, C. Petrovic, at light.

11. *Cariblatta* sp. 3, NEW RECORD (Fig. 10)

Diagnosis. Female adult 12 mm, elongate and narrow, with full tegmina; uniformly pale reddish-orange, with antennae of similar color; pronotum without spots or bars; costal cell of tegmina with inner margin pale like legs, but not white and therefore not as contrasting as in *Cariblatta* sp. 2 (Species 10); 7–8 costal veins thickened, clubbed radiate reddish; cerci entirely pale brown with each article weakly darker at base; underside mostly reddish brown, with lateral and posterior margins of each segment narrowly paler; venter and legs without black spots.

Comments. This species is slightly redder than its two congeners and superficially resembles *Symploce ruficollis* (Species 20) in color and size. It is known from one apparently gravid female collected by sweeping roadside vegetation (C. Bartlett, pers. comm. 2009); new collecting efforts, especially for males, will better define its taxonomic status.

Specimen examined. BDVC—1 female, BVI, Tortola Is., 28.X.1997, C. R. Bartlett.

12. *Euthlastoblatta diaphana* (Fabricius) (Table 1)

Blatta diaphana Fabricius 1793: 11; West Indies.

Comments. Shelford (1910) first reported this species from St. Thomas, USVI, and Cuba; it is also recorded from Puerto Rico (Wolcott 1948), Lesser Antilles, Jamaica, Hispaniola, and Bermuda (Princis 1969). We have not yet found it and are not certain of its identity.

13. *Euthlastoblatta facies* (Walker) (Fig. 11)

Blatta facies Walker 1868: 102; locality not recorded.

Diagnosis. Adults 9–11 mm, oval, with full tegmina in both sexes; yellowish brown; head pale brown with a narrow dark band between eyes; pronotum pale brown with a dark brown central 'T' that is reduced to a transverse band or even absent in a few individuals, and a dark brown medial posterior margin connecting 2 sinuate stripes that are often weakly in touch anteriorly; tegmina almost or completely covering abdomen, pale brown, each with a prominent dark-brown 'S' marking that connects anteriorly with the dark sinuate stripe on pronotum; legs all pale; abdomen dark brown with pale lateral margins; cerci flattened, widest in middle, with lateral and ventral but not dorsal setae.

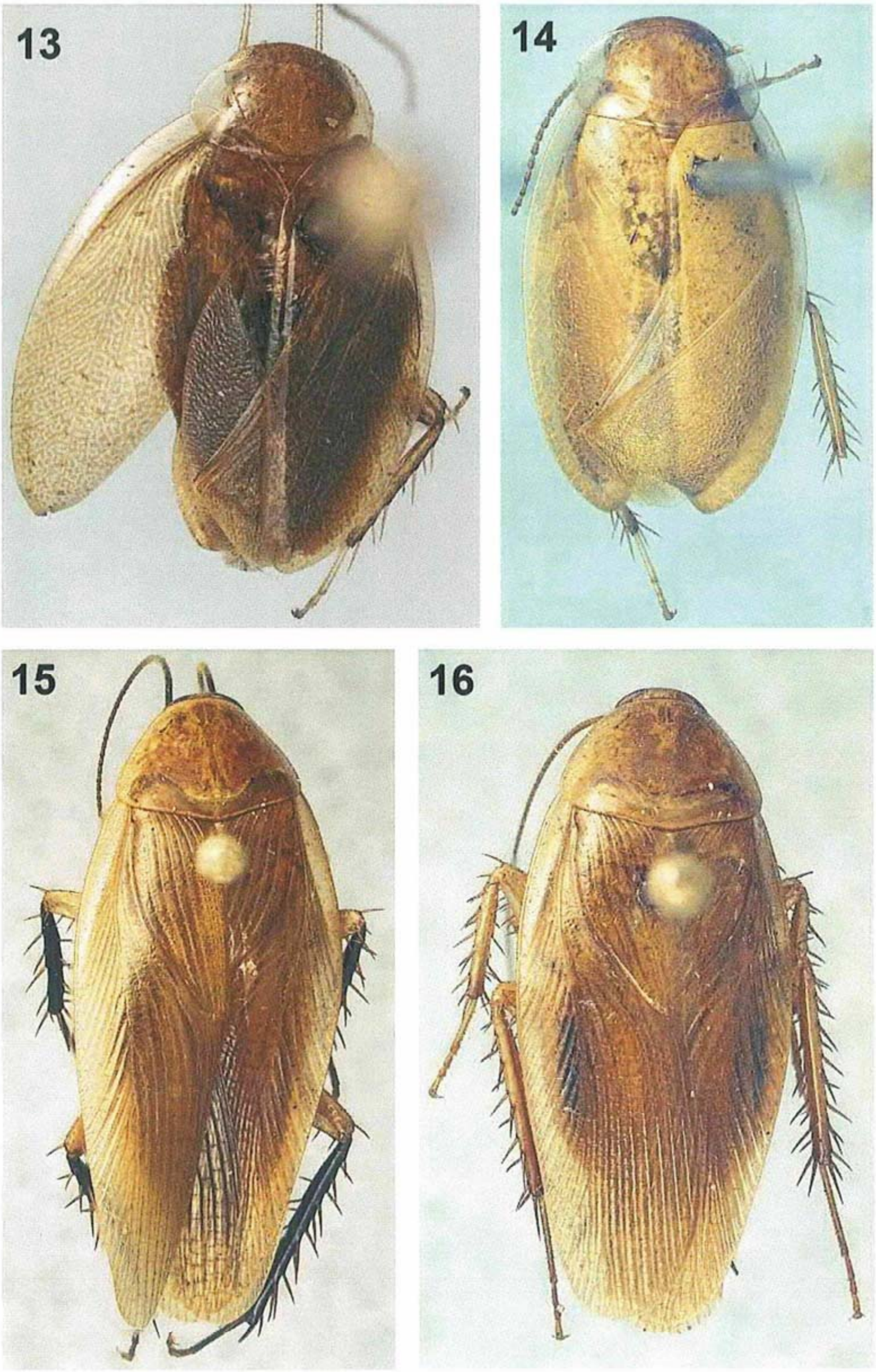
Nymphs similar to adults in having a central but much more distinct dark brown 'T' on pronotum; additionally, an inverted 'Y' on mesonotum and (less distinct) on metanotum; each notum with a dark brown posterior margin that connects two sinuate, lateral, dark brown stripes, more so on pronotum; like adults, head, thorax, and legs all pale, abdomen dark brown. The dark markings in first instars are grayish, vague, and suggestive. Nymphs can be sorted according to head width categories of 0.5–0.6, 0.7–0.8, 0.9–1.0, 1.1–1.3, 1.5–1.8, and 2.0–2.3 mm, suggesting six instars (adult 2.3–2.6 mm). A female caught in a Malaise trap during July 2011 carried an oothecum that had tufts of long hairs greater than the length of the abdomen. The sex ratio is about 1:1.

Comments. *Euthlastoblatta facies* is arboreal and nocturnal; individuals were very active at night on tree trunks and branches but never under ground cover (Table 1). At least some nymphs of this species are termite runway dwellers; in October 2008 Dr. Barbara Thorne discovered seven nymphs 3–7 mm long in arboreal tunnels of the termite *Nasutitermes acajutlae* (Holmgren).

The abundance pattern showed only one high in summer (Table 2), contrary to other species frequently captured in the forest edge Malaise trap. Abundance was particularly high in 2010 (40 individuals in August, all nymphs) (Fig. 3, Table 3), when annual rainfall of prior three years was below 2.0 mm (Fig. 2). Prolonged drought may have induced abundance increase, which was concurrent with the pattern of only one abundance peak each year (Table 2). However, a spike of 15.8 mm heavy rainfall in November 2003 was followed by a sizable abundance increase in November 2004 (Fig. 3).

A subsequent species, *E. absimilis* (Gurney 1937), was also described from Puerto Rico. According to Princis (1969), both *E. absimilis* and *E. diaphana* (Species 12) are distinct from, closely related to, and sympatric with *E. facies*, suggesting a possible Puerto Rican origin. Roth (1994) first recorded this species from Guana Island, where it is fairly common. It is herein recorded for the first time on St. John of USVI, Great Camanoe, Jost Van Dyke, Little Thatch, Moskito, Necker, Tortola, and Virgin Gorda of BVI, in addition to other previous records on St. Thomas of USVI, Mona Island, Culebra Island, Puerto Rico, Dominica, and Barbados (Rehn 1932, Princis 1969).

Specimens examined. BDVC—1 nymph, BVI, Great Camanoe Is., 20.X.2008, S. C. Valentine-Cooper, at night; 2 males, BVI, Guana Is., 17-19.X.2000, 1-7.X.2001, B. & B. Valentine; 2 males, BVI, Guana Is., 25.X.2003, 30.IX.2005, B. D. Valentine & S. Valentine-Cooper, Malaise trap; 1 male, BVI, Guana Is., 14.X.2007, W. Lu, sweep; 1 male, BVI, Guana Is., 26.IX.2006, J. Cokendolpher, at UV; 2 females, BVI, Guana Is., Quail Dove Ghut, 17-23.X.2000, 22-28.X.2001, B. & B. Valentine, Malaise trap; 2 females, BVI, Guana Is., 26.IX/12.X.2006, B. D. Valentine family; 11 males, BVI, Guana Is., Quail Dove Ghut, X/XI.2001, XII.2002, VII/VIII/IX.2004, VII.2005, XI.2005, II/V/VI/VII/XI.2006, W.-P. Liao, Malaise trap; 1 female, BVI, Guana Is., 17.IX.2006, J. Cokendolpher, at UV; 9 nymphs, BVI, Guana Is., I-II, V, VII, IX, and X; 1 nymph, BVI, Guana Is., 26.X.2008, [B. Thorne, in runways of *Nasutitermes acajutlae* (Holmgren)]; 2 adults/1 nymph, Jost Van Dyke, 18-19.X.2010, W. Lu & S. C. Valentine-Cooper; 1 adult, BVI, Little Thatch Is., 11.X.2010, E. Wright; 2 nymphs, BVI, Moskito Is., 25.X.2007, S. C. Valentine-Cooper & W. Lu; 1 adult/1 nymph, BVI, Moskito Is., 23.X.2012, E. Hill; 1 nymph, BVI, Necker Is., 16.X.2006,



Figures 13–16. Blattellidae. **13)** *Plectoptera infulata* adult from Tortola Island. **14)** *Plectoptera rhabdota* adult from Guana Island. **15)** *Symploce pararuficollis* adult from Guana Island. **16)** *Symploce ruficollis* adult from Guana Island (all specimens in BDVC).

S. C. Valentine-Cooper; 1 nymph, BVI, Necker Is., 2-5.VI.2005, W. Lu; 2 adults/3 nymphs, BVI, Necker Is., 16.X.2010, W. Lu; 1 male, BVI, Tortola Is., Sage Mt., 1600-1700 ft., 6.X.2001, B. & B. Valentine. **MCZ**—5 adults, BVI, Guana Is., B. & B. Valentine. **NMNH**—2 specimens, BVI, Guana Is., 1-6.X.1999, 8.IX-8.X.2000, W. Lu, Malaise trap; 6 specimens, BVI, Guana Is., 9.V-9.VI.2000, 9.VIII-8.IX.2000, 8.IX-9.X.2000, II.2003, W. P. Liao, Malaise trap; 1 specimen, BVI, Guana Is., hotel area, 6-13.X.2001, D. E. Perez-Gelabert; 4 specimens, BVI, Necker Is., 25.X.2000, W. Lu. **UDCC**—1 nymph, BVI, Guana Is., 29.X.1997, C. R. Bartlett, beat/sweep; 1 male, BVI, Virgin Gorda Is., 11.X.1994, C. R. Bartlett. **VIIS**—1 adult, USVI, St. John Is., Lameshur Bay, 18-27.VII.1972, A. Gray.

14. *Nyctibora lutzi* Rehn and Hebard (Fig. 12), NEW RECORD

Nyctibora lutzi Rehn and Hebard 1927: 193; Puerto Rico.

Diagnosis. Adults 31–36 mm, with full tegmina in both sexes; broadly oval, dorsum entirely dark brown and densely covered with very short, fine, cinereous setae. Nymphs very dark reddish-brown to almost black, densely covered with similar setae which can be partially absent (especially on pronotum) due to abrasion. Adults and larger nymphs with one or more pairs of faint, glabrous, pronotal grooves, each pair convergent anteriorly; last tergite narrow and triangular with weak apical emargination; male supra-anal plate trilobate apically.

Comments. Among the cockroach species in the Virgin Islands, *Nyctibora lutzi* is readily recognized by its large size (>30 mm), densely and finely tomentose dorsum, full tegmina, and uniform dark brown color in both sexes. The pronotal widths of 11 nymphs suggest six instars. It is a nocturnal ground dweller (Table 1). On Guana Island in October 2008 adults were observed at night actively foraging and courting on the orchard flat. Nymphs were often found in rotten *Agave*; this habitat is similar to that in epiphytic bromeliads for the Dominican Republic species (Gutiérrez and Perez-Gelabert 2000). A female specimen collected in June 1996 from St. John carried an oothecum. Originally described from Puerto Rico, this is not a common species on Guana and is recorded for the first time on St. John of USVI, Guana, Little Thatch, and Tortola of BVI, in addition to a previous record on Puerto Rico (Gutiérrez and Fisk 1998).

Specimens examined. BDVC—1 male, BVI, Guana Is., 26.X.2004, B. D. Valentine & S. C. Valentine-Cooper; 7 nymphs, BVI, Guana Is., 10.X.2003, B. & B. Valentine; 2 nymphs, BVI, Guana Is., 11/13.X.2004, B. D. Valentine & S. C. Valentine-Cooper, at UV; 1 nymph, BVI, no other data; 1 female, BVI, Little Thatch Is., 19.X.2012, W. Lu; 2 males/1 female/1 nymph, BVI, Tortola Is., Lock Hill, 15.VI.2002, C. Petrovic, at light. **MCZ**—1 female [with oothecum], USVI, St. John, Great Cruz Bay, 15-23.VI.1996, B. & B. Valentine. **NMNH**—1 male, BVI, Guana Is., 27.IX.2003, W. Lu & S. Lazell; 1 female, BVI, Guana Is., 8.X.2003, W. Lu.

15. *Nyctibora noctivaga* Rehn

Nyctibora noctivaga Rehn 1902: 3; Nicaragua.

Comments. This species differs from *N. lutzi* (Species 14) mainly in the male supra-anal plate. Shelford (1910) first recorded it from "Loango Island" (Lovango Cay) near St. Thomas, USVI; Rehn and Hebard (1927) state that "the latter record, however, was based on an immature male individual, and in consequence the specific determination may be open to question." We have not recognized any specimen of this taxon and question the record from the Virgin Islands until Lovango is revisited. It was recorded from Nicaragua; Panama; Jamaica; and Colombia, and considered adventive in Canada, USA, and Europe (Princis 1967).

16. *Plectoptera infulata* Rehn and Hebard (Fig. 13), NEW RECORD

Plectoptera infulata Rehn and Hebard 1927: 314; Puerto Rico, Vieques Island.

Diagnosis. Adults 6.5–7 mm, oval, with full tegmina in both sexes; pale yellowish brown; pronotum in 6 of 12 specimens with dull white, opaque, lateral margins (transparent in 6 others); tegmina with major veins opaque but not white, cells lacking any complex reticulum as in *P. rhabdota* (Species 17); interocular space with a dark band above a pale field (in one specimen this entire area is brown); abdomen and cerci paler than those of congeners.

Comments. A unique feature of this genus is the hindwing, which, at rest, is folded forward so that the wing apex rests above and near the wing base, thus explaining the generic name where *'plectos'* means folded in Latin and *'ptera'* wings. Another unique feature is that the tegmina meet in a straight line down the back, overlap less than other cockroaches. *Plectoptera infulata* is a new record and second species in the genus from the Virgin Islands. It is arboreal and probably diurnal (Table 1), not as common as *P. rhabdota* on Guana Island, suggesting a preference for wetter habitats. A female carried a partly visible oothecum in November 2001. It is herein recorded for the first time on Guana and Tortola of BVI in addition to a previous record from Puerto Rico (Princis 1965).

Specimens examined. BDVC—1 male, BVI, Tortola Is., Chalwell, 470 m, VI-VII.2001, C. Petrovic, at light; male/1 female [with oothecum], BVI, Tortola Is., Chalwell, 470 m, XI.2001, C. Petrovic; 2 males, BVI, Tortola Is., Chalwell, 16-24.X.2003, 470 m, C. Petrovic, at light. **NMNH**—1 specimen, BVI, Tortola Is., Chalwell, 16/24.X.2003, C. Petrovic, at light. **UDCC**—1 female [with oothecum], BVI, Guana Is., 26.X.1997, C. R. Bartlett; 2 males, BVI, Tortola Is., Sage Mt., 14.X.1993, C. Bartlett & J. Cryan; 1 adult, BVI, Tortola Is., 28.X.1997, C. Bartlett.

17. *Plectoptera rhabdota* Rehn and Hebard (Fig. 14)

Plectoptera rhabdota Rehn and Hebard 1927: 305; Puerto Rico.

Diagnosis. Adults 5–6 mm, with full tegmina in both sexes; oval, smooth, pale brown; pronotum with transparent lateral margins (in some specimens cloudy); tegmina with major veins white to pale (transparent in some specimens), enclosing cells each with a darker, irregular area, forming a complex reticulum; interocular space with a dark band above a paler one; abdomen and cerci darker than those of congeners.

Nymphs can be sorted based on head width to at least five instars. Oothecum is approximately 2 mm long, roughly triangular in cross-section, with hinge side weakly convex, without external indications of egg chambers, bluntly rounded at one end, broadly and triangularly produced at the other; the open edge has 10 very short, acute, evenly-spaced marginal teeth, with the three central teeth smallest.

Comments. *Plectoptera rhabdota* is one of the smallest cockroaches in the Virgin Islands; the network of white veins and the intracellular pattern of the tegmina distinguish this from *P. infulata* (Species 16). It is arboreal and probably diurnal (Table 1). Five females collected in May 2006 and Octobers of 1997 and 2001 carried oothecae.

Like *Euthlastoblatta facies* (Species 13), the abundance pattern showed only one high from late spring to early summer. Abundance was particularly high in 2010 (Table 3) (10 individuals in August, 50% nymphs) when annual rainfall of prior three years was below 2.0 mm (Fig. 3, Table 3), also similar to that of *E. facies*. Prolonged drought may have induced abundance, which was concurrent with the pattern of only one abundance peak each year (Table 2). However, a spike of 15.8 mm heavy rainfall in November 2003 was followed by a sizable abundance increase in June 2004 (Fig. 3).

Originally described from Puerto Rico, this species was first recorded on Guana (Roth 1994). It is herein recorded for the first time on St. John of USVI, Moskito, Necker, and Tortola of BVI, in addition to other previous records on St. Thomas of USVI (Princis 1965), Vieques Island, Puerto Rico, Dominica, Guadeloupe, and Marie Galante (Bonfils 1969).

Specimens examined. BDVC—1 nymph, BVI, Guana Is., 23.X.2007, B. D. Valentine family, sweep; 40 females, BVI, Guana Is., II-X, XII, at UV, at light, Malaise trap; 43 males, BVI, Guana Is., I-II, IV, VII-X, at UV, Malaise trap, sweep; 1 female, BVI, Moskito Is., 23.X.2008, Valentine-Cooper & Lu;

1male/1 female, BVI, Necker Is., 16.X.2010, W. Lu; 2 females, BVI, Tortola Is., Sage Mt., 1600-1700 ft., 22.X.2000, 6.X.2001, B. & B. Valentine; 1 female, BVI, Tortola Is., Chalwell, IV.2006, C. Petrovic, at light; 1 female/1 nymph, BVI, Tortola Is., Sage Mt., 11.X.2007, W. Lu; 3 males, BVI, Tortola Is., Sage Mt., 11.X.2007, W. Lu; 2 males/1 gravid female, BVI, Tortola Is., Sage Mt., 1600-1700 ft., 6.X.2001, B. & B. Valentine. **NMNH**—3 specimens, BVI, Guana Is., 9.V-9.VI.2000, 9.VII-9.VIII.2000, V.2004, W. P. Liao, Malaise trap; 2 females, BVI, Guana Is., 9.VII-9.VIII.2000/VIII.2005, W. P. Liao, Malaise trap. **UDCC**—10 adults, BVI, Tortola Is., 28.X.1997, C. R. Bartlett. **VIIS**—2 adults, USVI, St. John Is., Lameshur Bay, 18-27.VII.1972, A. Gray.

18. *Plectoptera* sp. 3, NEW RECORD

Diagnosis. Female adult 4 mm, very small, pale brown, delicate, abnormally shriveled, not completely sclerotized, with full tegmina; pronotum transparent, minutely aspirate with scattered long setae; tegmina transparent, venation obsolete, cells lacking any complex reticulum as in *Plectoptera rhabdota* (Species 17), with widely scattered long setae; abdomen and cerci more uniformly brown than those of congeners.

Comments. This unique specimen is a newly emerged adult that has shrunk; it was found by sweeping and beating bushes along the roadside to Sage Mountain, Tortola (Table 1). It is different from but closely related to *Plectoptera dorsalis* (Burmeister 1838) described from Puerto Rico. This is the first record of a third *Plectoptera* species for the Virgin Islands; Roth (1994) reported but did not differentiate two undetermined species from Tortola. We also found other specimens different from this *Plectoptera* sp. 3, *P. infulata* (Species 16), and *P. rhabdota* (Species 17). The generic placement of this taxon is tentative; further study is required.

Specimen examined. BDVC—1 female, BVI, Tortola Is., Sage Mt. 14.X.1993, C. R. Bartlett & J. R. Cryan.

19. *Symploce pararuficollis* Roth (Fig. 15)

Symploce pararuficollis Roth 1994: 45; BVI: Guana Island.

Diagnosis. Adults 15–19 mm, elongate oval, with full tegmina in both sexes; reddish brown with tibiae dark brown to black in contrast to pale reddish femora; underside lighter, with 1 (rarely 2) lateral pair of black spots on each sternite, plus 1 ventral and 2–3 dorsal black spots on each coxa.

Comments. *Symploce pararuficollis* is the second species originally described from the Virgin Islands on the Greater Puerto Rico Bank. The black tibia distinguishes it from the following congener. It is probably arboreal and nocturnal; individuals were active on vegetation and never under ground cover at night (Table 1). The sex ratio is about 1:1. This is the most commonly seen and most numerous species on Guana Island. However, we collected few nymphs to distinguish *S. pararuficollis* from the congener (Species 20) other than the black tibiae. The nymphs are ground dwellers of leaf litter and probably diurnal because they were actively escaping from us when disturbed during the day. Surprisingly, the nymphs have not been found in the forest edge Malaise trap, suggesting that they are very much terrestrial and do not behaviorally climb, unlike their arboreal adults.

The abundance pattern showed two highs; the fall increase topped the spring increase, unlike other species frequently captured in the forest edge Malaise trap (Table 2). Abundance was particularly high in June 2000 (209 individuals), followed by November 2004 and December 2007 (Fig. 3, Table 3). In these three cases, annual rainfall was 1.7, 2.8, and 1.6 mm with that of prior three years averaging above 3.1, 2.6, and 2.6 mm, respectively. The annual rainfall was 3.5 mm with a spike of 15.8 mm in November 2003; it did not induce a striking abundance increase like that in 2000, but may have contributed to a delayed and sharp abundance increase in 2004.

Roth (1994) first described this species from Guana Island; it is herein recorded for the first time on St. John of USVI, Anegada, Great Camanoe, Little Thatch, Moskito, and Tortola of BVI, in addition to a previous record on Puerto Rico (Gutiérrez and Fisk 1998, Gutiérrez 1999a). We have not found it on Necker, even though it occurs on Anegada, the easternmost island on the Puerto Rico Bank.

Specimens examined. BDVC—1 male, BVI, Anegada Is., 26/27.X.2009, W. Lu & S. Valentine-Cooper; 1 male/1female, BVI, Great Camanoe Is., 20.X.2008, Lu & S. C. Valentine-Cooper, at night; 20 females, BVI, Guana Is., I, III, IX-X, at UV, Malaise trap; 17 males, BVI, Guana Is., I, II, VIII-IX, Malaise trap; 1 adult, BVI, Little Thatch Is., 11.X.2010, E. Wright; 1 adult, BVI, Little Thatch Is., 11-12.X.2010, S. C. Valentine-Cooper; 1 nymph, BVI, Moskito Is., 23.X.2012, E. Hill; 1 female, BVI, Tortola Is., Chalwell, XI.2002, C. Petrovic, at light; 2 females, BVI, Tortola Is., Chalwell, XII.2009, C. Petrovic, Malaise trap. **MCZ**—6 adults, BVI, Guana Is., B. & B. Valentine; 5 adults, USVI, St. John, Great Cruz Bay, 15-23. VI.1996, B. & B. Valentine. **UDCC**—4 adults, BVI, Guana Is., 10.X.1994, 23/26.X.1997, C. R. Bartlett. **VIIS**—2 adults, USVI, St. John Is., Lameshur Bay, 18-27.VII.1972, A. Gray; 1 female, USVI, St. John Is., Trunk Bay, BS; 1 male, USVI, St. John Is., 26.I.1970.

20. *Symploce ruficollis* (Fabricius) (Fig. 16)

Blatta ruficollis Fabricius 1787: 226; "India." USVI: St. Thomas Island (lectotype by Princis 1949: 362).

Diagnosis. Adults 12–14 mm, with full tegmina in both sexes; elongate oval, reddish brown with legs and venter lighter; venter with 1 lateral pair of black spots on each sternite, plus 1 and 3–4 dorsal black spots on each forecoxa, mesocoxa, and metacoxa, respectively.

Comments. *Symploce ruficollis* has the entire leg reddish in contrast to its congener *S. pararuficollis* (Species 19) who has contrasting black tibiae. It is probably arboreal and nocturnal; adult individuals were active on vegetation at night and never under ground cover (Table 1). The sex ratio is about 1:1. It is not as frequently seen or numerous as *S. pararuficollis* (Tables 2–3). Though a relatively common species on Guana Island, we collected few nymphs to distinguish *S. ruficollis* from the congener other than the tibia color.

The abundance pattern showed a spring high. This is the only species caught frequently in the Malaise trap, whose monthly abundance synchronized closely with the spring rainfall peak (Table 2); notably the abundance increase did not lag behind the spring rainfall peak. Abundance was particularly high in June 2000 (20 individuals), followed by May 2005, April and October 2008, and March-April 2011 (Fig. 3, Table 3). A spike of 15.8 mm heavy rainfall in November 2003 did not seem to impact abundance (Fig. 3).

Roth (1994) first recorded this species from Guana Island; it is herein recorded for the first time on Anegada, Great Camanoe, Jost Van Dyke, Little Thatch, Moskito, Tortola, and Virgin Gorda of BVI, in addition to other previous records on Guana and Necker of BVI, St. John and St. Thomas of USVI, Culebra Island, and Puerto Rico (Princis 1969, Roth 1994, Gutiérrez and Fisk 1998, Lazell 2005).

Specimens examined. BDVC—1 male/1 female, BVI, Anegada Is., 26/27.X.2009, W. Lu & S. Valentine-Cooper; 2 females, BVI, Great Camanoe Is., 20.X.2008, Lu & S. C. Valentine-Cooper; 19 males, BVI, Guana Is., III, IX-X, at UV, Malaise trap; 27 females, BVI, Guana Is., I, IX-X, at UV, Malaise trap; 3 adults, BVI, Little Thatch Is., 11.X.2010, E. Wright; 2 males, BVI, Moskito Is., 25.X.2007, W. Lu, sweep; 1 female, BVI, Moskito Is., 23.X.2008, Valentine-Cooper & Lu; 1 male, BVI, Necker Is., 2-5. VI.2005, W. Lu; 3 adults, BVI, Necker Is., 16.X.2010, W. Lu. **MCZ**—10 adults, USVI, St. John, Great Cruz Bay, 15-23.VI.1996, B. & B. Valentine; 10 adults, BVI, Guana Is., B. & B. Valentine. **NMNH**—3 adults, BVI, Anegada Is.; 4 adults, BVI, Jost Van Dyke Is.; 4 adults, BVI, Tortola Is.; 20 adults, BVI, Virgin Gorda Is. **UDCC**—1 adult, BVI, Guana Is., 23.X.1997, C. R. Bartlett. **VIIS**—2 adults, USVI, St. John Is., Lameshur Bay, 18-27.VII.1972, A. Gray; 1 male; USVI, St. John Is., Lameshur Ranger Station, 23XI.1958, C. F. Adams.

Family Blattidae

152

21. *Eurycotis improcera* Rehn (Fig. 17)

Eurycotis improcera Rehn 1930: 48; USVI: St. Croix.

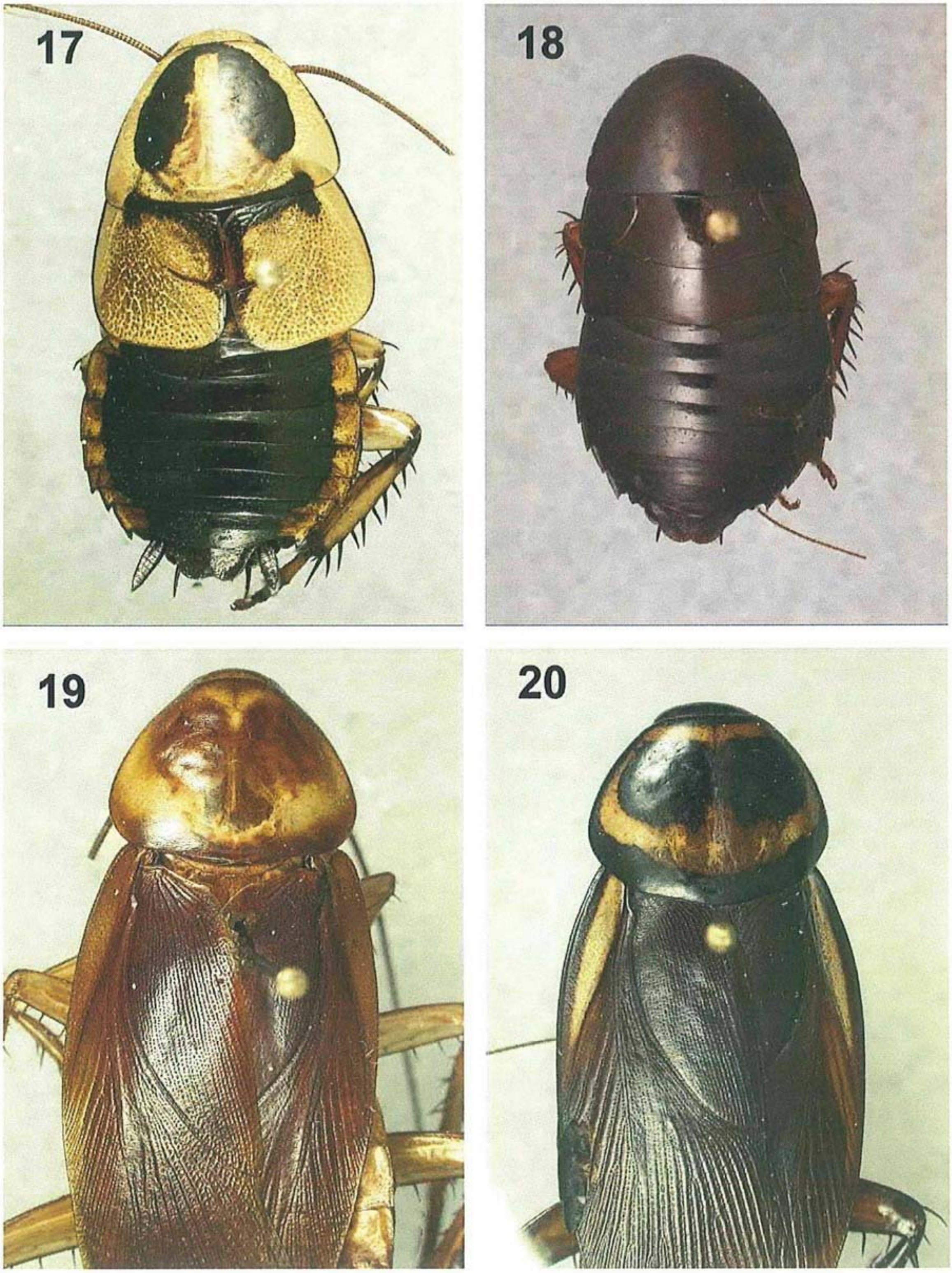
Diagnosis. Adults 16–24 mm, brachypterous with quadrate tegmina in both sexes that barely overlap; oval, yellowish brown with dark brown pattern; dorsum shiny, tegmina densely and finely punctate; head yellowish with a distinct dark band across vertex between eyes and another across frons above clypeus, and an irregular, often weakly defined, dark area between antennal insertions; pronotum broader than long, with 2 large, elongate-oval, oblique, dark brown spots connected anteriorly, and sometimes weakly connected to a dark basal band, which does not reach lateral margins; tegmina with basal margins, suture, and transverse discal grooves variably dark brown; anteroventral margin of fore femur with a row of 13 progressively decreasing spines and 3 larger distal spines (Type A_3); basal and apical tarsomeres darker than intermediate; 4 or 5 hind tarsomeres (sometimes 4 on one leg and 5 on the other); abdomen dark brown with yellowish lateral margins, each segment slightly darker anteriorly than posteriorly; segment 7 broadly convex dorsally in female, last tergite triangular with apex broadly excavated in both sexes.

Nymphs have the same yellowish lateral margins of the abdomen but are duller and the number of segments with yellowish margins is variable, increasing with age, suggesting a random ontogenetic progression. Legs are darker in younger nymphs. The largest nymphs (~18 mm long) have no external indication of wing pads. An oothecum is twice as long as broad, 11 mm long, with 8 egg chambers on each side; each opening side (lip) has a submarginal, longitudinal ridge across the egg chambers, and 17 small, marginal teeth.

Comments. *Eurycotis improcera* is a common species on Guana Island and probably arboreal and nocturnal; individuals were active at night on tree branches at >2 m high, never under ground cover, but were caught in pitfall traps, probably during dispersal (Table 1). The sex ratio is about 1:1. Nymphs can be sorted according to head width categories of 2.0, 3.5, 4.0, 5.0–5.5, 6.5–7.0, 7.5–8.0, and 8.5–9.0 mm (adult 9.0–11 mm), suggesting seven instars. We observed active females carrying oothecae at night in Octobers of 2007, 2008, and 2009.

Originally described from St. Croix, *Eurycotis improcera* has three congeners from Puerto Rico (Gutiérrez 2004): *E. decipiens* (Kirby), *E. gurneyi* Gutiérrez, and *E. victori* Gutiérrez. The misidentification of *E. improcera* as *E. decipiens* from Guana Island (Lazell 2005) suggests morphological similarity of the two. It is herein recorded for the first time on St. John of USVI, Great Camanoe, Jost Van Dyke, Little Thatch, Moskito, Tortola, and Virgin Gorda of BVI, in addition to another previous record on St. Croix (Princis 1966).

Specimens examined. AMNH—1 male, USVI, St. John, Virgin Island National Park, 19-27.VII.1972, A. Gray. **BDVC**—1 nymph, BVI, Great Camanoe Is., 20.X.2008, S. C. Valentine-Cooper; 1 male, BVI, Guana Is., 22.X.2000, B. & B. Valentine; 1 male, BVI, Guana Is., N shore, 17-23.X.2007, B. D. Valentine family; 1 male, BVI, Guana Is., White Beach, 15.X.2007, W. Lu; 1 female [with oothecum], BVI, Guana Is., Pyramid, 22.X.2007, B. D. Valentine family, sweep; 1 female, BVI, Guana Is., 8.X.2004, B. D. & S. C. Valentine-Cooper, at UV; 1 female, BVI, Guana Is., 17-23.X.2000, B. & B. Valentine; 1 female, BVI, Guana Is., Palm Ghut, 18.X.2007, B. D. Valentine family; 4 female nymphs, BVI, Guana Is., Quail Dove Ghut, 9.VI-9.VII.2000, V/VIII.2003, VII.2006, W.-P. Liao, Malaise trap; 1 nymph, BVI, Guana Is., 16-22.X.2002, B. D. Valentine; 1 nymph, BVI, Guana Is., 5-19.X.2005, B. D. & B. S. Valentine; 2 nymphs, BVI, Guana Is., 16.X.2007, W. Lu; 1 nymph, BVI, Guana Is., 2.X.2009, D. M. Dennis & W. Lu; 1 female, BVI, Jost Van Dyke [as Pyke] Is., 19.X.2008, W. Lu; 1 female, BVI, Little Thatch Is., 25.X.2008, Valentine-Cooper & Lu; 1 adult, BVI, Little Thatch Is., 11.X.2010, E. Wright; 1 nymph, BVI, Moskito Is., 23.X.2012, E. Hill; 2 males, BVI, Tortola Is., Sage Mt., 750 m, 24.X.2002, B. & B. Valentine, beat; 1 female/1 male, BVI, Tortola Is., Chalwell, XI.2002/IV.2011, C. Petrovic, at light; 2 nymphs, BVI, Tortola Is., Sage Mt., 15.X.1999/28.X.2006, W. Lu; 1 nymph, BVI, Tortola Is., Sage Mt., 22/28.X.2009, S. Valentine-Cooper; 1 male, BVI, Virgin Gorda Is., SW coast, 14.X.2004, B. S. Valentine, at UV; 1 male nymph, BVI, Virgin Gorda Is., Oil Nut Bay, 12.X.2008, [B. S. Barker]. **MCZ**—2 adults, BVI, Guana Is., B. & B. Valentine. **NMNH**—2 males/1 female, BVI, Guana Is., hotel area, 6-13.X.2001,



Figures 17–20. Blattidae. **17)** *Eurycotis improcera* adult from Guana Island. **18)** *Eurycotis* sp. 1 adult from Tortola Island. **19)** *Periplaneta americana* adult from Guana Island. **20)** *Periplaneta australasiae* adult from Guana Island (all specimens in BDVC).

154

D. E. Perez-Gelabert; 1 female, BVI, Guana Is., Quail Dove Ghut, I.2003, W.-P. Liao, Malaise trap; 1 male, BVI, Guana Is., 9.X.2002, W. Lu. **UDCC**—1 male, BVI, Guana Is., 8.X.1994, C. R. Bartlett.

22. *Eurycotis* sp. 2 (Fig. 18), NEW RECORD

Diagnosis. Adults 18–19 mm, with small, full, widely separated tegmina in both sexes that are rounded-triangular and barely surpass the mesonotal posterior margin, no transverse discal grooves, no hindwings; dorsum totally blackish brown, shiny, without punctures or wrinkles, with a fine, median, longitudinal carina on each notum, only visible at certain light angles; head dark without any marking; pronotum broader than long; anteroventral margin of fore femur with a row of 13 progressively decreasing spines and 3 larger distal spines (Type A_3); tarsomeres 1–5 each with a pale apical pad, that of 5 much smaller and partly hidden by 4; each pulvillus forming a ventral pad, which appears bilobed on metatarsi; abdominal segments slightly lighter anteriorly than posteriorly, supra-anal plate sub-trapezoidal with apical emargination and rounded angles.

Comments. *Eurycotis* sp. 2 may be a new species closely related to *E. gurneyi* Gutiérrez (1999b) described from Puerto Rico; further comparative study of both will determine its taxonomic status. It does not come to light and is a nocturnal ground-dweller (Table 1). We found them by sweeping dead vegetation, in rotten *Agave* in daytime, and at night active on the forest floor in the wet zone of Sage Mountain. This is the first report for the Virgin Islands; *E. improcera* (Species 21) was thought to be the only Virgin Islands species in the genus until the discovery of this species.

Specimens examined. BDVC—2 males/2 female nymphs, BVI, Tortola Is., Sage Mt., 11.X.2007/28.X.2008, W. Lu; 1 male nymph, BVI, Tortola Is., Sage Mt., 22/28.X.2009, S. Valentine-Cooper.

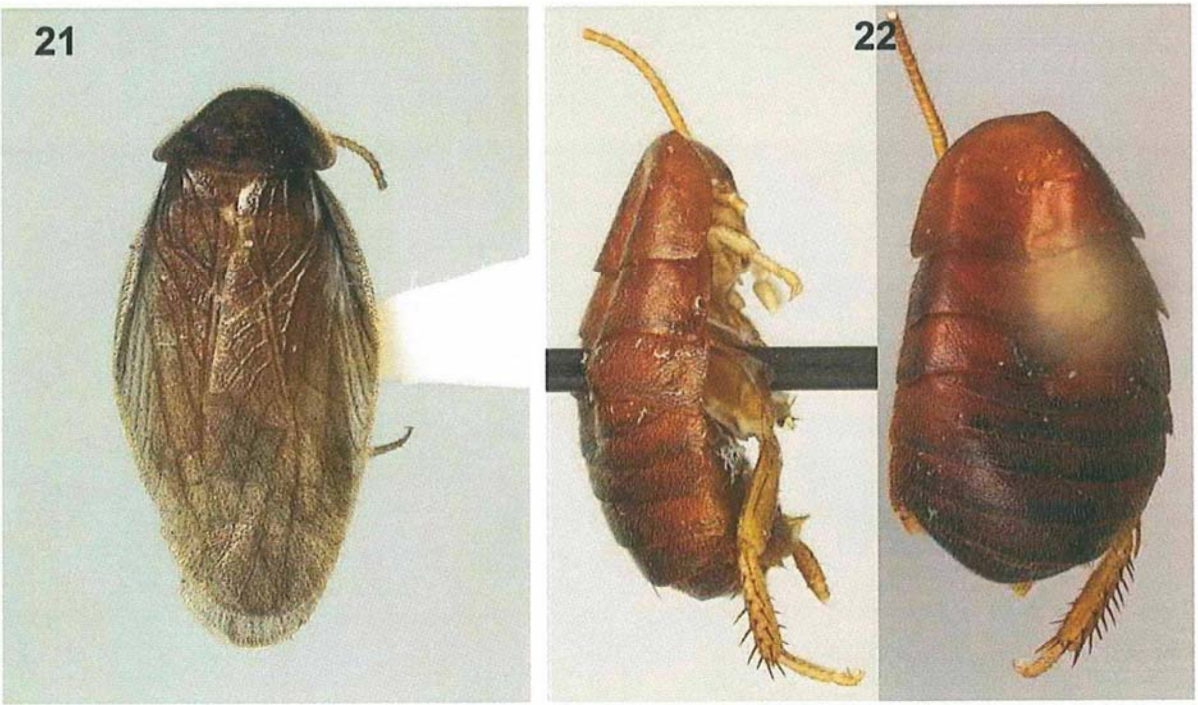
23. *Periplaneta americana* (Linnaeus) (Fig. 19)

Blatta americana Linnaeus 1758: 424; America.

Diagnosis. Adults 27–38 mm, with full tegmina in both sexes; elongate oval, reddish-brown; pronotum bicolored, disc with yellow encircling a large, irregular, central, reddish-brown area that is sometimes weakly divided into two; outer basal margin of tegmina without a contrasting yellow stripe; supra-anal plate sub-triangular, elongate, strongly bilobed, semi-transparent; cerci slender, almost as long as mid tarsi, apical 1/2 (female) or 1/3 (male) articles longer than broad. Nymphs are shades of brown without yellow spots or bands.

Comments. Cosmopolitan spread has produced multiple synonyms for *Periplaneta americana*. This edificarian pest is easily distinguished from another widespread congener *P. australasiae* (Species 24), by the tegmina color pattern. This is a common species on Guana Island; it is a nocturnal ground-dweller; individuals scurried around fallen tree trunks and rocks behind the hotel area (Table 1). Familiarity and abundance explain the fact that few specimens were collected for island records. Ledru (1810) first reported it from St. Thomas and St. Croix, and Lazell (2005) from Guana Island. A local BVI pest control agent has confirmed its presence in major edificarian habitats on Virgin Gorda and Tortola (J. Egelhoff, pers. comm. 24.X.2011). It is herein recorded for the first time on Anegada and Little Thatch of BVI, and St. John of USVI, in addition to other previous records on St. Croix, St. Thomas, Puerto Rico, and other Antillean islands (Shelford 1910, Princis 1966).

Specimens examined. BDVC—1 male, BVI, Anegada Is., airport vicinity, 20-21.X.2004, Valentines & Sibleys, at UV; 2 males, BVI, Guana Is., 8-9.X.2004, B. D. Valentine & S. C. Valentine-Cooper, at UV; 2 males, BVI, Guana Is., 6.X.2006/24.X.2007, B. D. Valentine family, at UV/under debris; 3 males/4 females, BVI, Guana Is., 1-7/15-21/22-28.X.2001, 9-15/23-30.X.2002, 8.X.2003, B. & B. Valentine, at UV; 2 males, BVI, Little Thatch Is., 23.X.2008, W. Lu. **MCZ**—5 adults, BVI, Guana Is., B. & B. Valentine. **NMNH**—1 male, BVI: Guana Is., hotel area, 6-13.X.2001, D. E. Perez-Gelabert. **UDCC**—1 male/1 female, BVI, Guana Is., 21/23.X.1997, C. R. Bartlett. **VIIS**—1 male, USVI, St. John Is., Lameshur Bay,



Figures 21–22. Polyphagidae. **21)** Polyphagid sp. 1 (*Compsodes* sp. 1) adult from Guana Island. **22)** Polyphagid sp. 2 nymph from Guana Island (all specimens in BDVC).

18-27.VII.1972, A. Gray; 1 male, USVI, St. John Is., Lameshur Bay, 7.VII.1968, R. Philibosian; 1 female, USVI, St. John Is., Lameshur Ranger Station, 15.XI.1958, C. F. Adams.

24. *Periplaneta australasiae* (Fabricius) (Fig. 20)

Blatta australasiae Fabricius 1775: 271; the Pacific and unknown regions ("nave e mare Pacifico et regionibus incognitis revertente"...).

Diagnosis. Adults 27–30 mm, with full tegmina in both sexes; elongate oval, dark brown; pronotum bicolored, disc with yellow encircling a large brown central area, which is sometimes weakly divided into two; outer basal margin of tegmina with a yellow costal edge; supra-anal plate of male rectangular, with a shallow emargination, opaque, reddish brown; supra-anal plate in female folded downward on each side, apically emarginate with apices rounded, dark brown; cerci flat, elongate spindle-like, almost as long as mid tarsi, articles broader than long except last one. Nymphs black, with 2 yellow transverse bands strikingly on pronotum and irregular lateral spots on rest of dorsum.

Comments. The likely tropical origin and spread around the world have created multiple synonyms for *Periplaneta australasiae*. This is an edificarian pest like its congener *P. americana* (Species 23), and probably arrived via cargo shipments from abroad. Because of its superficial resemblance to *P. americana* and collector bias, specimens were rarely collected. Its spread over the Virgin Islands should be interesting for geological, historical, and ecological aspects. Collecting efforts on other islands, especially those not inhabited, should be made. It can be easily distinguished from the widespread *P. americana* by the yellow costal edge of its tegmina. It is a nocturnal ground-dweller (Table 1); individuals were active at night in the orchard and in the hotel area, mingling with *P. americana*. Shelford (1910) reported this species from St. Thomas; it is common and herein recorded for the first time on Anegada, Guana, Jost Van Dyke, Moskito, and Tortola of BVI, in addition to other previous records on St. Thomas, Puerto Rico, and other Antillean islands (Princis 1966).

Specimens examined. BDVC—1 nymph, BVI, Anegada Is., airport vicinity, 22.X.2004, Valentines & Sibleys; 1 male, BVI, Guana Is., 2003, W.-P. Liao; 1 adult (abdomen missing), BVI, Guana Is., 27.IX.2005, B. D. Valentine & S. C. Valentine-Cooper, at UV; 1 female/1 nymph, BVI, Guana Is., 14.X.2007, W. Lu, sweep; 1 female, BVI, Guana Is., 9-15.X.2002, B. & B. Valentine, at UV; 1 female, BVI, Guana Is., 26.IX.2005, B. D. Valentine & S. C. Valentine-Cooper; 1 nymph, Jost Van Dyke, 18-19.X.2010, W. Lu & S. C. Valentine-Cooper; 1 male/1 female, BVI, Moskito Is., 23.X.2008, Valentine-Cooper & Lu; 1 nymph, BVI, Tortola Is., Chalwell, 16-24.X.2003, C. Petrovic, at light.

Family Polyphagidae

25. Polyphagid sp. 1 (*Compsodes* sp. 1) (Fig. 21), NEW RECORD

Diagnosis. Male adults very small, delicate, 5 mm, elongate, with full tegmina; pale brown but head and pronotum slightly darker; pronotum and tegmina finely setose; anterior and lateral margins of pronotum pale; tegmina membranous with raised veins, cells minutely reticulate with larger setose punctures; venter and legs entirely paler; subgenital plate apically truncate; cerci as long as mid tarsi, with dense long setae, with intermediate articles thicker, apical articles sometimes darker.

Comments. Hebard (1917) described the genus *Compsodes*; the online catalogue (Beccaloni 2007) indicates that it contains four species and ranges from Panama to southern USA. *Compsodes* was first recorded from the Antilles based on five specimens taken in semi-dry forests in the Dominican Republic (Gutiérrez and Perez-Gelabert 2000) and was recently described as *Compsodes perezgelaberti* by Gutiérrez (2012b). Our species is different from the Dominican species and may be new. It is the first record of the genus for the Virgin Islands, and the second record for the Antillean region. It seems to be rare and comes to lights (Table 1). Roth (1994) recorded a possible polyphagid nymph from Guana Island, which may be this species.

Specimens examined. BDVC—1 male, BVI, Guana Is., 9-15.X.2002, B. & B. Valentine, at UV; 1 male, BVI, Guana Is., 17.X.2007, W. Lu, at light; 1 male, BVI, Guana Is., 2-7.X.2003, B. & B. Valentine, at UV. **NMNH**—1 specimen, BVI, Guana Is., 16-22.X.2002, B. & B. Valentine, sandpit Malaise trap.

26. Polyphagid sp. 2 (Fig. 22), NEW RECORD

Diagnosis. Nymph about 5 mm (abdomen somewhat down-curled), wingless, dorsum entirely shades of red, shining, with pronotum lightest and apical abdominal segments darkest, each segment darker anteriorly; dorsum finely and densely punctate, covered with short, pale, appressed setae that do not conceal the underlying derm, and a row of longer but sparse setae on each posterior abdominal tergite, most visible on segment 5; head pale, reddish-brown, with a darker transverse band between antennal insertions; clypeal apex and labrum much paler than frons; palpi almost white; antennae paler than head; venter mostly dark reddish, with many short, non-overlapping setae on abdominal segments; forecoxa and posterior apices of meso- and metacoxa bright creamy white; foreleg (1 missing) pale yellowish white; cerci short, widest in middle, segmentation obscure, with 5 or more articles; styli very small with perhaps 4 or 5 articles.

Comments. We tentatively place the single nymph in this family but need adults for further determination. It was collected on Guana Island in 2003 by Dr. Barbara Thorne, in an arboreal termite runway of *Nasutitermes corniger* (Motschulsky), identified then as *N. costalis* (Holmgren), which is now a junior synonym of *N. corniger*. She sent additional specimens in the same year to the late Dr. Louis M. Roth, but we have not been able to locate them. The termite is reported from more than 20 islands from Cuba to Trinidad; including Guana, Tortola, St Thomas, and St Croix (Collins et al. 1997) and more since then (Thorne and Haverty 2000). The cockroach may be host-specific and limited to islands with the same termite. In October 2008, Dr. Thorne revisited the Guana site, but found no additional specimens; she also checked colonies of the related and more common *Nasutitermes acajutlae* (Holmgren), and found only nymphs of *Euthlastoblatta facies* (Walker).

Specimen examined. BDVC—1 nymph, BVI, Guana Is., 4.X.2003, B. Thorne, gallery of *Nasutitermes costalis* (Holmgren).

Discussion

Most cockroaches of the Virgin Islands are definitively related to those of Puerto Rico. From Cretaceous times (100 million years ago) intermittently until the present interglacial, Puerto Rico and the Virgin Islands (except St. Croix) formed a single large land mass more than double the size of modern Puerto Rico. Beginning about 20,000 years ago, melting glaciers raised sea level, isolating the present islands. Many of the species shared with Puerto Rico were probably isolated on the Virgin Islands when these islands were separated by sea level rise in the late Pleistocene. Of the 14 genera identified, 10 genera have additional species on the other Antilles and the adjacent continental areas: *Eurycotis*, *Hemiblabera*, and *Symploce* are Antillean; *Cariblatta*, *Euthlastoblatta*, *Plectoptera*, and *Nyctibora* are also Antillean, but perhaps centered on the Puerto Rican Bank; *Colapteroblatta* is in the Antilles and northern South America; *Compsodes* has Central American relatives; and *Panchlora* is widespread neotropical. Of the 19 species identified to specific level, five are edificarian: *Blattella germanica*, *Periplaneta americana*, *P. australasiae*, *Pycnoscelus surinamensis*, and *Rhyparobia maderae*. The first three are thought to be introduced from the Old World and now have cosmopolitan distributions. *Pycnoscelus surinamensis* is largely a parthenogenetic species (Roth 1967, 1998) that has spread over the tropical and humid areas of the world. *Rhyparobia maderae* is the largest; its disappearance from the Virgin Islands may be coincident with the fading animal husbandry. Ten of the remaining 14 species are shared with Puerto Rico and two of them, *Panchlora nivea* and *Euthlastoblatta diaphana*, were previously reported but have not been rediscovered from the Virgin Islands. The extreme similarity of *P. nivea* to *P. sagax* and *E. diaphana* to *E. facies* suggests misidentifications or synonymy. Among the four that are not recorded from Puerto Rico, *Cariblatta antiguensis* may also be present on Puerto Rico as *Cariblatta plagia* Rehn and Hebard (1927); type comparison is necessary to confirm this. The remaining three species absent from Puerto Rico are *Panchlora viridis*, described from "America," *Nyctibora noctivaga*, from Nicaragua, and *Eurycotis improcera*, from St. Croix. Although all three have a wide distributional range, we could not rediscover the first two species on the Virgin Islands and question their identities. For these four, as well as the seven unidentified species, we refrain from drawing biogeographic conclusions until there is a much-needed thorough comparison of cockroaches between Puerto Rico and the Virgin Islands.

Species diversity has more to do with altitude and habitat differences than just island size (Lazell 2005). Tortola is 5,494 hectares with a maximum BVI elevation of 521 m on Sage Mountain and a suggestion of a unique cloud forest; St. Thomas is 8,091 hectares and attains a maximum USVI elevation of 474 m at Crown Mountain — not a national park; St. John is 5,180 hectares with a height of 389 m on Bordeaux Mountain — lower than St. Thomas but in the USVI national park; and Guana is 297 hectares with a height of 246 m. The Virgin Islands have been extensively degraded by human activity; Sage Mountain on Tortola and Bordeaux Mountain on St. John were designated national parks not long ago. However, nearby Guana was only partially cleared a century ago (Lazell 2005) and has been protected for many years and recovering. Tortola is 18 times larger than Guana and twice the altitude, but is less well protected. Of the 21 species found, Tortola has 19 and Guana 15. Two Guana species are still unknown on Tortola (*Compsodes* sp. 1 and polyphagid sp. 2), but are expected because they are either common or associated with termites that are also abundant on Tortola. Six species on Tortola are not known from Guana where most collection efforts have been made (*Blattella germanica*, *Colapteroblatta* sp. 1, *Cariblatta* spp. 2–3, *Eurycotis* sp. 2, and *Plectoptera* sp. 3). Excluding the edificarian *B. germanica*, the three *Cariblatta and Plectoptera* species have full wings and appear arboreal, so flight ability cannot explain their absence on Guana Island. Lower altitude and drier forest on Guana suggest that habitat diversity may be the limiting factor. Though similar to Tortola in island size, St. John and St. Thomas may prove to have species numbers closer to Guana than to Tortola due to the lack of cloud forest. Furthermore, we have not found *Euthlastoblatta facies* on Necker despite extensive efforts, even though it occurs on Anegada, the easternmost island on the Puerto Rico Bank. Necker is a small island of 30 hectares (Lazell 2006), 1/130 the area of Anegada and slightly higher above sea level. The limited habitat of only a small patch of natural woods may explain the absence *E. facies* from

Necker. Anegada is a flat, elongate, limestone and sand bar of 3,872 hectares and its maximum 8.5 m height is a sand dune; it has seven widespread or edificarian species, which have full wings except the most abundant *Hemiblabera brunneri*, all shared with and probably derived from nearby islands.

Diverse collecting techniques, search image, effort, and natural tendency to concentrate on rarer species, all make estimates of abundance and island distribution imprecise. *Periplaneta* is a good example: we have a combined total of <30 specimens of the two common species on Guana (*P. americana* and *P. australasiae*); this contrasts with >20 specimens for each of the 10 native species. The absence of the edificarian *Periplaneta* from the Malaise trap may be explained by the trap location in a wooded area, away from edifices. This Malaise trap has been operated almost continuously for >12 years and has collected in excess of 5,000 cockroach specimens, but only eight species are represented and are all associated with wooded habitats. Two of these (*Symploce pararuficollis* and *Cariblatta antiguensis*) far outnumber the others and account for over 4,000 specimens. Total counts for the six remaining species range from <20 to <200 per species over 12 years. Even considering all collecting methods, five species in our collection are represented by single specimens. These are *Cariblatta* spp. 2 and 3 (Tortola), *Colapteroblatta* sp. 1 (Tortola), *Plectoptera* sp. 3 (Tortola), and polyphagid sp. 2 (Guana). Their rarity indicates strong habitat preferences; therefore, it is reasonable to expect their absence on smaller islands.

Morphological and behavioral variation may partially explain abundance and island distribution. Of the eight species coming to the Malaise trap, *Cariblatta antiguensis*, *Euthlastoblatta facies*, *Plectoptera rhabdota*, *Symploce pararuficollis*, and *S. ruficollis* are commonly found perched on shrubs at night. These five species are relatively small, have full wings, and fly readily, so they can be expected in the Malaise trap frequently. On the other hand, *Eurycotis improcera* is relatively large, brachypterous, and arboreal. *Nyctibora lutzi* has full wings, but is a heavy cockroach and may not fly high and far; it is usually found on detritus close to or on the ground. Thus, they are infrequent visitors to the Malaise trap. *Panchlora sagax* has full wings and comes to electric lights and UV light traps in good numbers, but is surprisingly low in frequency in the Malaise trap. Ground level of the trap hints that this species is a canopy dweller. For an abundance estimate, use of UV light traps in combination with Malaise traps should be more informative for this species. The early abundance peak of *Symploce ruficollis* in April contrasts the latter abundance peaks of *S. pararuficollis* in June and December (Table 2), which suggests alternating ecologies of the congeners to avoid competition: when one is abundant the other is scarce. Each species has unique behavior and ecology; varied ecologies generate different abundance maxima and different slopes of abundance increase at different times; thus phenology varies among species.

Local weather also influences abundance and island distribution. The Virgin Islands in general have two rainy seasons, April-May and September-October-November. Total Malaise trap captures indicate that abundance fluctuated greatly among months and over years and differed in reference to these two rainy seasons (Fig. 2, 3). When looking at changes across months, the delayed burst of cockroach abundance after the spring rainfall and the small but steady increase during the fall rainfall (Fig. 2A) illustrate seasonality of abundance. Our cockroaches are mostly scavengers; vegetation boom in rainy seasons should provide them fresh palatable food sources. The spring rainy season is most important in affecting abundance for most species. When looking at changes over years, the ups and downs of cockroach abundances become perplexing, however. On one hand, the average numbers were tracking the annual rainfall (Fig. 2B); on the other hand, irregularity of fluctuation within a species (Fig. 3, Table 3) contradicts this yearly pattern of abundance and makes it difficult to predict. Of all five species frequently captured in the Malaise trap, the high abundance of three species (*Cariblatta antiguensis*, *Symploce pararuficollis*, and *S. ruficollis*) in June 2000 has not been surpassed in >12 years (Fig. 3). Neither the prior three years of heavy rainfall nor the low annual rainfall in 2000 can explain these high numbers of individuals, because these rainfall conditions are not essential to bursts of abundance. For example, in 2007 *S. pararuficollis* increased abruptly but *C. antiguensis* did not (Fig. 3, Table 3). If continuous drought for three years induced a sharp increase in *Plectoptera rhabdota* in 2010, then drought does not explain its leap in 2004 after a spike of heavy rainfall in 2003 (Fig. 3). We have observed a downward impact of a prior annual rainfall threshold below a daily average of 2.0 mm on abundance in some species and an upward affect of low annual rainfall consistently below that threshold in others. There may have been another rainfall threshold above a certain amount to trigger a big spike in abundance, or timing of heavy rainfall in each spring and fall season may have affected abundance responses rapidly or be more extended into the next season. Also, seasonality is not obvious in the Virgin Islands because temperature does not fluctuate much in time and space due to latitude and low mountain ranges. Therefore, temperature is not regarded as a major factor affecting changes in cockroach abundance in the Virgin Islands. The lowest abundance of total Malaise trap captures coincided with the winter rainfall low, and could be the result of the combined affect of low moisture and temperature. Furthermore, use of the arithmetic average of the rainfall gauge measurements may be comparable to the "optimal interpolation" technique used to create a global data set. This technique merges satellite information with available gauge data over land and modifies the calculation of average values (Adler et al. 2003). The resultant rainfall data may be more pertinent in terms of climatic changes than just rain. Overall, complexity calls for evaluation of different climatic data sets and partition of data into crucial periods for further analysis of the effects of drought, heavy rainfall, and temperature.

Conclusions

Of the 26 cockroach species historically recorded or recently found during this long term research, nine are new records for the Virgin Islands and five are new for Guana Island. Excluding five edificarian species, more than half of these cockroaches are definitively present on Puerto Rico or related to those of the Greater Puerto Rico Bank. This close biogeographic relationship may increase with further taxonomic study of the Puerto Rican fauna. Most of these cockroaches are nocturnal but *Panchlora sagax* and perhaps the three *Plectoptera* species may be diurnal because we have not observed them actively moving around in the habitat at night. Nymphs of *Euthlastoblatta facies* and a polyphagid species have been taken in active termite nests. Phenology of five species frequently captured in the Malaise trap demonstrated distinct seasonality with abundance highs in spring and fall for two species, and with only one high in spring or early summer for three other species. The abundance increases were correlated closely, but not necessarily synchronic, with the spring and fall rainy peaks. An annual average rainfall below a threshold of 2.0 mm appears to impact abundance. Fluctuation over >12 years indicates further analysis of the relationship of cockroach abundance with rainfall is imperative.

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