

9

West Indian Mammals The Old, the New, and the Recently Extinct

Liliana M. Dávalos and Samuel T. Turvey

Abstract

The West Indian mammal fauna has played a key role in the development of biogeographic ideas for over a century, but a synthesis explaining regional patterns of mammal diversity and distribution in a historical framework has not emerged. We review recent phylogenetic, population genetic, and radiocarbon dating studies of West Indian mammals and explore the biological and historical drivers of colonization, speciation, and extinction in this region of endemism. We also present the first complete list of all its extant and extinct mammals. The mammalian biota is older than was earlier presumed, with many ancient endemic lineages, even among highly vagile organisms such as bats. Land bridges, Cenozoic eustatic sea-level changes, and Pleistocene glacial cycles have been proposed to explain the colonization of the islands, but phylogenetic divergence analyses often conflict with the timing of these events and favor alternative biogeographic histories. The loss of West Indian biodiversity is incompletely understood, but new radiometric chronologies indicate that anthropogenic impacts rather than glacial-interglacial environmental changes are responsible for most Quaternary extinction and extirpation events involving land mammals. However, many outstanding questions of historical biogeography remain unresolved, including appropriate methods for interpreting phylogenies and divergence estimates in a biogeographic context, and whether to use vicariance or dispersal as the null hypothesis when investigating regional patterns of colonization, speciation, and extinction in comparative analyses. We propose synthetic approaches drawing from phylogenetics, population genetics, paleogeography, paleontology, and even archaeology to resolve persisting questions in Caribbean biogeography.

9.1 Introduction

The mammals of the West Indies have been crucial to the development of biogeography from its very inception (Wallace 1876). The endemism of the Antillean biota, for example, led Wallace to propose land interconnections

and subsequent subsidence that isolated the islands first from South America and later from Central America (Wallace 1876). This was the first cogent—if incorrect—biogeographic hypothesis for the region. Even this early biogeographic work highlighted two critical aspects of the Caribbean mammalian fauna: its poverty in comparison to continental areas of equal size, and its sharp divergence from the nearby continental fauna. By proposing an ancient interconnection, severed in the Miocene, his geological hypothesis accounted for the endemism of the mammals, while the subsidence of a large proportion of the land mass was proposed to explain the small number of surviving lineages (Wallace 1876).

Although Caribbean mammals, particularly bats, were key to developing the equilibrium theory of island biogeography (e.g., Koopman 1958; MacArthur and Wilson 1967), the importance of endemism and geological changes in regional biogeographic studies declined with growing interest in mechanistic explanations of island diversity (MacArthur and Wilson 1963). The goal of explaining the origin and diversity of West Indian mammals in a historical framework, however, was not completely forgotten, especially among systematists (e.g., Williams 1952; Williams and Koopman 1951). Initial systematic zoogeography reviews (e.g., Baker and Genoways 1978; Koopman 1989) gave way to increasingly formal biogeographic analyses (e.g., Griffiths and Klingener 1988; Woods 1989; Woods, Ottenwalder, and Oliver 2001), culminating in the explicit use of phylogenies to infer biogeographic history (e.g., Dávalos 2004b, 2005, 2006, 2007; Roca et al. 2004). Whether informed by phylogeny or not, these studies have shared a historical perspective and focus on the origin and diversification of multiple mammalian lineages.

Aside from questions on the origins and colonization routes of Caribbean mammals, another main focus of biogeographic research has been quantifying and explaining extinction. As Quaternary fossil findings accumulated (e.g., Anthony 1918; Koopman and Williams 1951; MacPhee and Iturralde-Vinent 1995a, 1995b; MacPhee, White, and Woods 2000; MacPhee, Iturralde-Vinent, and Gaffney 2003; Miller 1918, 1922, 1929a, 1929b; Williams and Koopman 1951), new competing hypotheses on the drivers of regional Pleistocene and Holocene extinctions were proposed (MacPhee and Marx 1997; Pregill and Olson 1981; Steadman et al. 2005). An extensive literature has sought to explain the extinction and extirpation of numerous terrestrial mammal species (MacPhee 2008; MacPhee, Ford, and McFarlane 1989; Morgan 2001; Morgan and Woods 1986; Turvey, Gądy, and Rye 2006; Turvey et al. 2007). At present, three main questions remain on the region's historical biogeography: (1) What

is the geographic origin of the endemic mammal fauna?; (2) How did mammals, especially nonvolant ones, reach the Antilles?; and (3) What drove most of the nonvolant mammal fauna to extinction? In this chapter, we synthesize recent evidence from molecular phylogenetics, population genetics, paleontology, zoology, and archaeology to address these questions. Our goals are to present the status of historical biogeography of Caribbean mammals and to point to new methodological and analytical approaches that will resolve persistent gaps in understanding Antillean historical biogeography.

9.1.1 GEOGRAPHIC AND TAXONOMIC SCOPE

In this chapter, "West Indies," "Antilles," and "Caribbean" refer to the islands of the Caribbean Sea that have an insular biota (Koopman 1989; Morgan 2001; Morgan and Woods 1986), including San Andrés, (Old) Providence, and Swan Island (see fig. 9.1). Phylogenetic studies and analyses of fossil remains have overlapped most frequently in the Greater Antilles—Cuba, Jamaica, Hispaniola, and Puerto Rico—so we devote particular attention to these islands. The mammal faunas of Trinidad, Tobago, Margarita, Aruba, Bonaire, and Curaçao are not discussed here because these islands are characterized by a South American biota (e.g., Hooijer 1959, 1966, 1967; Trejo-Torres and Ackerman 2001; Vázquez-Miranda, Navarro-Sigüenza, and Morrone 2007; Voss and Weksler 2009). We have included data on extinct rice rat species from Grenada and the Grenadines because the terrestrial mammal fauna of these islands, though poorly known, is apparently endemic (Turvey et al. 2010). The bats of those islands, however, are not discussed, as most of these insular populations maintain gene flow with South American populations and are better thought of as being at the northern margin of their distributions (Genoways, Phillips, and Baker 1998; Koopman 1989; Presley and Willig 2008). A total of 55 extant and 12 regionally or globally extinct bats have been recorded in the West Indian Holocene, representing about 45 independent lineages. Only 16% (16 species) of an estimated 99 Quaternary nonvolant mammals survive to this day. Fossil and subfossil remains have been described for many lineages, both volant and not, but the bat lineages are better covered than other mammals in molecular phylogenetic and population genetic analyses, largely because of ongoing problems with extracting sequence data from degraded Caribbean Quaternary subfossil and zooarchaeological mammal material. We review both endemic and widespread species, briefly summarize the diversity of all native West Indian mammals (table 9.1), and provide a complete mammal species list in appendix 9.1.

Table 9.1 Orders and families of native Holocene (or putatively Holocene) West Indian mammals. Taxonomy follows contributors to Wilson and Reeder (2005) and Turvey (2009), with additional data from White and MacPhee (2001) and Rega et al. (2002) for sloths, MacPhee and Fleming (2003), Borroto-Páez et al. (2005), and Turvey et al. (2006) for rodents, and Dávalos (2006), Morgan (2001), and Tejedor (2006) for bats.

| Order | Family | Common name | Genera | | Species | |
|------------|------------------|--------------------------------|---------|-------|---------|-------|
| | | | Endemic | Total | Endemic | Total |
| Pilosa | Megalonychidae | Sloths | 6 | 6 | 15 | 15 |
| | Solenodontidae | Solenodons | 1 | 1 | 4 | 4 |
| Rodentia | Nesophontidae | Island shrews | 1 | 1 | 8 | 8 |
| | Echimyidae | Spiny rats | 4 | 4 | 6 | 6 |
| | Capromyidae | Hutias | 9 | 9 | 39 | 39 |
| | Hepaxodontidae | Giant hutias | 4 | 4 | 4 | 4 |
| | Cricetidae | Rice rats | 2 | 2 | ≤18 | ≤18 |
| | Inertaezidae | "Giant hutias" | 2 | 2 | 2 | 2 |
| Primates | Pitheciidae | Antillean monkeys | 3 | 3 | 3 | 3 |
| Chiroptera | Natalidae | Funnel-eared bats | 2 | 3 | 8 | 8 |
| | Nocilionidae | Fishing bat | 0 | 1 | 0 | 1 |
| | Mormoopidae | Ghost-faced and mustached bats | 0 | 2 | 9 | 12 |
| | Phyllostomidae | New World leaf-nosed bats | 9 | 16 | 23 | 30 |
| | Vespertilionidae | Various | 0 | 5 | 8 | 12 |
| | Molossidae | Free-tailed bats | 0 | 5 | 1 | 8 |
| | | | 43 | 66 | 148 | 176 |
| Total | | | | | 95 | |

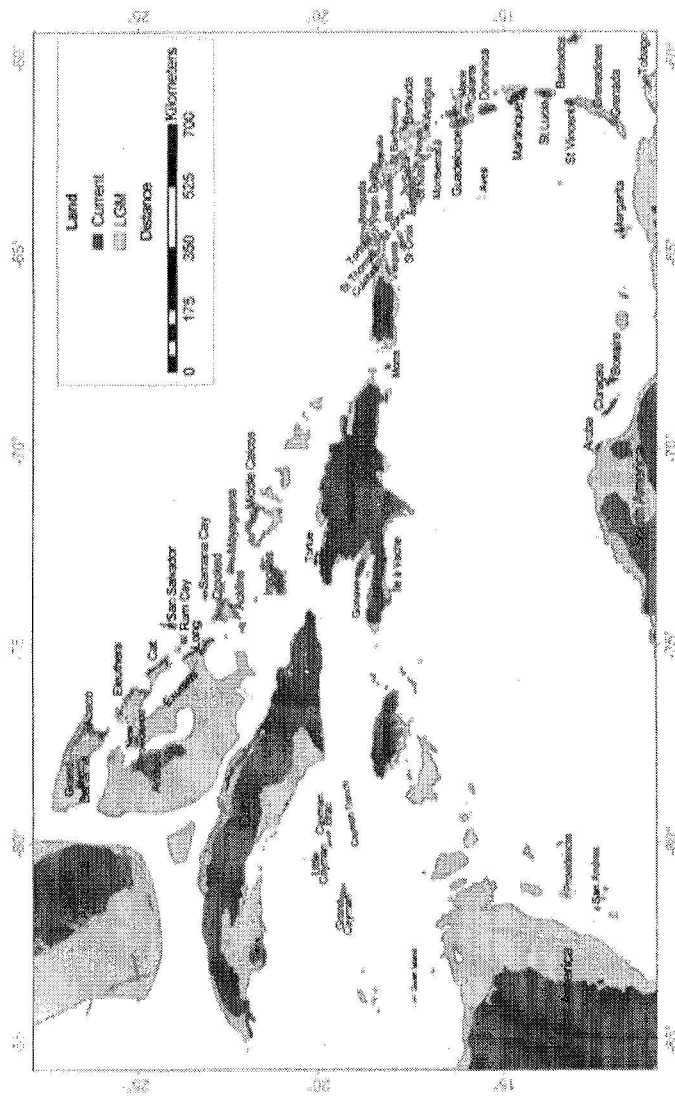


Figure 9.1 Relief map (1 km² grid) of the Caribbean basin with present-day continental outlines.

9.2 The Old: Origin and Phylogeny of West Indian Mammals

Early proponents of West Indian vicariance cited the vulnerability of mammals to refute “flotsam or jetsam dispersal” and argue instead for land interconnections, both between islands and between islands and continents (Allen 1911; Barbour 1916). In contrast, proponents of dispersal as the main mechanism responsible for biotic assembly pointed to the low diversity and peculiar composition of the Antillean biota compared to continental islands, such as Trinidad, or island-sized continental regions (Darlington 1938; Matthew 1918). By the time of Simpson’s (1956) review of the West Indian mammal fauna, dispersal explanations held sway, but vicariant mechanisms were current enough to merit a thorough rebuttal. Despite advances in Antillean geology, paleontology, and mammalogy, the arguments for vicariance or dispersal relied on similar evidence, which remained virtually unchanged over the first half of the twentieth century: (1) classification or, at best, evolutionary systematics; (2) static continents (Simpson 1943); and (3) estimates of probability of dispersal across water gaps and, sometimes, their relationship to hurricanes, ocean currents, and drainage basins.

The development of phylogenetics (Edwards and Cavalli-Sforza 1964) and the establishment of plate tectonics as the mechanism underlying continental drift (Hess 1962) helped revive vicariance in the Antilles but did not close the debate on the prevalent mechanism of biotic assembly. Formal studies of Caribbean biogeography started with the first biogeographic methods using a form of phylogenetic information, such as generalized tracks (Rosen 1975). That analysis compiled the distribution of dozens of monophyletic or presumed monophyletic groups (mainly vertebrates) to identify patterns of overlap across independent groups of close relatives. The patterns were then interpreted to support a multistep vicariant explanation for the origin of the insular biota (Rosen 1975, 1985). In particular, a proto-Antillean archipelago bridging North and South America was postulated in the Cretaceous, followed by separation of the three landmasses by the Oligocene, concluding with the consolidation of Central America and closure of the Isthmus of Panama in the late Cenozoic. Almost immediately, Rosen’s vicariant model was criticized for its outdated geological framework, very ancient dates for the majority of lineages, and inability to explain the absence of major continental groups on the islands (Pregill 1981). Despite its gaps, the proto-Antillean archipelago hypothesis was the basis for the first phylogeny-based biogeography of Antillean insectivores (MacFadden 1980). In fact, because of the complexity of Carib-

bean plate tectonics, Rosen's geological framework was, at the time, considered plausible and in the mainstream of biogeographic explanations (Hedges 1982; MacFadden 1981).

The more recent West Indian dispersal versus vicariance debate traces back to the early 1990s, when molecular clocks were first applied to date the colonization of multiple amphibian and reptile lineages (Hedges et al. 1992). The absence of phylogenies in that initial salvo was quickly identified as a key methodological problem, requiring reanalysis and reinterpretation using cladistic biogeography methods (Page and Lydeard 1994). The land bridge hypothesis of MacPhee and Iturralde-Vinent (1995b) emerged as the vicariant alternative to the molecular clock-based dispersal model. Articulated more fully elsewhere (Iturralde-Vinent and MacPhee 1999), the Greater Antillean and Aves Ridge hypothesis—or GAARlandia—drew on both geological and biological lines of evidence to postulate a temporary land bridge connecting the Greater Antillean Ridge and northwestern South America through the Aves Ridge. The GAARlandia hypothesis proposed a two-step mechanism to explain the patterns of diversity and distribution of land mammals in the West Indies. Initially, the land bridge enabled dispersal from the mainland without crossing ocean barriers, and the eventual disappearance of the bridge then led to vicariant speciation and subsequent independent evolution of the Antillean lineages.

As at the beginning of the twentieth century, the dispersal counterhypothesis invoked prevailing ocean currents and river drainages to explain repeated dispersal across ocean barriers, again criticizing the new land bridge hypothesis for its inability to explain the diversity and distribution of the Caribbean fauna (Hedges 1996). If a land bridge existed, why wasn't the fauna a random subsample of the continental fauna? This question overlooks the possibility of ecological filtering leading to the dispersal and establishment of some lineages but not others; for example, primates but not marsupials. Another tenet of the contemporary dispersal hypothesis is that the entire pre-Tertiary Caribbean biota went extinct because of the dust clouds, tsunamis, and earthquakes that would have followed the asteroid impact at nearby Chicxulub (Yucatán) 65 Ma (Alvarez et al. 1980; Grajales Nishimura et al. 2000) and the subsidence of the West Indies in the Eocene (Graham 2003).

Although the resurrected dispersal and vicariance hypotheses initially lacked phylogenies, multiple morphology-based phylogenies for Antillean mammals soon became available (Horovitz and MacPhee 1999; MacPhee, Iturralde-Vinent, and Gaffney 2003; White and MacPhee 2001; Woods, Borroto, and Kilpatrick 2001), and the first targeted molecular phylogenies soon followed (Dávalos

2005, 2006, 2007; Roca et al. 2004). A reconciled-tree approach applied to Caribbean mammal phylogenies identified a few instances of congruence with the GAARlandia hypothesis, but also pointed to contradictory nodes across several trees, and difficulties reconciling dated molecular phylogenies with the timing of the land bridge (Dávalos 2004b). In particular, the colonization of most nonvolant West Indian lineages was dated to the middle Miocene, but not to the late Eocene/early Oligocene boundary as required by GAARlandia (Dávalos 2004b; Iturralde-Vinent 2006). At the same time, a third alternative, the interconnection of North America and South America through the proto-Antilles in the Cretaceous, was revived by Mesozoic-age molecular divergence estimates for the soricomorph *Solenodon* and the xantusiid lizard *Crotosaura* (Roca et al. 2004). Congruence with GAARlandia has further eroded, as the timing of mammalian colonization for most remaining lineages has been dated to either before or after the proposed land bridge (Dávalos 2010; table 9.2). Finally, the timing of divergence between insular and continental bat lineages has been traced to periods of low sea level, contributing to a fourth biogeographic model of facilitated dispersal (Dávalos 2010).

Rather than revisit the implications of the hypothetical land bridge (Dávalos 2004b), eustatic sea level changes (Dávalos 2010), or the Cenozoic fossil record in the Caribbean (MacPhee 2005; Turvey 2009), we focus instead on the avenues to resolve outstanding biogeographic questions. Current biogeography studies face two practical challenges: how best to use phylogenies to inform biogeography, and how to incorporate fossil calibrations in phylogeny and then interpret the results of divergence analyses. Beyond these methodological concerns, however, lies the question of which conceptual framework is appropriate in historical biogeography.

First, we concur with earlier analyses that reaffirm the central role of phylogeny in biogeographic research (Page and Lydeard 1994). There seems to be little debate on this point, as even the strongest recent proponents of dispersal currently rely on phylogenies to show that divergences between West Indian endemics and their closest extant mainland relatives are not clustered, but rather interspersed through time (Heinicke, Duellman, and Hedges 2007). Although phylogenies have become available in recent years for bats (Dávalos 2005, 2006, 2007) and *Solenodon* (Roca et al. 2004), phylogenies for rodents and vespertilionid and molossid bats are still lacking. How to use phylogenies to inform biogeography remains an open question. Mapping areas as characters (Dávalos 2007, 2010; Roca et al. 2004), dispersal-vicariance analyses (Dávalos 2005, 2006), and phylogeny-reconciliation approaches (Dávalos 2004b) have all

Table 9.2 Geographic origin of Antillean mammals (endemic species or higher-level taxa), and estimated age of divergence from mainland taxa.

| Antillean lineage | Closest mainland relatives | Inferred geographic origin | Molecular divergence (Ma) | Fossil divergence (Ma) | Sources |
|---|--|-----------------------------------|---------------------------|------------------------|--|
| Pilosa | | | | | |
| Choloepodinae (Acratocnus and Neocnus) | <i>Choloepus</i> | South America | | ≥33–34? | MacPhee and Iturralde-Vinent 1995b; White and MacPhee 2001 |
| Megalocninae (<i>Megalocnus</i> and <i>Parocnus</i>) | <i>Bradypus</i> | South America | | ≥33–34? | MacPhee and Iturralde-Vinent 1995b; White and MacPhee 2001 |
| Soricomorpha | | | | | |
| <i>Solenodon</i> | Eulipotyphlan insectivores (Talpidae + (Erinaceidae + Soricidae) | Proto-Antilles plus North America | 76 (72–81) | | Roca et al. 2004 |
| <i>Nesophontes</i> | Soricidae? | Unknown | | | Asher 1999, 2005; Asher, Emry, and McKenna 2005 |
| Rodentia | | | | | |
| Capromyidae (+ Hep-taxodontidae?) | <i>Clyomys</i> + <i>Euryzygomatomys</i> (<i>Myocasto</i> ?) | South America | 18 (11–27) | ≥17.5–18.5 | Galewski et al. 2005; MacPhee, Iturralde-Vinent, and Gaffney 2003; Woods, Borroto, and Kilpatrick 2001 |
| Heteropsomyinae (<i>Boromys</i> , <i>Brotomys</i> and <i>Heteropsomys</i>) | Mainland echimyd rodents/ capromyids | South America/ Greater Antilles | | | Wilson and Reeder 2005; Woods, Borroto, and Kilpatrick 2001 |
| " <i>Megalomys</i> " <i>audreyae</i> | Unknown | South America? | | | Turvey et al. 2010 |

(continued)

Table 9.2 (continued)

| Antillean lineage | Closest mainland relatives | Inferred geographic origin | Molecular divergence (Ma) | Fossil divergence (Ma) | Sources |
|--|---|---|---------------------------|------------------------|---------------------------|
| <i>Megalomys desmarestii</i> and <i>luciae</i> | <i>Sigmodontomys aphrastus</i> | South America | | | Turvey et al. 2010 |
| <i>Oligoryzomys victus</i> | Other <i>Oligoryzomys</i> spp. | South America | | | Turvey et al. 2010 |
| <i>Oryzomys antillarum</i> | <i>Oryzomys couesi</i> | Mesoamerica | | | Morgan 1993 |
| <i>Pennatomys nivalis</i> | <i>Oryzomyini</i> "Clade D" (<i>Aegialomys</i> , <i>Amphinctomys</i> , <i>Melanomys</i> , <i>Nectomys</i> + <i>Sigmodontomys</i>) | South America | | | Turvey et al. 2010 |
| Primates | | | | | |
| <i>Xenotrichini</i> | <i>Callicebus</i> | South America | | ≥17.5–18.5 | MacPhee and Horovitz 2004 |
| Chiroptera | | | | | |
| <i>Nyctiellus</i> , <i>Chilonatalus</i> , <i>Natalus</i> | Mainland Natalidae | Equivocal: Eurasia/ North America | 50 (45–56) | | Teeling et al. 2005 |
| <i>Mormoops blainvilliei</i> | <i>Mormoops megalophylla</i> | Equivocal: Meso-america/northern South America/ West Indies | 15 (11–24) | | Dávalos 2006, 2010 |
| <i>Mormoops magna</i> | <i>Mormoops megalophylla</i> | Unknown | | | Silva-Taboada 1974 |
| <i>Pteronotus parnellii</i> sensu lato (Antillean spp.) | <i>Pteronotus parnellii</i> sensu lato (mainland spp.) | Equivocal: Mesoamerica/ northern South America | 5 (3–8) | | Dávalos 2006, 2010 |

Table 9.2 (continued)

| Antillean lineage | Closest mainland relatives | Inferred geographic origin | Molecular divergence (Ma) | Fossil divergence (Ma) | Sources |
|---|---|---|---------------------------|------------------------|--|
| <i>Pteronotus pristinus</i> <i>Pteronotus quadridens</i> and <i>macleanii</i> | <i>Pteronotus parnellii</i> <i>Pteronotus davyi</i> and <i>P.</i> <i>gymnonotus</i> | Unknown Equivocal: Mesoamerica/ northern South America/Cuba/ Jamaica | 14 (9–21) | | Simmons and Conway 2001 Dávalos 2006, 2010 |
| <i>Desmodus puntajudensis</i> | <i>Desmodus stocki</i> and <i>D.</i> <i>archaeodaptes</i> | North America | | | Suárez 2005 |
| <i>Macroton waterhousii</i> sensu lato (Antillean spp.) | <i>Macroton waterhousii</i> sensu lato (mainland sp.) | Mexico | | | Fleming, Murray, and Carstens 2010 |
| <i>Palynophil</i> (<i>Erophylla</i> , <i>Phyllonycteris</i> , <i>Brachy-</i> <i>phylla</i>) | <i>Glossophaga</i> | Equivocal: Meso- america/northern South America/ West Indies | 17 (12–26) | | Dávalos 2010 |
| <i>Monophyllus</i> | <i>Glossophaga</i> | Equivocal: Meso- america/northern South America/ West Indies | 14 (10–22) | | Dávalos 2010 |
| <i>Sturnira thomasi</i> | <i>Sturnira luisi</i> sp. complex | Northern South America | | | Villalobos and Valerio 2002; C. Iudica, pers. comm. |
| <i>Chiroderma improvisum</i> | <i>C. villosum</i> | Northern South America | | | Baker et al. 1994 |
| <i>Artibeus anthonyi</i> | Other <i>Artibeus</i> | Unknown | | | based on systematics—see Simmons 2005 |

(continued)

Table 9.2 (continued)

| Antillean lineage | Closest mainland relatives | Inferred geographic origin | Molecular divergence (Ma) | Fossil divergence (Ma) | Sources |
|--|--|---|---------------------------|------------------------|---|
| <i>Stenodermatina</i> : <i>Arctops</i> , <i>Ariteus</i> , <i>Cubanactris</i> , <i>Phyllips</i> , <i>Stenoderma</i> | <i>Artibeus</i> | Equivocal: Meso- america/northern South America/ West Indies | 10 (7–16) | | Dávalos 2007, 2010 |
| <i>Myotis dominicensis</i> , and <i>martiniensis</i> | <i>M. atacamensis</i> , <i>M. yuman-</i> <i>ensis</i> and <i>M. velifer</i> | Neotropical | 4 (3–5) | | Stadelmann et al. 2007 |
| <i>Eptesicus guadeloupensis</i> | <i>E. fuscus</i> sp. complex | Unknown | | | Jones et al. 2002 |
| <i>Lasiurus degelidus</i> | <i>L. seminolus</i> | North America | | | Baker et al. 1988 |
| <i>Lasiurus insularis</i> | <i>L. ega</i> and <i>L. intermedius</i> | North America (in- cluding Mexico) | | | Morales and Bickham 1995 |
| <i>Lasiurus minor</i> | <i>L. borealis</i> , <i>L. blossvillii</i> , and <i>L. seminolus</i> | North America | | | based on systematics—see Sim- mons 2005 |
| <i>Lasiurus pfeifferi</i> | <i>L. seminolus</i> | North America | | | Morales and Bickham 1995 |
| <i>Nycticeius cubanus</i> | <i>Nycticeius humeralis</i> | North America | | | inferred from systematics—see Simmons 2005 |
| <i>Mormopterus minutus</i> | <i>M. phrudus</i> and <i>M.</i> <i>kalinowskii</i> | South America | | | Jones et al. 2002 |

been used recently, but these methods used neither branch lengths (and hence dates — Ree and Smith 2008) nor accounted for environmental change in areas over time (Yesson and Culham 2006). The use of character-mapping methods that do account for branch lengths seems a logical next step in phylogeny-based biogeography, because there is greater probability of change over long branches than over short branches (e.g., Brumfield and Edwards 2007; McGuire et al. 2007). Molecular dating estimates place the earliest divergence of Caribbean clades as far back as the Mesozoic (Roca et al. 2004), so the net effect of applying these methods might be to increase uncertainty on the geographic origin, mechanism of range expansion, and subsequent diversification of mammals. Greater uncertainty might be more consistent with the dynamic geological history and complex biotic history of the region than a single all-encompassing dispersal or vicariance model.

Second, a similar reassessment of molecular divergence dates is in order, as their uncertainty is often large. Rather than confirm a particular date, molecular divergence dates can only exclude periods of time, such as when GAARlandia would have existed. There are many dating methods, and most rely on hard boundaries set by the date of last occurrence as inferred from the fossil record (Rutschmann 2006). There is also uncertainty associated with the stratigraphy of the fossils used in these calibrations, a fact not always considered in molecular analyses. A minimal requirement for reporting molecular divergence dates should be a sensitivity analysis of the dates to the fossils available (Dávalos 2010), the use of soft boundaries to account for stratigraphic uncertainty (Yang and Rannala 2006), and the use of a frequency distribution rather than a point estimate of the age of each fossil calibration (Drummond et al. 2006). Divergence dates varied up to 10% depending on parameters modeling the age of the root of a clade in a sensitivity analysis of molecular dates for Caribbean mammals (Dávalos 2010). If the biogeographic hypothesis being tested requires precise divergence times, sensitivity analyses could reveal greater variation, thereby increasing uncertainty in biogeographic inference.

Third, what is the appropriate null for testing historical biogeography? At the core of the vicariance versus dispersal debate is the struggle to define the null model of biogeography. This choice is crucial. Individual phylogenies can simultaneously be congruent with vicariance and dispersal hypotheses because both processes can give rise to indistinguishable patterns. Congruence in biogeographic patterns between phylogenies is taken to indicate vicariance, another way of saying that vicariance should be the null hypothesis. This makes

intuitive sense, but it ignores the possibility of congruent dispersal. Conversely, dispersal as null hypothesis is difficult to test because it requires somehow testing the predictions of isolated events across different lineages.

One quantitative approach to dispersal, the equilibrium theory of island biogeography (MacArthur and Wilson 1963), has been largely overlooked in discussions of West Indian mammal biogeography despite the early role of Caribbean continental-shelf islands in developing the theory (Koopman 1958). One early island biogeography analysis calibrated species-area curves with extant Caribbean bats (Griffiths and Klingener 1988), without estimating colonization or extinction rates from the data. Another application included both extinct and extant mammals to calibrate species-area curves, and calculated extinction and immigration rates based on then-available phylogenies and rough estimates of colonization times (Morgan and Woods 1986).

Island biogeographic analyses of Caribbean mammals have been limited, perhaps because paleontologists, phylogenetic systematists, and ecologists have questioned the central tenets of island biogeography, particularly as it applies over evolutionary history (Brown and Lomolino 2000; Heaney 2000, 2007; Olson and James 1982; Steadman 1995). The equilibrium theory of island biogeography has been criticized because: (1) both extant and extinct island faunas reveal many instances of nonequilibrium; (2) the theory reduces individual islands to their isolation and area; and (3) by reducing individual species into interchangeable units, the theory ignores the differences in speciation, extinction, and colonization rates arising from a species' characteristics. But it is precisely the expectation of equilibrium and factoring out of phylogeny that makes island biogeography appropriate as a null model for quantitative tests of dispersal. If periods of high dispersal are driven by lowered sea levels, then immigration rates should not be uniform but instead show nonequilibrium dynamics with peaks around glacial periods. Changes in sea level should also dictate the size of islands, producing higher rates of extinction during periods of high sea levels. This approach has been used to analyze community assembly in Lesser Antillean birds (Ricklefs and Bermingham 2001), identifying a rise in colonization rate or a mass extinction event before the last glaciation.

Analyzing dispersal in the framework of island biogeography would complement, not replace, vicariance analyses. Vicariance models are appropriate null hypotheses when paleoclimate or paleogeographic reconstructions indicate continuous habitats at certain periods (e.g., between Grand Terre and Basse Terre in Guadeloupe, or between the Exumas in the Bahamas). Choosing a dispersal or vicariance hypothesis as a null model will depend on geological

data. When geological data indicate a plausible mechanism of vicariance, this can be the null model. In the absence of such data, and based on island biogeographic theory, dispersal becomes the null model, and quantitative tests based on dated phylogenies become possible.

9.3 The New: Population Genetics of West Indian Mammals

Historical biogeography has traditionally focused on the study of endemic taxa and their origins (Dávalos 2004b; Kluge 1989; Page and Lydeard 1994); the overlapping ranges of endemics help to outline areas of endemism (Platnick 1991). With the increasing use of molecular markers in biogeography, it has become possible to analyze patterns of population expansion, stasis, or contraction, as well as origins of island populations (Lessa, Cook, and Patton 2003; Russell et al. 2007; Russell, Goodman, and Cox 2008; Russell et al. 2008b). In the Antilles, only two population-genetic studies, for *Artibeus jamaicensis* and *Macrotus waterhousii*, have encompassed both continental and island populations, with different results in each case (Fleming, Murray, and Carstens 2010; Larsen et al. 2007). The population structure of the widespread frugivorous phyllostomid *Artibeus jamaicensis* has been studied using mitochondrial restriction sites and RFLP (restriction fragment length polymorphisms) mapping (Phillips et al. 1989; Phillips et al. 1991; Pumo et al. 1988), mitochondrial sequences (Carstens et al. 2004; Fleming, Murray, and Carstens 2010; Pumo et al. 1988; Pumo et al. 1996), and, more recently, amplified fragment-length polymorphisms (AFLPs; Larsen, Marchán-Rivadeneira, and Baker 2010). Traditionally, thirteen subspecies of *Artibeus jamaicensis* have been recognized, three—*parvipes*, *jamaicensis*, and *schwartzi*—confined to the West Indies (Koopman 1994; Simmons 2005). Large amounts of genetic variation were detected in the earliest genetic analyses of *Artibeus jamaicensis* (e.g., Phillips et al. 1989; Pumo et al. 1988), with highly divergent haplotypes found coexisting in the Lesser Antilles (Carstens et al. 2004; Pumo et al. 1996).

Multiple hypotheses have been proposed to account for these highly divergent haplotypes: (1) hybridization between differentiated subspecies of a single species (Jones 1989); (2) relictual diversity from an ancient invasion that was subsequently swamped by new arrivals (Phillips et al. 1989; Pumo et al. 1996); and (3) a ring species arriving from the confluence in the Lesser Antilles of an eastward Mesoamerican invasion and a northward South American invasion (Carstens et al. 2004). An analysis of mitochondrial sequences offered an alternative interpretation: species-level recognition for three reciprocally-

monophyletic clades, two of them sympatric in St. Kitts, Nevis, Montserrat, St. Lucia, and Barbados, and all three present in St. Vincent (Larsen et al. 2007). The proposed species limits did not follow the traditionally recognized subspecies, but they accommodate the clades obtained in analyses of the mitochondrial cytochrome-b gene. This last interpretation implied that populations of *Artibeus jamaicensis*, *A. planirostris*, and *A. schwartzi* were cryptic in the Lesser Antilles and have converged on a similar phenotype, despite divergent phylogenetic and geographic origins (Larsen et al. 2007). A subsequent study of nuclear markers revealed that patterns of genomic variation in *A. schwartzi* are consistent with this population originating through hybridization between *A. jamaicensis* and *A. planirostris* (Larsen, Marchán-Rivadeneira, and Baker 2010). Hybridization would have been possible by imperfect reproductive isolation between the two parent species. The biogeographic origin of the parent species would indicate an eastward invasion of *A. jamaicensis* from Mesoamerica, with *planirostris* originating in South America. Targeted studies are needed to determine if these populations have recently grown, as expected from recent colonization leading to hybridization.

While *Artibeus jamaicensis* appears to maintain gene flow with mainland populations on Mesoamerica, Antillean populations of the insectivorous phyllostomid *Macrotus waterhousii* seem completely isolated from the mainland counterparts (Fleming, Murray, and Carstens 2010). Although *Macrotus waterhousii* has been thought to comprise one widespread population from Mexico through the Bahamas and Greater Antilles, rapidly evolving mitochondrial sequences represent at least four reciprocally monophyletic groups, each corresponding to islands or island banks. These populations are effectively isolated, without shared haplotypes. Morphology-based systematics would suggest a very recent colonization from Mexico (Griffiths and Klingener 1988; Koopman 1989), but the molecular data showed no evidence of recent population expansion and dozens of fixed differences with respect to the mainland population, indicating a more ancient colonization date than previously thought (Fleming, Murray, and Carstens 2010). As with *Artibeus*, additional markers and more research on the ecology and morphology of *Macrotus* are needed to understand how these highly divergent allopatric populations maintain their nearly identical morphology.

Population genetic analyses are available for only three other phyllostomid endemics: flower-visiting *Brachyphylla* (Carstens et al. 2004; Dávalos 2004a) and *Erophylla* (Fleming and Murray 2009; Fleming, Murray, and Carstens 2010) and the frugivorous *Ardops* (Carstens et al. 2004). Mitochondrial sequences of *Brachyphylla* revealed the reciprocal monophyly of *Brachyphylla nana* populations

on Cuba and Grand Cayman versus Hispaniola and Middle Caicos (Dávalos 2004a). Conversely, detailed analyses of the population genetic structure of *Brachyphylla cavernarum* showed no evidence of interisland monophyly and instead were consistent with incomplete lineage sorting following recent expansion into the Lesser Antilles from Puerto Rico (Carstens et al. 2004). A mirror image of this pattern of stasis in one part of the range and expansion in another is shown by *Erophylla*, whose western populations (Bahamas, Cuba, Caymans, and Jamaica) have expanded recently, in contrast with the stable populations of Hispaniola and Puerto Rico (Fleming, Murray, and Carstens 2010). Unlike *Brachyphylla*, *Erophylla* populations have not attained reciprocal monophyly, indicating much more recent isolation and only incipient speciation. In contrast with these two species, which maintain gene flow across most shallow water barriers, the Lesser Antillean *Ardops* is relatively well-differentiated on individual islands. Coalescent analyses could not reject island monophyly across the northern Antilles (Carstens et al. 2004).

None of these endemic genera — *Brachyphylla*, *Erophylla*, and *Ardops* — have a sister genus on the mainland, and *Brachyphylla cavernarum* and *Ardops* originated west of their current range. This can be inferred for *Brachyphylla* from its basal relatives in Hispaniola and Cuba (Dávalos 2004a), and for *Ardops* from its common ancestry with the Jamaican *Ariteus* (Dávalos 2007). In contrast, in *Erophylla*, it is the western populations that are recent, likely as a result of sea-level changes that made the banks of the Bahamas and Cuba much larger than at present (Fleming, Murray, and Carstens 2010). *Brachyphylla* and *Erophylla* share a common ancestor with the (mostly) Mesoamerican *Glossophaga* and *Leptonycteris*, indicating an origin in that Neotropical subregion. *Ardops* could either be part of an Antillean endemic radiation or the descendent of an ancient mainland colonizer (table 9.1; Dávalos 2007, 2010).

Population genetic approaches are needed in Caribbean mammal biogeography to close two gaps in higher-level analyses: to delimit species and identify species complexes and to expand biogeographic understanding of widespread species. One example of the first gap is the recent revision of *Artibeus jamaicensis*. Although superficially similar, the island populations hitherto called *Artibeus jamaicensis* have complex evolutionary histories and rightfully should be called a species complex. In-depth examination of Antillean *Natalus* has revealed isolated populations on Cuba, Jamaica, and Hispaniola (Dávalos 2005; Tejedor, Tavares, and Silva-Taboada 2005). The last time these ancient lineages exchanged genes was 1.3 million years ago (Dávalos 2010). Other populations, including *Lasiurus* (Morales and Bickham 1995), *Eptesicus*, and *Tadarida*, remain to be studied and might also reveal much greater diversity than currently rec-

ognized. Although related to the gap in species delimitation, the biogeography of widespread species is indispensable to understand community assembly, current structure, and to prioritize areas for conservation (Gannon et al. 2005; Rodríguez Durán and Kunz 2001). By identifying routes of colonization and providing estimates of the age of colonization, population genetic studies can help resolve whether recent colonizers have outcompeted and replaced endemic lineages (e.g., *Artibeus* replacing *Brachyphylla* in Jamaica; Koopman and Williams 1951), if the absence of a species on an island indicates extinction or failure to colonize (e.g., *Natalus* in Puerto Rico; Tejedor 2006), or whether colonization patterns are similar among ecologically distinct genera (Fleming, Murray, and Carstens 2010).

9.4 The Recently Extinct: Caribbean Mammal Species Losses

In addition to its importance in developing key ideas in biogeography, the Antillean biota has also been used to identify fundamental ecological processes of faunal turnover and extinction (Ricklefs 1970; Ricklefs and Bermingham 2001; Ricklefs and Cox 1972), and the region's historical land mammal fauna has been the subject of considerable investigation into mammalian extinction dynamics. The Tertiary terrestrial fossil record of the insular Caribbean is still highly incomplete, posing a major obstacle to understanding ancient patterns of colonization and biogeography across the region (MacPhee, Iturralde-Vinent, and Gaffney 2003; Portell, Donovan, and Domning 2001). Conversely, from the mid-nineteenth century onwards (Castro 1864; Leidy 1868), investigation of Quaternary deposits on numerous Caribbean islands has revealed increasingly diverse assemblages of recently extinct mammal species, containing both megafaunal and pygmy arboreal sloths, an endemic Caribbean clade of primates, and extensive insular radiations of rodents and insectivores, as well as numerous bats (see appendix 9.1). Most Quaternary fossils from the Caribbean have been reported from cave deposits, but additional material is also known from asphalt seeps and sinkholes (Iturralde-Vinent et al. 2000; Steadman et al. 2007).

It is still difficult to generate an accurate estimate of the diversity of the prehuman Caribbean mammal fauna. Extinct Late Quaternary mammal species continue to be discovered from all of the major Caribbean islands (e.g., MacPhee and Flemming 2003; Mancina and Garcia-Rivera 2005; Rega et al. 2002; Suárez and Díaz-Franco 2003; Turvey, Grady, and Rye 2006), and large numbers of additional species, notably Lesser Antillean oryzomyine rice rats,

remain undescribed (see appendix 9.1), often because they have been studied only by zooarchaeologists (Newsom and Wing 2004; Pregill, Steadman, and Watters 1994; Turvey 2009; Turvey et al. 2010). There are also major unresolved problems with available taxonomies for extinct Caribbean mammals, notably for Cuban and Hispaniolan capromyid rodents, and many supposed species are likely to represent synonyms (Díaz-Franco 2001; Rímoli 1976). However, despite these taxonomic uncertainties, over 100 species or island populations of volant and nonvolant land mammals can be interpreted as having become extinct during the Late Quaternary (Morgan 2001; Turvey 2009). Nevertheless, it is clear that the Caribbean mammal fauna has experienced the highest level of recent species loss of any mammal fauna in the world, both for the period following 1500 AD and across the entire Holocene (MacPhee 2008; MacPhee and Flemming 1999; Morgan 2001; Turvey 2009). For example, the Lesser Antillean Windward and Leeward Islands alone have lost approximately 20 island populations of oryzomyine rice rats, many of which were probably distinct species; these rice rat extinctions are equivalent in magnitude to the much better known historical-era loss of marsupials and rodents in Australia (Johnson 2006; MacPhee and Flemming 1999; Turvey 2009; Turvey et al. 2010), but they comprise only part of the much greater series of land mammal extinctions so far documented across Caribbean islands.

Investigation of the Late Quaternary Caribbean mammal mass extinction event may provide novel insights into the putatively human-caused, Late Pleistocene megafaunal extinctions in North America (see Barnosky et al. 2004; Martin 1984; Martin and Steadman 1999), and a wider base for developing appropriate conservation management plans for surviving Caribbean hutias and insectivores, almost all of which are threatened with extinction (International Union for Conservation of Nature [IUCN] 2008). As with megafaunal extinction on the mainland, two major competing hypotheses have been proposed to account for Quaternary Caribbean mammal extinctions. Pregill and Olson (1981) noted that many now-extinct terrestrial vertebrates (particularly reptiles and birds) present in Late Quaternary deposits in the West Indies were characteristic of xeric habitats (arid savanna, grassland, and scrub forest) and obligate xerophiles that are still extant had wider distributions in the Recent fossil record. Nonanthropogenic environmental change at the Pleistocene-Holocene boundary at the end of the last glaciation, notably a large-scale shift to more mesic forested habitats, may have been a major driver of faunal extinction in the region. This hypothesis was adopted to explain West Indian bat extinctions by Morgan (2001), who demonstrated that most regional bat population or species

losses affected obligate or facultative cave-dwelling species—these extinctions may therefore have been driven by changes in cave microclimates or the inundation of large cave systems by rising sea levels or erosional collapse during the Pleistocene-Holocene climatic transition. In contrast, other authors have considered that most or all of the region's mammal extinctions occurred later in time, and were instead driven by mid-late Holocene anthropogenic actions such as overhunting, habitat destruction, and introduction of exotic predators, competitors, and diseases following the arrival of humans in the Caribbean around 6000 BP (Burney, Burney, and MacPhee 1994; MacPhee 2008; Morgan and Woods 1986; Wilson 2007).

The question of the timing and causation of Caribbean mammal extinctions is truly interdisciplinary, with potential contributions from paleontology, zoology, and archaeology. However, analyses based on approaches such as population genetics have not yet been able to provide useful insights into this question, in part because of the continuing difficulty of extracting DNA from Caribbean Quaternary specimens, as well as the challenge of obtaining sufficient genetic samples from extant but threatened and cryptic land mammal species. Distinguishing between the two extinction hypotheses requires establishing “last-occurrence” dates for extinct species based on historical, radiometric, or constrained stratigraphic data; meaningful extinction chronologies are lacking for most of the region's extinct mammal fauna (MacPhee 2008; MacPhee, Ford, and McFarlane 1989). Some last-occurrence dates are available for a handful of mammal species that persisted into the nineteenth or twentieth centuries (e.g., *Megalomys* rice rats and the hutia, *Geocapromys thoracatus*; Allen 1942; Clough 1976), but there are few records from earlier centuries and they seldom identify particular species with any accuracy (MacPhee and Fleagle 1991; Miller 1929a). Dubious twentieth-century reports of several now-extinct mammal species have generated additional confusion (MacPhee et al. 1999; Miller 1930; Raffaele 1979; Woods, Ottenwalder, and Oliver 1985). Collagen degradation under moist, humid subtropical conditions has hindered radiometric dating of even young subfossil material (Turvey et al. 2007), and direct radiometric last-occurrence dates are published for 11 extinct Caribbean insular mammal species. A wider series of terminus post quem dates have been generated with reasonable confidence from the apparent stratigraphic co-occurrence of extinct species with introduced mammals (particularly *Rattus rattus*) in superficial cave sediments, although this approach may also be problematic and open to alternative interpretations (MacPhee and Flemming 1999; Woods and Ottenwalder 1992). Information on key variables such as pre-Columbian hu-

man population densities and prehistoric levels of habitat conversion is also highly speculative (e.g., Watts 1987), and evidence on past human exploitation of most native Caribbean mammal species, especially large-bodied mammals, is typically lacking.

Despite these obstacles, stratigraphic studies and applied dating efforts since the 1980s (e.g., Steadman, Pregill, and Olson 1984) have provided direct or indirect evidence that most of the region's Late Quaternary mammal species persisted into the Holocene. These studies have therefore disproved the environmental change hypothesis of Pregill and Olson (1981) as a general explanation for Caribbean mammal extinctions, and have led to the development of a two-stage human-driven extinction model for nonvolant Caribbean land mammals. Although there is evidence for relatively intensive pre-Columbian Amerindian exploitation of some rodents, notably in the Lesser Antilles (Newsom and Wing 2004), many or most of the extinct small- and medium-sized rodent and insectivore species (nesophontid island-shrews, heteropsomyine echimyids, hutias, rice rats), and the Jamaican monkey *Xenothrix mcgregori* are now thought to have survived until around the time of European arrival. Few of these appear to have survived much beyond first European contact (Flemming and MacPhee 1999; MacPhee and Flemming 1999; MacPhee et al. 1999; McFarlane et al. 2000; Turvey et al. 2007; Turvey 2009).

It is probable that the extinction of most of the smaller nonvolant land mammal fauna was driven by interactions with *Rattus rattus*, which reached the Caribbean by the early 1500s, although the subsequent deliberate introduction of the mongoose *Herpestes javanicus* and massive forest clearing for sugarcane and other crops were also key drivers in extinctions of some native small mammals. Although further data are required to clarify the ecological mechanism(s) by which exotic *Rattus* species cause extinctions, rats have been implicated in the disappearance of small mammals and many other taxa on island systems across the world through competition, predation, disease transmission, and habitat modification (Drake and Hunt 2009; Harris 2009; Harris, Gregory, and Macdonald 2006; Harris and Macdonald 2007; Towns, Atkinson, and Daugherty 2006; Wyatt et al. 2008).

Recent direct radiometric studies have also demonstrated the protracted survival of Caribbean large-bodied mammals (MacPhee, Iturralde-Vinent, and Vazquez 2007; Steadman et al. 2005; Turvey et al. 2007), with at least some megalonychid sloths (*Megalocnus rodens*, *Neocnus comes*) and heptaxodontid rodents (*Elasmodontomys obliquus*) apparently persisting for millennia beyond first human arrival in the Greater Antilles. These taxa apparently became extinct

through attrition, possibly driven by low-level exploitation before Columbus or by indirect factors such as progressive habitat modification—"sitzkrieg"-style events (sensu Diamond 1989)—rather than through a rapid "blitzkrieg"-style overkill following Amerindian colonization.

This two-stage pattern of extinction—protracted survival after human arrival, but eventually leading to extinction—may reflect either different levels of human exploitation of large-bodied and small-bodied mammal taxa or the intrinsically higher vulnerability of larger-bodied species to human impacts due to size-dependent scaling of ecological and life-history traits (Cardillo et al. 2005). The delayed extinction of even the large-bodied Caribbean land mammals contrasts markedly with rapid extinctions of other large-bodied insular taxa overexploited by early hunters (e.g., New Zealand moas; Holdaway and Jacomb 2000), and instead resembles the protracted late Holocene declines of large-bodied mammals on Madagascar (Burney et al. 2004). Several extinct Caribbean bats are known to have persisted into the Holocene (Jiménez Vázquez, Condis, and García 2005; Steadman, Pregill, and Olson 1984), and there is little or no evidence that humans ever consumed bats in the Caribbean (Mickleburgh, Waylen, and Racey 2009). It should be noted that many Caribbean bats (e.g., *Natalus*) are severely threatened by invasive mammals such as feral cats (Tejedor et al. 2005) and by loss of foraging habitat through deforestation (Gannon et al. 2005). These anthropogenic factors may also have contributed to past bat extirpations and extinctions in the region. Large congregations of cave-roosting bats may enhance their vulnerability to introduced predators such as rats, cats, and mongooses. This risk becomes particularly acute as natural or anthropogenic change confines populations to single caves (e.g., *Natalus* in Cuba or Jamaica; Tejedor, Silva-Taboada, and Rodríguez Hernández 2004; Tejedor, Tavares, and Silva-Taboada 2005).

Although most Caribbean land mammal extinctions have been caused by prehistoric and historic-era human impacts during an interval of relatively modest environmental change, there is some evidence to suggest that other regional extinction events may have occurred as a result of environmental change before humans reached the islands. Uranium-series disequilibrium dates support a nonanthropogenic Late Pleistocene extinction for the giant hutia *Amblyrhiza inundata*, probably caused by inundation of the Anguilla Bank at the end of the last glaciation (McFarlane, MacPhee, and Ford 1998). Pre-Holocene extinctions have also been postulated for other species, including the Jamaican giant rodent *Clidomys osborni*, the Puerto Rican rodent *Puerti-*

comys corozalus, and the Cuban monkey *Paralouatta varonai*, on the basis of the heavy fossilization of all known specimens and their absence from well-studied Late Quaternary deposits (MacPhee and Meldrum 2006; MacPhee, Ford, and McFarlane 1989; Morgan and Wilkins 2003; Williams and Koopman 1951). However, the apparent absence of these species may also reflect incomplete palaeontological sampling rather than early extinction. Although none of the Greater Antillean islands experienced catastrophic late Quaternary fluctuations in exposed areas from eustatic changes in sea level, severe climatic events in the Antilles have been postulated for the last interglacial period (McFarlane and Lundberg 2004)—glaciers may even have formed at higher elevations on the largest islands (Schubert and Medina 1982)—with unexplored consequences for the regional fauna. Understanding of Caribbean mammal extinctions is thus still incomplete and in need of further investigation and testing; we expect that the temporal framework for extinctions we have sketched will have to be revised as new data emerge.

9.5 Prospects for the Historical Biogeography of West Indian Mammals

There are three main gaps in our understanding of Antillean historical biogeography: (1) resolving species limits and phylogenetic relationships for several endemic lineages (e.g., hutias, *Lasiurus*); (2) undertaking revisionary morphological and population genetics analyses of widespread lineages (e.g., *Mormoops megalophylla* and *Eptesicus fuscus*); and (3) combining phylogenetics, population genetics, and ecological biogeography with paleontology, zoology, and archaeology to detail the history of both colonization and extinction across Caribbean communities. Despite recent progress in resolving relationships among the majority of the endemic West Indian lineages (e.g., Dávalos 2007; Horovitz and MacPhee 1999; White and MacPhee 2001), the largest radiation of nonvolant mammals—the hutias—remains only partly resolved (Woods, Borroto, and Kilpatrick 2001). Revisionary work (e.g., Turvey, Grady, and Rye 2006) has demonstrated the need to examine species limits of both extant and fossil material. This also holds for lineages with fewer species, such as *Lasiurus*, that have never been included simultaneously in a phylogenetic analyses and whose phylogenetic relationships are still poorly understood (Simmons 2005). Quantifying rates of colonization, speciation, and extinction over time requires as many phylogenies and instances of colonization as possible, and a

phylogeny of hutias would add the largest number of nonvolant species in the region. The phylogenies of these taxa would be much more than single data points in historical biogeography—they would illuminate the mechanisms of dispersal from the mainland, interisland colonization, and further clarify drivers of extinction risk.

A second remaining gap in Caribbean mammal biogeography involves widespread species and species complexes whose population genetic structure and geographic origin remain largely unexplored. Both morphological measurements and the few mitochondrial sequences available suggest that insular populations of *Pteronotus parnellii* constitute distinct species (Dávalos 2006; Lewis-Oritt, Porter, and Baker 2001). *Mormoops megalophylla* requires similar revisionary work to determine if the fossils found throughout North America, the West Indies, and northern South America are conspecific (Czaplewski and Cartelle 1998; Silva-Taboada 1974). Although population structure in large, vagile, wide-ranging species such as *Tadarida brasiliensis* or *Eptesicus fuscus* should be detectable only at very broad geographic scales, the distances and depths separating West Indian and mainland populations might still prove to be significant barriers to gene flow (Russell and McCracken 2006; Russell, Medellín, and McCracken 2005).

Closing the third gap will require extending population genetic studies to continental populations, and using ecological modeling, radiometric dating of fossils and subfossils, and even sequencing genetic samples from extinct populations. Despite several recent studies tackling the population genetics and phylogeography of West Indian bats (e.g., Carstens et al. 2004; Fleming and Murray 2009; Fleming, Murray, and Carstens 2010; Larsen et al. 2007; Larsen, Marchán-Rivadeneira, and Baker 2010), there has been no research investigating both population genetic structure and timing of colonization in widespread bats (e.g., Russell, Goodman, and Cox 2008). By combining timing of divergence or colonization from population genetics analyses with modeling of the climatic niche of the populations in question, new insights on the relationship between climate change, colonization, and persistence are possible (e.g., Carnaval and Moritz 2008; Carnaval et al. 2009). Dating fossil remains (McFarlane and Lundberg 2004), and even the use of ancient DNA from subfossils (Shapiro et al. 2004), would refine the timescale of decline and extinction of populations. These synthetic analyses would test climate change as the primary driver of extinction in the West Indies, particularly among bats (Morgan 2001). By directly evaluating the availability of suitable habitat for different species under alternative climate conditions, such studies would help clarify the relative roles

of overexploitation and habitat change in past Caribbean mammal extinctions (MacPhee, Iturralde-Vinent, and Vazquez 2007; Turvey et al. 2007).

Both traditional systematic approaches (e.g., to resolve species limits using morphological data, and syntheses of more novel methods) along with combining historical and ecological biogeography with radiometric dating of fossil remains, will be necessary to resolve the outstanding questions on the geographic origins and drivers of extinction in this biota. After reviewing the century-long history of the vicariance versus dispersal debate, we conclude that quantitative approaches, including equilibrium models hitherto absent from most historical analyses, can better serve as null hypotheses than single-mechanism hypotheses such as dispersal or vicariance.

Literature Cited

- Allen, G. M. 1911. "Mammals of the West Indies." *Bulletin of the Museum of Comparative Zoology* 54:175–263.
- . 1942. *Extinct and Vanishing Mammals of the Western Hemisphere with the Marine Species of All the Oceans*. Washington, DC: American Committee for International Wildlife Protection, Special Publication, 11.
- Alvarez, L. W., W. Alvarez, F. Asaro, and H. V. Michel. 1980. "Extraterrestrial Cause for the Cretaceous Tertiary Extinction." *Science* 208:1095–108.
- Anthony, H. E. 1918. "The Indigenous Land Mammals of Porto Rico, Living and Extinct." *Memoirs of the American Museum of Natural History* 2:331–435.
- Asher, R. J. 1999. "A Morphological Basis for Assessing the Phylogeny of the 'Tenrecoidea' (Mammalia, Lipotyphla)." *Gladistics* 15:231–52.
- . 2005. "Insectivoran-Grade Placentals." In *The Rise of Placental Mammals: Origins and Relationships of the Major Extant Clades*, edited by K. D. Rose and J. D. Archibald, 50–70. Baltimore: Johns Hopkins University Press.
- Asher, R. J., R. J. Emry, and M. C. McKenna. 2005. "New Material of *Centetodon* (Mammalia, Lipotyphla) and the Importance of (Missing) DNA Sequences in Systematic Paleontology." *Journal of Vertebrate Paleontology* 25:911–23.
- Baker, R. J., and H. H. Genoways. 1978. "Zoogeography of Antillean Bats." *Special Publication, Academy of Natural Sciences of Philadelphia* 13:53–97.
- Baker, R. J., J. C. Patton, H. H. Genoways, and J. W. Bickham. 1988. "Genic Studies of *Lasiurus* (Chiroptera: Vespertilionidae)." *Occasional Papers, Museum of Texas Tech University* 117:1–15.
- Baker, R. J., V. A. Taddei, J. L. Hudgeons, and R. A. Van Den Bussche. 1994. "Systematic Relationships within Chiroderma (Chiroptera: Phyllostomidae) Based on Cytochrome b Sequence Variation." *Journal of Mammalogy* 75:321–27.
- Barbour, T. 1916. "Some Remarks upon Matthew's 'Climate and Evolution.'" *Annals of the New York Academy of Sciences* 27:1–15.
- Barnosky, A. D., P. L. Koch, R. S. Feranec, S. L. Wing, and A. B. Shabel. 2004. "Assessing the Causes of Late Pleistocene Extinctions on the Continents." *Science* 306:70–75.
- Borotto-Páez, R., C. A. Woods, and C. W. Kilpatrick. 2005. "Sistemática de las Jutías de las Antillas (Rodentia, Capromyidae)." In *Proceedings of the International Symposium Insular Vertebrate Evolution: the Palaeontological Approach*, edited by J. A. Alcover and P. Bover, 33–50. Palma de Mallorca: Monografies de la Societat d'Història Natural de les Balears, 12.
- Brown, J. H., and M. V. Lomolino. 2009. "Concluding Remarks: Historical Perspective and the Future of Island Biogeography Theory." *Global Ecology and Biogeography* 9:87–92.
- Brumfield, R. T., and S. V. Edwards. 2007. "Evolution into and out of the Andes: A Bayesian Analysis of Historical Diversification in *Thamnophilus antshrikes*." *Evolution* 61:346–67.
- Burney, D. A., L. P. Burney, L. R. Godfrey, W. L. Jungers, S. M. Goodman, H. T. Wright, and A. J. T. Jull. 2004. "A Chronology for Late Prehistoric Madagascar." *Journal of Human Evolution* 47:25–63.
- Burney, D. A., L. P. Burney, and R. D. E. MacPhee. 1994. "Holocene Charcoal Stratigraphy from Laguna Tortuguero, Puerto Rico, and the Timing of Human Arrival on the Island." *Journal of Archaeological Science* 21:273–81.
- Cardillo, M., G. M. Mace, K. E. Jones, J. Bielby, O. R. P. Bininda-Emonds, W. Sechrest, C. D. L. Orme, et al. 2005. "Multiple Causes of High Extinction Risk in Large Mammal Species." *Science* 309:1239–41.
- Carnaval, A. C., M. J. Hickerson, C. F. B. Haddad, M. T. Rodrigues, and C. Moritz. 2009. "Stability Predicts Genetic Diversity in the Brazilian Atlantic Forest Hotspot." *Science* 323:785–89.
- Carnaval, A. C., and C. Moritz. 2008. "Historical Climate Modelling Predicts Patterns of Current Biodiversity in the Brazilian Atlantic Forest." *Journal of Biogeography* 35:1187–201.
- Carstens, B. C., J. Sullivan, L. M. Dávalos, P. A. Larsen, and S. C. Pedersen. 2004. "Exploring Population Genetic Structure in Three Species of Lesser Antillean Bats." *Molecular Ecology* 13:2557–66.
- Castro, M. F. de 1864. *De la Existencia de Grandes Mamíferos Fósiles en la Isla de Cuba*. *Anales de la Academia de Ciencias Médicas, Físicas y Naturales de la Habana* 1:17–21.
- Clough, G. C. 1976. "Current Status of Two Endangered Caribbean Rodents." *Biological Conservation* 10:43–47.
- Czaplewski, N. J., and C. Cartelle. 1998. "Pleistocene Bats from Cave Deposits in Bahia, Brazil." *Journal of Mammalogy* 79:784–803.
- Darlington, R. J., Jr. 1938. "The Origin of the Fauna of the Greater Antilles, with Discussion of Dispersal of Animals over Water and through the Air." *Quarterly Review of Biology* 13:274–300.
- Dávalos, L. M. 2004a. "Historical Biogeography of the Antilles: Earth History and Phylogenetics of Endemic Chiropteran Taxa." Unpublished PhD diss., Columbia University, New York.

- . 2004b. "Phylogeny and Biogeography of Caribbean Mammals." *Biological Journal of the Linnean Society* 81:373–94.
- . 2005. "Molecular Phylogeny of Funnel-Eared Bats (Chiroptera: Natalidae), with Notes on Biogeography and Conservation." *Molecular Phylogenetics and Evolution* 37:91–103.
- . 2006. "The Geography of Diversification in the Mormoopids (Chiroptera: Mormoopidae)." *Biological Journal of the Linnean Society* 88:101–18.
- . 2007. "Short-Faced Bats (Phyllostomidae: Stenodermatina): A Caribbean Radiation of Strict Frugivores." *Journal of Biogeography* 34:364–75.
- . 2010. "Earth History and the Evolution of Caribbean Bats." In *Island Bats: Ecology, Evolution, and Conservation*, edited by T. H. Fleming and P. A. Racey, 96–115. Chicago: University of Chicago Press.
- Diamond, J. M. 1989. "Quaternary Megafaunal Extinctions: Variations on a Theme by Paganini." *Journal of Archaeological Science* 16:167–75.
- Díaz-Franco, S. 2001. "Situación taxonómica de *Geocapromys megas* (Rodentia: Capromyidae)." *Caribbean Journal of Science* 37:72–80.
- Drake, D. R., and T. L. Hunt. 2009. "Invasive Rodents on Islands: Integrating Historical and Contemporary Ecology." *Biological Invasions* 11:1483–87.
- Drummond, A. J., S. Y. W. Ho, M. J. Phillips, and A. Rambaut. 2006. "Relaxed Phylogenetics and Dating with Confidence." *PLoS Biology* 4:e88.
- Edwards, A. W. F., and L. L. Cavalli-Sforza. 1964. "Reconstruction of Evolutionary Trees." In *Phenetic and Phylogenetic Classification*, edited by V. H. Heywood and J. McNeill, 67–76. London: Systematics Association.
- Fleming, T. H., and K. L. Murray. 2009. "Population and Genetic Consequences of Hurricanes for Three Species of West Indian Phyllostomid Bats." *Biotropica* 41:250–56.
- Fleming, T. H., K. L. Murray, and B. C. Carstens. 2010. "Phylogeography and Genetic Structure of Three Evolutionary Lineages of West Indian Phyllostomid Bats." In *Island Bats: Evolution, Ecology, and Conservation*, edited by T. H. Fleming and P. A. Racey, 116–50. Chicago: University of Chicago Press.
- Fleming, C., and R. D. E. MacPhee. 1999. "Redetermination of Holotype of *Isolobodon portoricensis* (Rodentia, Capromyidae), with Notes on Recent Mammalian Extinctions in Puerto Rico." *American Museum Novitates* 3278:1–11.
- Galewski, T., J.-F. Mauffrey, Y. L. R. Leite, J. L. Patton, and E. J. P. Douzery. 2005. "Ecomorphological Diversification Among South American Spiny Rats (Rodentia; Echimyidae): A Phylogenetic and Chronological Approach." *Molecular Phylogenetics and Evolution* 34:601–15.
- Gannon, M. R., A. Kurta, A. Rodriguez Duran, and M. R. Willig. 2005. *Bats of Puerto Rico: An Island Focus and a Caribbean Perspective*. Lubbock: Texas Tech University Press.
- Genoways, H. H., C. J. Phillips, and R. J. Baker. 1998. "Bats of the Antillean Island of Grenada: A New Zoogeographic Perspective." *Occasional Papers, Museum of Texas Tech University* 177:1–28.
- Graham, A. 2003. "Geohistory Models and Cenozoic Paleoenvironments of the Caribbean Region." *Systematic Botany* 28:378–86.

- Grajales Nishimura, J. M., E. Cedillo Pardo, C. Rosales Domínguez, D. J. Moran Zenteno, W. Alvarez, P. Claeys, J. Ruiz Morales et al. 2000. "Chicxulub Impact: The Origin of Reservoir and Seal Facies in the Southeastern Mexico Oil Fields." *Geology* 28:307–10.
- Griffiths, T. A., and D. Klingener. 1988. "On the Distribution of Greater Antillean Bats." *Biotropica* 20:240–51.
- Harris, D. B. 2009. "Review of Negative Effects of Introduced Rodents on Small Mammals on Islands." *Biological Invasions* 11:1611–30.
- Harris, D. B., S. D. Gregory, and D. W. Macdonald. 2006. "Space Invaders? A Search for Patterns Underlying the Coexistence of Alien Black Rats and Galápagos Rice Rats." *Oecologia* 149:276–88.
- Harris, D. B., and D. W. Macdonald. 2007. "Interference Competition between Introduced Black Rats and Endemic Galápagos Rice Rats." *Ecology* 88:2330–44.
- Heaney, L. R. 2000. "Dynamic Disequilibrium: A Long-Term, Large-Scale Perspective on the Equilibrium Model of Island Biogeography." *Global Ecology and Biogeography* 9:59–74.
- . 2007. "Is a New Paradigm Emerging for Oceanic Island Biogeography?" *Journal of Biogeography* 34:753–57.
- Hedges, S. B. 1982. "Caribbean Biogeography: Implications of Recent Plate Tectonic Studies." *Systematic Zoology* 31:518–22.
- . 1996. "Historical Biogeography of West Indian Vertebrates." *Annual Review of Ecology and Systematics* 27:163–96.
- Hedges, S. B., C. A. Hass, and L. R. Maxson. 1992. "Caribbean Biogeography: Molecular Evidence for Dispersal in West Indian Terrestrial Vertebrates." *Proceedings of the National Academy of Sciences, USA* 89:1909–13.
- Heinicke, M. P., W. E. Duellman, and S. B. Hedges. 2007. "Major Caribbean and Central American Frog Faunas Originated by Ancient Oceanic Dispersal." *Proceedings of the National Academy of Sciences, USA* 104:10092–97.
- Hess, H. H. 1962. "History of Ocean Basins." In *Petrologic Studies: A Volume in Honor of A. F. Buddington*, edited by A. E. J. Engel, H. L. James, and B. F. Leonard, 599–620. New York: Geological Society of America.
- Holdaway, R. N., and C. Jacomb. 2000. "Rapid Extinction of the Moas (Aves: Dinornithiformes): Model, Test, and Implications." *Science* 287:2250–54.
- Hooijer, D. A. 1959. "Fossil Rodents from Curaçao and Bonaire." *Studies on the Fauna of Curaçao and Other Caribbean Islands* 9:1–27.
- . 1966. "Fossil Mammals of the Netherlands Antilles." *Archives Néerlandaises de Zoologie* 16:531–32.
- . 1967. "Pleistocene Vertebrates of the Netherlands Antilles." In *Pleistocene Extinctions: The Search for a Cause*, edited by P. S. Martin and H. E. Wright Jr., 399–406. New Haven: Yale University Press.
- Horovitz, I., and R. D. E. MacPhee. 1999. "The Quaternary Cuban Platyrrhine *Paralouatta avaronai* and the Origin of Antillean Monkeys." *Journal of Human Evolution* 36:33–68.
- International Union for Conservation of Nature. (IUCN). 2008. "2008 IUCN Red List of Threatened Species." Available at <http://www.iucnredlist.org/>.

- Iturralde-Vinent, M. A. 2006. "Mesozoic Caribbean Paleogeography: Implications for the Historical Biogeography of the Region." *International Geology Review* 48:791-827.
- Iturralde-Vinent, M. A., and R. D. E. MacPhee. 1999. "Paleogeography of the Caribbean Region: Implications for Cenozoic Biogeography." *Bulletin of the American Museum of Natural History* 238:1-95.
- Iturralde-Vinent, M. A., R. D. E. MacPhee, S. Díaz-Franco, R. Rojas-Consuegra, W. Suárez, and A. Lomba. 2000. "Las Breas de San Felipe, a Quaternary Fossiliferous Asphalt Seep Near Martí (Matanzas Province, Cuba)." *Caribbean Journal of Science* 36:300-23.
- Jiménez Vázquez, O., M. M. Condís, and C. E. García. 2005. "Vertebrados Post-glaciales en un Residuario Fósil de *Tyto alba scopoli* (Aves: Tytonidae) en el Occidente de Cuba." *Revista Mexicana de Mastozoología* 9:85-112.
- Johnson, C. 2006. "Australia's Mammal Extinctions: A 50,000 Year History." Cambridge: Cambridge University Press.
- Jones, J. K., Jr. 1989. "Distribution and Systematics of Bats in the Lesser Antilles." In *Biogeography of the West Indies: Past, Present, and Future*, edited by C. A. Woods, 645-60. Gainesville: Sandhill Crane Press.
- Jones, K. E., A. Purvis, A. MacLarnon, O. R. P. Bininda-Emonds, and N. B. Simmons. 2002. "A Phylogenetic Supertree of the Bats (Mammalia: Chiroptera)." *Biological Reviews* 77:223-59.
- Kluge, A. G. 1989. "A Concern for Evidence and a Phylogenetic Hypothesis of Relationships Among *Epicrates* (Boidae, Serpentes)." *Systematic Zoology* 38:7-25.
- Koopman, K. F. 1958. "Land Bridges and Ecology in Bat Distribution on Islands off the Northern Coast of South America." *Evolution* 12:429-39.
- . 1989. "A Review and Analysis of the Bats of the West Indies." In *Biogeography of the West Indies: Past, Present, and Future*, edited by C. A. Woods, 635-44. Gainesville: Sandhill Crane Press.
- . 1994. "Chiroptera: Systematics." *Handbuch der Zoologie* 8:1-217.
- Koopman, K. F., and I. E. Williams. 1951. "Fossil Chiroptera Collected by H. E. Anthony in Jamaica, 1919-1920." *American Museum Novitates* 1519:1-29.
- Larsen, P. A., S. R. Hooper, M. C. Bozeman, S. C. Pedersen, H. H. Genoways, C. J. Phillips, D. E. Pumo et al. 2007. "Phylogenetics and Phylogeography of the *Artibeus jamaicensis* Complex Based on Cytochrome-b DNA Sequences." *Journal of Mammalogy* 88:712-27.
- Larsen, P. A., M. R. Marchán-Rivadeneira, and R. J. Baker. 2010. "Natural Hybridization Generates Mammalian Lineage with Species Characteristics." *Proceedings of the National Academy of Sciences, USA* 107:11447-52.
- Leidy, J. 1868. "Notice of Some Vertebrate Remains from the West Indian Islands." *Proceedings of the Academy of Natural Sciences of Philadelphia* 20:178-80.
- Lessa, E. P., J. A. Cook, and J. L. Patton. 2003. "Genetic Footprints of Demographic Expansion in North America, But Not Amazonia, During the Late Quaternary." *Proceedings of the National Academy of Sciences, USA* 100:10331-34.
- Lewis-Oritt, N., C. A. Porter, and R. J. Baker. 2001. "Molecular Systematics of the Family Mormoopidae (Chiroptera) Based on Cytochrome b and Recombination Activating Gene 2 Sequences." *Molecular Phylogenetics and Evolution* 20:426-36.

- MacArthur, R. H., and E. O. Wilson. 1963. "An Equilibrium Theory of Insular Zoogeography." *Evolution* 17:373-87.
- . 1967. *The Theory of Island Biogeography*. Monographs in Population Biology, 1. Princeton: Princeton University Press.
- MacFadden, B. J. 1980. "Rafting Mammals or Drifting Islands?: Biogeography of the Greater Antillean Insectivores *Nesophontes* and *Solenodon*." *Journal of Biogeography* 7:11-22.
- . 1981. "Comments on Pregill's Appraisal of Historical Biogeography of Caribbean Vertebrates: Vicariance, Dispersal, or Both?" *Systematic Zoology* 30:370-72.
- MacPhee, R. D. E. 2005. "'First' Appearances in the Cenozoic Land-Mammal Record of the Greater Antilles: Significance and Comparison with South American and Antarctic Records." *Journal of Biogeography* 32:551-64.
- . 2008. "Insulae Infortunatae: Establishing a Chronology for Late Quaternary Mammal Extinctions in the West Indies." In *American Megafaunal Extinctions at the End of the Pleistocene*, edited by G. Haynes, 169-93. Dordrecht: Springer Science + Business Media B.V.
- MacPhee, R. D. E., and J. G. Fleagle. 1991. "Postcranial Remains of *Xenothrix mcgregori* (Primates, Xenotrichidae) and Other Late Quaternary Mammals from Long Mile Cave, Jamaica." *Bulletin of the American Museum of Natural History* 206:287-321.
- MacPhee, R. D. E., and C. Flemming. 1999. "Requiem /Eternam: The Last Five Hundred Years of Mammalian Species Extinctions." In *Extinctions in Near Time: Causes, Contexts, and Consequences*, edited by R. D. E. MacPhee, 333-71. New York: Kluwer Academic/Plenum.
- . "A Possible Heptaxodontine and Other Caviidan Rodents from the Quaternary of Jamaica." *American Museum Novitates* 3422:1-42.
- MacPhee, R. D. E., C. Flemming, D. P. Domning, R. W. Portell, and B. Beatty. 1999. "Eocene? Primate Petrosal from Jamaica: Morphology and Biogeographical Implications." *Journal of Vertebrate Paleontology* 19:61.
- MacPhee, R. D. E., D. C. Ford, and D. A. McFarlane. 1989. "Pre-Wisconsinan Mammals from Jamaica and Models of Late Quaternary Extinction in the Greater Antilles." *Quaternary Research* 31:94-106.
- MacPhee, R. D. E., and I. Horowitz. 2004. "New Craniodental Remains of the Quaternary Jamaican Monkey *Xenothrix mcgregori* (Xenotrichini, Callicebinae, Pitheciidae), with a Reconsideration of the Aotus Hypothesis." *American Museum Novitates* 3434:1-51.
- MacPhee, R. D. E., and M.-A. Iturralde-Vinent. 1995a. "Earliest Monkey from Greater Antilles." *Journal of Human Evolution* 28:197-200.
- . 1995b. "Origin of the Greater Antillean Land Mammal Fauna, 1: New Tertiary Fossils from Cuba and Puerto Rico." *American Museum Novitates* 3141:1-30.
- MacPhee, R. D. E., M. A. Iturralde-Vinent, and E. S. Gaffney. 2003. "Domo de Zaza, an Early Miocene Vertebrate Locality in South-Central Cuba, with Notes on the Tectonic Evolution of Puerto Rico and the Mona Passage." *American Museum Novitates* 3394:1-42.
- MacPhee, R. D. E., M. A. Iturralde-Vinent, and O. J. Vazquez. 2007. "Prehistoric Sloth Extinctions in Cuba: Implications of a New 'Last' Appearance Date." *Caribbean Journal of Science* 43:94-98.

- MacPhee, R. D. E., and P. A. Marx. 1997. "The 40,000-Year Plague: Humans, Hyperdisease, and First-Contact Extinctions." In *Natural Change and Human Impact in Madagascar*, edited by S. M. Goodman and B. D. Patterson, 169–217. Washington, DC: Smithsonian Institution Press.
- MacPhee, R. D. E., and J. Meldrum. 2006. "Postcranial Remains of the Extinct Monkeys of the Greater Antilles, with Evidence for Semiterrestriality in *Paralouatta*." *American Museum Novitates* 3516:1–65.
- MacPhee, R. D. E., J.-L. White, and C.-A. Woods. 2000. "New Megalonychid Sloths (Phyllophaga, Xenarthra) from the Quaternary of Hispaniola." *American Museum Novitates* 3303:1–32.
- Mancina, C. A., and L. Garcia-Rivera. 2005. "New Genus and Species of Fossil Bat (Chiroptera: Phyllostomidae) from Cuba." *Caribbean Journal of Science* 41:22–27.
- Martin, P. S. 1984. "Prehistoric Overkill: The Global Model." In *Quaternary Extinctions: A Prehistoric Revolution*, edited by P. S. Martin and R. G. Klein, 354–404. Tucson: University of Arizona Press.
- Martin, P. S., and D. W. Steadman. 1999. "Prehistoric Extinctions on Islands and Continents." In *Extinctions in Near Time: Causes, Contexts, and Consequences*, edited by R. D. E. MacPhee, 17–55. New York: Kluwer Academic/Plenum.
- Matthew, W. D. 1918. "Affinities and Origin of the Antillean Mammals." *Bulletin of the Geological Society of America* 29:657–66.
- McFarlane, D. A., and J. Lundberg. 2004. "Reliquiae Diluviane Alter: Last Interglacial Flood Deposits in Caves of the West Indies." In *Studies of Cave Sediments*, edited by I. D. Sasowsky and J. Mylroie, 313–22. New York: Kluwer/Plenum Press.
- McFarlane, D. A., R. D. E. MacPhee, and D. C. Ford. 1998. "Body Size Variability and a Sangamonian Extinction Model for *Amblyrhiza*, a West Indian Megafaunal Rodent." *Quaternary Research* 50:80–89.
- McFarlane, D. A., A. Vale, K. Christenson, J. Lundberg, G. Atilles, and S. E. Lauritzen. 2000. "New Specimens of Late Quaternary Extinct Mammals from Caves in Sanchez Ramirez Province, Dominican Republic." *Caribbean Journal of Science* 36:163–66.
- McGuire, J. A., C. C. Witt, D. L. Altshuler, and J. V. Remsen Jr. 2007. "Phylogenetic Systematics and Biogeography of Hummingbirds: Bayesian and Maximum Likelihood Analyses of Partitioned Data and Selection of an Appropriate Partitioning Strategy." *Systematic Biology* 56:837–56.
- Mickleburgh, S., K. Waylen, and P. Racey. 2009. "Bats as Bushmeat: A Global Review." *Oryx* 43:217–34.
- Miller, G. S. 1918. "Three New Bats from Haiti and Santo Domingo." *Proceedings of the Biological Society of Washington* 31:39–40.
- . 1922. "Remains of Mammals from Caves in the Republic of Haiti." *Smithsonian Miscellaneous Contributions* 74:1–8.
- . 1929a. "A Second Collection of Mammals from Caves Near St. Michel, Haiti." *Smithsonian Miscellaneous Contributions* 81:1–30.
- . 1929b. "Mammals Eaten by Indians, Owls, and Spaniards in the Coast Region of the Dominican Republic." *Smithsonian Miscellaneous Contributions* 82:1–16.

- . 1930. "Three Small Collections of Mammals from Hispaniola." *Smithsonian Miscellaneous Contributions* 82:1–15.
- Morales, J. C., and J. W. Bickham. 1995. "Molecular Systematics of the Genus *Lasiurus* (Chiroptera: Vespertilionidae) Based on Restriction-Site Maps of the Mitochondrial Ribosomal Genes." *Journal of Mammalogy* 76:730–49.
- Morgan, G. S. 1993. "Quaternary Land Vertebrates of Jamaica." In *Biostratigraphy of Jamaica*, edited by R. M. Wright and E. Robinson, 417–42. Boulder: Geological Society of America. Memoir 182.
- . 2001. "Patterns of Extinction in West Indian Bats." In *Biogeography of the West Indies: Patterns and Perspectives*, edited by C. A. Woods and F. E. Sergile, 369–407. Boca Raton: CRC Press.
- Morgan, G. S., and L. Wilkins. 2003. "The Extinct Rodent *Clidomys* (Heptaxodontidae) from a Late Quaternary Cave Deposit in Jamaica." *Caribbean Journal of Science* 39:34–41.
- Morgan, G. S., and C. A. Woods. 1986. "Extinction and the Zoogeography of West Indian Land Mammals." In *Island Biogeography of Mammals*. *Biological Journal of the Linnean Society*, 28, edited by L. R. Heaney and B. D. Patterson, 167–203. New York: Academic Press.
- Newsom, L. A., and E. S. Wing. 2004. *On Land and Sea: Native American Uses of Biological Resources in the West Indies*. Tuscaloosa: University of Alabama Press.
- Olson, S. L., and H. F. James. 1982. "Fossil Birds from the Hawaiian Islands: Evidence for Wholesale Extinction by Man Before Western Contact." *Science* 217:633–35.
- Page, R. D. M., and C. Lydeard. 1994. "Towards a Cladistic Biogeography of the Caribbean." *Cladistics* 10:21–41.
- Phillips, C. J., D. E. Pumo, H. H. Genoways, and P. E. Ray. 1989. "Caribbean Island Zoogeography: A New Approach Using Mitochondrial DNA to Study Neotropical Bats." In *Biogeography of the West Indies: Past, Present, and Future*, edited by C. A. Woods, 661–84. Gainesville: Sandhill Crane Press.
- Phillips, C., J. D. E. Pumo, H. H. Genoways, P. E. Ray, and C. Briskay. 1991. "Mitochondrial DNA Evolution and Phylogeography in Two Neotropical Fruit Bats, *Artibeus jamaicensis* and *Artibeus lituratus*." In *Latin American Mammalogy: History, Biodiversity, and Conservation*, edited by M. Mares and D. Schmidly, 97–123. Norman: University of Oklahoma Press.
- Platnick, N. I. 1991. "On Areas of Endemism." *Australian Systematic Botany* 4:ix–xii.
- Portell, R. W., S. K. Donovan, and D. P. Domning. 2001. "Early Tertiary Vertebrate Fossils from Seven Rivers, Parish of St. James, Jamaica, and their Biogeographical Implications." In *Biogeography of the West Indies*, edited by C. A. Woods and F. E. Sergile, 191–200. Boca Raton: CRC Press.
- Pregill, G. K. 1981. "An Appraisal of the Vicariance Hypothesis of Caribbean Biogeography and its Application to West Indian Terrestrial Vertebrates." *Systematic Zoology* 30:147–55.
- Pregill, G. K., and S. L. Olson. 1981. "Zoogeography of West Indian Vertebrates in Relation to Pleistocene Climatic Cycles." *Annual Review of Ecology and Systematics* 12:75–98.
- Pregill, G. K., D. W. Steadman, and D. R. Watters. 1994. "Late Quaternary Vertebrate

- Faunas of the Lesser Antilles: Historical Components of Caribbean Biogeography." *Bulletin of Carnegie Museum of Natural History* 30:1–51.
- Presley, S. J., and M. R. Willig. 2008. "Composition and Structure of Caribbean Bat (Chiroptera) Assemblages: Effects of Inter-Island Distance, Area, Elevation and Hurricane-Induced Disturbance." *Global Ecology and Biogeography* 17:747–57.
- Pumo, D. E., E. Z. Goldin, B. Elliot, C. Phillips, and H. H. Genoways. 1988. "Mitochondrial DNA Polymorphism in Three Antillean Island Populations of the Fruit Bat, *Artibeus jamaicensis*." *Molecular Biology and Evolution* 5:79–89.
- Pumo, D. E., K. Iksoo, J. Remsen, C. J. Phillips, and H. H. Genoways. 1996. "Molecular Systematics of the Fruit Bat, *Artibeus jamaicensis*: Origin of an Unusual Island Population." *Journal of Mammalogy* 77:491–503.
- Raffaele, H. A. 1979. "The Status of Some Endangered Species in Puerto Rico with Particular Emphasis on *Isolobodon* (Rodentia)." In *Memorias del Tercer Simposio*, 100–104. San Juan: Departamento de Recursos Naturales.
- Ree, R. H., and S. A. Smith. 2008. "Maximum-Likelihood Inference of Geographic Range Evolution by Dispersal, Local Extinction, and Cladogenesis." *Systematic Biology* 57:4–14.
- Rega, E., D. A. McFarlane, J. Lundberg, and K. Christenson. 2002. "A New Megalonychid Sloth from the Late Wisconsinan of the Dominican Republic." *Caribbean Journal of Science* 38:11–19.
- Ricklefs, R. E. 1970. "Stage of Taxon Cycle and Distribution of Birds on Jamaica, Greater Antilles." *Evolution* 24:475–77.
- Ricklefs, R. E., and E. Bermingham. 2001. "Nonequilibrium Diversity Dynamics of the Lesser Antillean Avifauna." *Science* 294:1522–24.
- Ricklefs, R. E., and G. C. Cox. 1972. "Taxon Cycles in the West Indian Avifauna." *American Naturalist* 106:195–219.
- Rímoli, R. O. 1976. "Roedores Fósiles de la Hispaniola." *Universidad Central del Este, Serie Científica III* 95:1–93.
- Roca, A. L., G. Kahila Bar-Gal, E. Eizirik, K. M. Hölgen, R. Maria, M. S. Springer, S. J. O'Brien et al. 2004. "Mesozoic Origin for West Indian Insectivores." *Nature* 429:649–51.
- Rodríguez Durán, A., and T. H. Kunz. 2001. "Biogeography of West Indian Bats: An Ecological Perspective." In *Biogeography of the West Indies: Patterns and Perspectives*, edited by C. A. Woods and F. E. Sergile, 355–68. Boca Raton: CRC Press.
- Rosen, D. E. 1975. "A Vicariance Model of Caribbean Biogeography." *Systematic Zoology* 24:431–64.
- . 1985. "Geological Hierarchies and Biogeographic Congruence in the Caribbean." *Annals of the Missouri Botanical Garden* 72:636–59.
- Russell, A., and G. F. McCracken. 2006. "Population Genetic Structure of Very Large Populations: The Brazilian Free-Tailed Bat, *Tadarida brasiliensis*." In *Functional and Evolutionary Ecology of Bats*, edited by A. Zubaid, G. F. McCracken, and T. H. Kunz, 227–47. New York: Oxford University Press.
- Russell, A. L., R. A. Medellín, and G. F. McCracken. 2005. "Genetic Variation and Migration

- tion in the Mexican Free-Tailed Bat (*Tadarida brasiliensis mexicana*)." *Molecular Ecology* 14:2207–22.
- Russell, A. L., J. Ranivo, E. P. Palkovacs, S. M. Goodman, and A. D. Yoder. 2007. "Working at the Interface of Phylogenetics and Population Genetics: A Biogeographical Analysis of *Triaenops* spp. (Chiroptera: Hipposideridae)." *Molecular Ecology* 16:839–51.
- Russell, A. L., S. M. Goodman, and M. P. Cox. 2008. "Coalescent Analyses Support Multiple Mainland-to-Island Dispersals in the Evolution of Malagasy *Triaenops* bats (Chiroptera: Hipposideridae)." *Journal of Biogeography* 35:995–1003.
- Russell, A. L., S. M. Goodman, I. Fiorentino, and A. D. Yoder. 2008. "Population Genetic Analysis of *Myzopoda* (Chiroptera: Myzopodidae) in Madagascar." *Journal of Mammalogy* 89:209–21.
- Rutschmann, F. 2006. "Molecular Dating of Phylogenetic Trees: A Brief Review of Current Methods That Estimate Divergence Times." *Diversity and Distributions* 12:35–48.
- Schubert, C., and E. Medina. 1982. "Evidence of Quaternary Glaciation in the Dominican Republic: Some Implications for Caribbean Paleoclimatology." *Palaeogeography, Palaeoclimatology, Palaeoecology* 39:281–94.
- Shapiro, B., A. J. Drummond, A. Rambaut, M. C. Wilson, P. E. Matheus, A. V. Sher, O. G. Pybus et al. 2004. "Rise and Fall of the Beringian Steppe Bison." *Science* 306:1561–65.
- Silva-Taboada, G. 1974. "Fossil Chiroptera from Cave Deposits in Central Cuba, with Description of Two New Species (Genera *Pteronotus* and *Mormoops*) and the First West Indian Record of *Mormoops megalophylla*." *Acta Zoologica Cracoviensia* 19:33–73.
- Simmons, N. B. 2005. "Order Chiroptera." In *Mammal Species of the World: A Taxonomic and Geographic Reference*, 3rd ed., edited by D. E. Wilson and D. M. Reeder, 313–529. Baltimore: Johns Hopkins University Press.
- Simmons, N. B., and T. M. Conway. 2001. "Phylogenetic Relationships of Mormoopid Bats (Chiroptera: Mormoopidae) Based on Morphological Data." *Bulletin of the American Museum of Natural History* 258:1–97.
- Simmons, G. G. 1943. "Mammals and the Nature of Continents." *American Journal of Science* 241:1–31.
- . 1956. "Zoogeography of West Indian Land Mammals." *American Museum Novitates* 1759:1–28.
- Stadelmann, B., L. K. Lin, T. H. Kunz, and M. Ruedi. 2007. "Molecular Phylogeny of New World *Myotis* (Chiroptera, Vespertilionidae) Inferred from Mitochondrial and Nuclear DNA Genes." *Molecular Phylogenetics and Evolution* 43:32–48.
- Steadman, D. W. 1995. "Prehistoric Extinctions of Pacific Island Birds: Biodiversity Meets Zooarchaeology." *Science* 267:1123–31.
- Steadman, D. W., R. Franz, G. S. Morgan, N. A. Albury, B. Kakuk, K. Broad, S. E. Franz et al. 2007. "Exceptionally Well Preserved Late Quaternary Plant and Vertebrate Fossils from a Blue Hole on Abaco, the Bahamas." *Proceedings of the National Academy of Sciences, USA* 104:19897–902.
- Steadman, D. W., P. S. Martin, R. D. E. MacPhee, A. J. T. Jull, H. G. McDonald, C. A. Woods, M. Iturralde-Vinent et al. 2005. "Asynchronous Extinction of Late Quater-

- nary Sloths on Continents and Islands." *Proceedings of the National Academy of Sciences, USA* 102:11763–68.
- Steadman, D. W., G. K. Pregill, and S. L. Olson. 1984. "Fossil Vertebrates from Antigua, Lesser Antilles: Evidence for Late Holocene Human-Caused Extinctions in the West Indies." *Proceedings of the National Academy of Sciences, USA* 81:4448–51.
- Suárez, W. 2005. "Taxonomic Status of the Cuban Vampire Bat (Chiroptera: Phyllostomidae: Desmodontinae: Desmodus)." *Caribbean Journal of Science* 41:761–67.
- Suárez, W., and S. Díaz-Franco. 2003. "A New Fossil Bat (Chiroptera: Phyllostomidae) from a Quaternary Cave Deposit in Cuba." *Caribbean Journal of Science* 39:371–77.
- Teeling, E. C., M. S. Springer, O. Madsen, P. Bates, S. J. O'Brien, and W. J. Murphy. 2005. "A Molecular Phylogeny for Bats Illuminates Biogeography and the Fossil Record." *Science* 307:580–84.
- Tejedor, A. 2006. "The Type Locality of *Natalus stramineus* (Chiroptera: Natalidae): Implications for the Taxonomy and Biogeography of the Genus *Natalus*." *Acta Chiropterologica* 8:361–80.
- . 2011. "Systematics of Funnel-Eared Bats (Chiroptera: Natalidae)." *Bulletin of the American Museum of Natural History* 353:1–40.
- Tejedor, A., G. Silva-Taboada, and D. Rodríguez Hernández. 2004. "Discovery of Extant *Natalus* major (Chiroptera: Natalidae) in Cuba." *Mammalian Biology* 69:153–62.
- Tejedor, A., V. d. C. Tavares, and G. Silva-Taboada. 2005. "Taxonomic Revision of Greater Antillean Bats of the Genus *Natalus*." *American Museum Novitates* 3493:1–22.
- Towns, D., I. Atkinson, and C. Daugherty. 2006. "Have the Harmful Effects of Introduced Rats on Islands Been Exaggerated?" *Biological Invasions* 8:863–91.
- Trejo-Torres, J. C., and J. D. Ackerman. 2001. "Biogeography of the Antilles Based on a Parsimony Analysis of Orchid Distributions." *Journal of Biogeography* 28:775–94.
- Turvey, S. T. 2009. "Holocene Mammal Extinctions." In *Holocene Extinctions*, edited by S. T. Turvey, 41–61. Oxford: Oxford University Press.
- Turvey, S. T., E. V. Grady, and P. Rye. 2006. "A New Genus and Species of 'Giant Hutia' (*Tai-notherium vlei*) from the Quaternary of Puerto Rico: An Extinct Arboreal Quadruped?" *Journal of Zoology* 270:585–94.
- Turvey, S., J. Oliver, Y. Narganes Storde, and P. Rye. 2007. "Late Holocene Extinction of Puerto Rican Native Land Mammals." *Biology Letters* 3:193–96.
- Turvey, S. T., M. Weksler, E. L. Morris, and M. Nöckert. 2010. "Taxonomy, Phylogeny, and Diversity of the Extinct Lesser Antillean Rice Rats (Sigmodontinae: Oryzomyini), with Description of a New Genus and Species." *Zoological Journal of the Linnean Society* 160:748–72.
- Vázquez-Miranda, H., A. G. Navarro-Sigüenza, and J. J. Morrone. 2007. "Biogeographical Patterns of the Avifaunas of the Caribbean Basin Islands: A Parsimony Perspective." *Cladistics* 23:180–200.
- Villalobos, F., and A. A. Valerio. 2002. "The Phylogenetic Relationships of the Bat Genus *Sturmia* Gray, 1842 (Chiroptera: Phyllostomidae)." *Mammalian Biology* 67:268–75.
- Voss, R. S., and M. Weksler. 2009. "On the Taxonomic Status of *Oryzomys curasoae* Mc-

- Farlane and Debrot, 2001, with Remarks on the Phylogenetic Relationships of *O. gorgasi* Hershkovitz, 1971." *Caribbean Journal of Science* 45:1–7.
- Wallace, A. R. 1876. *The Geographical Distribution of Animals: With a Study of the Relations of Living and Extinct Faunas as Elucidating the Past Changes of the Earth's Surface*. New York: Harper & Brothers.
- Watts, D. 1987. *The West Indies: Patterns of Development, Culture and Environmental Change Since 1492*. Cambridge: Cambridge University Press.
- White, J. L., and R. D. E. MacPhee. 2001. "The Sloths of the West Indies: A Systematic and Phylogenetic Overview." In *Biogeography of the West Indies*, edited by C. A. Woods and F. E. Sergile, 201–35. Boca Raton: CRC Press.
- Williams, E. E. 1952. "Additional Notes on Fossil and Subfossil Bats from Jamaica." *Journal of Mammalogy* 33:171–79.
- Williams, E. E., and K. F. Koopman. 1951. "A New Fossil Rodent from Puerto Rico." *American Museum Novitates* 1515:1–9.
- Wilson, D. E., and D. M. Reeder, eds. 2005. *Mammal Species of the World: A Taxonomic and Geographic Reference*, 3rd ed. Baltimore: Johns Hopkins University Press.
- Wilson, S. M. 2007. *The Archaeology of the Caribbean*. Cambridge: Cambridge University Press.
- Woods, C. A. 1989. "The Biogeography of West Indian Rodents." In *Biogeography of the West Indies: Past, Present, and Future*, edited by C. A. Woods, 741–98. Gainesville: Sandhill Crane Press.
- Woods, C. A., R. Borroto, and C. Kilpatrick. 2001. "Insular Patterns and Radiations of West Indian Rodents." In *Biogeography of the West Indies*, edited by C. A. Woods and F. E. Sergile, 335–53. Boca Raton: CRC Press.
- Woods, C. A., J. A. Ottenwalder, and W. L. R. Oliver. 1985. "Lost Mammals of the Greater Antilles: The Summarised Findings of a Ten Weeks Field Survey in the Dominican Republic, Haiti and Puerto Rico." *Dodo* 22:23–42.
- Woods, C. E., and J. A. Ottenwalder. 1992. *The Natural History of Southern Haiti*. Gainesville: Florida Museum of Natural History.
- Wyatt, K. B., P. F. Campos, M. T. P. Gilbert, S.-O. Kolokotronis, W. H. Hynes, R. DeSalle, P. Daszak et al. 2008. "Historical Mammal Extinction on Christmas Island (Indian Ocean) Correlates with Introduced Infectious Disease." *PLoS ONE* 3:e3602.
- Yang, Z., and B. Rannala. 2006. "Bayesian Estimation of Species Divergence Times under a Molecular Clock Using Multiple Fossil Calibrations with Soft Bounds." *Molecular Biology and Evolution* 23:212–26.
- Yesson, C., and A. Culham. 2006. "Phyloclimatic Modeling: Combining Phylogenetics and Bioclimatic Modeling." *Systematic Biology* 55:785–802.

Appendix 9.1

Table Ag.1 Complete taxonomic list, status, and distribution of extinct and extant West Indian mammals. Taxonomy follows contributors to Wilson and Reeder (2005) and Turvey (2009), with additional data from White and MacPhee (2001) and Rega et al. (2002) for sloths, MacPhee and Fleming (2003), Borroto-Pérez, Woods, and Kilpatrick (2005), and Turvey et al. (2006, 2010) for rodents, and Dávalos (2006), Larsen et al. (2007), Morgan (2001), and Tejedor (2011) for bats. Named subspecies of *Pteronotus parnellii*, *Chilonatalus micropus*, and *Brachyphylla nana* are treated as distinct based on morphological and molecular data in Dávalos (2004a, 2006), Morgan (2001), and Tejedor (2011). Five bat species found in the Antilles only on Grenada (*Anoura geoffroyi*, *Artibeus glaucus*, *Micronycteris megalotis*, and *Pteropteryx macrotis*) are not included in this list. An online version of this table is available at http://sites.google.com/site/lmdavalos/appendix9_1.csv.

| ORDER, FAMILY, and Genus | SPECIES | ENDEMIC | EXTINCT | DISTRIBUTION († indicates extirpated from an island) |
|--------------------------|---------------------|---------|---------|--|
| PILOSA | | | | |
| MEGALONYCHIDAE | | | | |
| <i>Acratocnus</i> | <i>odontrigonus</i> | + | † | Puerto Rico |
| | <i>antillensis</i> | + | † | Cuba |
| | <i>ye</i> | + | † | Hispaniola |
| | <i>simorhynchus</i> | + | † | Hispaniola |
| <i>Galerocnus</i> | <i>jaimenzi</i> | + | † | Cuba |
| <i>Megalocnus</i> | <i>rodens</i> | + | † | Cuba |
| | <i>zile</i> | + | † | Hispaniola, Ile de la Tortue |
| <i>Neocnus</i> | <i>gliriformis</i> | + | † | Cuba |
| | <i>major</i> | + | † | Cuba |
| | <i>comes</i> | + | † | Hispaniola |
| | <i>dousman</i> | + | † | Hispaniola |
| | <i>toupiti</i> | + | † | Hispaniola |
| <i>Paramiocnus</i> | <i>riveroi</i> | + | † | Cuba |
| <i>Parocnus</i> | <i>serus</i> | + | † | Hispaniola, Ile de la Tortue, Ile de la Gonave |
| | <i>browni</i> | + | † | Cuba |

(continues)

Table Ag.1 (continued)

| ORDER, FAMILY, and Genus | SPECIES | ENDEMIC | EXTINCT | DISTRIBUTION († indicates extirpated from an island) |
|--------------------------|-------------------|---------|---------|--|
| SORICOMORPHA | | | | |
| NESOPHONTIDAE | | | | |
| <i>Nesophontes</i> | <i>edithae</i> | + | † | Puerto Rico, Vieques, St. John, St. Thomas |
| | <i>hypomicrus</i> | + | † | Hispaniola, Ile de la Gonave |
| | <i>major</i> | + | † | Cuba |
| | <i>micrus</i> | + | † | Cuba, Isle of Pines |
| | <i>paramicrus</i> | + | † | Hispaniola |
| | <i>zamicrus</i> | + | † | Hispaniola, Ile de la Gonave |
| | sp. nov. A | + | † | Cayman Brac |
| | sp. nov. B | + | † | Grand Cayman |
| SOLENDONTIDAE | | | | |
| <i>Solenodon</i> | <i>arredondoi</i> | + | † | Cuba |
| | <i>cubanus</i> | + | | Cuba |
| | <i>marcanoi</i> | + | † | Hispaniola |
| | <i>paradoxus</i> | + | | Hispaniola, Ile de la Gonave |
| RODENTIA | | | | |
| CAPROMYIDAE | | | | |
| <i>Capromys</i> | <i>antiquus</i> | + | † | Cuba |
| | <i>arredondoi</i> | + | † | Cuba |
| | <i>latus</i> | + | † | Cuba |
| | <i>pappus</i> | + | † | Cuba |
| | <i>pilorides</i> | + | | Cuba, Isle of Pines, other Cuban offshore islands |
| | <i>robustus</i> | + | † | Cuba |
| | sp. nov. | + | | Cayo Ballentino del Medio (Camaguey, Cuba) |

| ORDER, FAMILY, and Genus | SPECIES | ENDEMIC | EXTINCT | DISTRIBUTION († indicates extirpated from an island) |
|--------------------------|-------------------------------|---------|---------|--|
| Geocapromys | brownii | + | | Jamaica |
| | columbianus | + | † | Cuba |
| | ingrahami | + | | Acklins, Crooked Island, Middle Caicos, Andros, Cat Island, Eleuthera Island, Great Exuma, Little Exuma, Long Island, New Providence, Ragged Island, Great Abaco, East Plana Cay, San Salvador, Samana Cay |
| | pleistocenicus | + | † | Cuba |
| | thoracatus | + | † | Little Swan Island |
| | sp. nov. A | + | † | Cayman Brac |
| | sp. nov. B | + | † | Grand Cayman |
| | phenax | + | † | Hispaniola, Ile de la Gonave |
| | gen. nov.? (aff. Hexalobodon) | + | † | Hispaniola |
| | montanus | + | † | Hispaniola, Ile de la Gonave |
| Hexalobodon | portoricensis | + | † | Hispaniola, Ile de la Gonave, Ile de la Tortue, Mona, Guana, Jost van Dyke, Puerto Rico, St. John, St. Thomas, Tortola, Vieques, St. Croix |
| | | | | |
| Mesocapromys | angelabrerae | + | | Cayos de Ana Maria (Cuba) |
| | aureus | + | | Cayo Fragoso (Archipelago de Samana, Cuba) |
| | barbouri | + | † | Cuba |
| | beatrizae | + | † | Cuba |
| | delicatus | + | † | Cuba |
| | gracilis | + | † | Cuba |
| | kraglievichi | + | † | Cuba |
| | melanurus | + | | Cuba |
| | minimus | + | † | Cuba |
| | nanus | + | | Cuba, Isle of Pines |
| | sanfelipensis | + | | San Felipe Cays (Cuba) |
| | silvii | + | † | Cuba |

(continues)

Table Ag.1 (continued)

| ORDER, FAMILY, and Genus | SPECIES | ENDEMIC | EXTINCT | DISTRIBUTION († indicates extirpated from an island) |
|--------------------------|--------------|---------|---------|--|
| Mysateles | garridoi | + | | Cayo Maya, Cayo Largo, Cayo de la Piedra (Cuba) |
| | gundlachi | + | | Isle of Pines |
| | jaumei | + | † | Cuba |
| | meridionalis | + | | Isle of Pines (Cuba) |
| | prehensilis | + | | Cuba |
| Plagiodontia | aedium | + | | Hispaniola, Ile de la Gonave |
| | araeum | + | † | Hispaniola, Ile de la Gonave |
| | ipnaeum | + | † | Hispaniola |
| Rhizoplagiodontia | lemkei | + | † | Hispaniola |
| Cricetidae | | | | |
| gen. nov.? | sp. nov.? | + | † | Anguilla, St. Martin, Tintamarre |
| gen. nov.? | sp. nov.? | + | † | Barbados |
| gen. nov.? | sp. nov.? | + | † | Carriacou |
| gen. nov.? | sp. nov.? | + | † | Grenada |
| gen. nov.? | sp. nov.? | + | † | Grenada |
| gen. nov.? | sp. nov.? | + | † | Guadeloupe |
| gen. nov.? | sp. nov.? | + | † | La Desirade |
| gen. nov.? | sp. nov.? | + | † | Marie Galante |
| gen. nov.? | sp. nov.? | + | † | Montserrat |
| gen. nov.? | sp. nov.? | + | † | Montserrat |
| gen. nov.? | sp. nov.? | + | † | Saba |
| gen. nov.? | sp. nov.? | + | † | Antigua, Barbuda |
| Megalomys | audreyae | + | † | Barbuda |
| | desmarestii | + | † | Martinique |
| | luciae | + | † | St. Lucia |

| ORDER, FAMILY, and Genus | SPECIES | ENDEMIC | EXTINCT | DISTRIBUTION († indicates extirpated from an island) |
|-------------------------------|--------------------|---------|---------|--|
| <i>Oligoryzomys</i> | <i>victus</i> | + | † | St. Vincent |
| <i>Oryzomys</i> | <i>antillarum</i> | + | † | Jamaica |
| <i>Pennatomys</i> | <i>nivalis</i> | + | † | Nevis, St. Eustatius, St. Kitts |
| ECHIMYIDAE | | | | |
| <i>Beromys</i> | <i>offella</i> | + | † | Cuba |
| | <i>torrei</i> | + | † | Cuba, Isle of Pines |
| <i>Stotomys</i> | <i>contractus</i> | + | † | Hispaniola |
| | <i>voratus</i> | + | † | Hispaniola, Ile de la Gonave |
| <i>Heteropsomys</i> | <i>insulans</i> | + | † | Puerto Rico, Vieques |
| <i>Puertoicomys</i> | <i>corozalus</i> | + | † | Puerto Rico |
| HEPTAXODONTIDAE | | | | |
| | | + | † | |
| <i>Chidomys</i> | <i>osborni</i> | + | † | Jamaica |
| <i>Elasmodontomys</i> | <i>obliquus</i> | + | † | Puerto Rico |
| <i>Quemisia</i> | <i>gravis</i> | + | † | Hispaniola |
| <i>Xaymaca incertae sedis</i> | <i>fulvopulvis</i> | + | † | Jamaica |
| gen. nov. | sp. nov. | + | † | Jamaica |
| <i>Tainotherium</i> | <i>volei</i> | + | † | Puerto Rico |
| PRIMATES | | | | |
| PITHECIIDAE | | | | |
| <i>Antillothrix</i> | <i>bernensis</i> | + | † | Hispaniola |
| <i>Paralouatta</i> | <i>varonai</i> | + | † | Cuba |
| <i>Xenothrix</i> | <i>mcgregori</i> | + | † | Jamaica |

(continues)

Table A9.1 (continued)

| ORDER, FAMILY, and Genus | SPECIES | ENDEMIC | EXTINCT | DISTRIBUTION († indicates extirpated from an island) |
|--------------------------|---------------------|---------|---------|--|
| CHIROPTERA | | | | |
| MOLOSSIDAE | | | | |
| <i>Eumops</i> | <i>auripendulus</i> | | | Jamaica |
| | <i>glauclus</i> | | | Cuba, Jamaica |
| | <i>perotis</i> | | | Cuba |
| <i>Molossus</i> | <i>molossus</i> | | | Cayman Brac, Cuba, Isle of Pines, Grand Cayman, Hispaniola, Ile de la Gonave, Jamaica, Culebra, Guana, Puerto Rico, St. John, St. Thomas, Tortola, Vieques, Virgin Gorda, St. Croix, Anguilla, St. Barthelemy, St. Eustatius, St. Martin, Antigua, Barbuda, Barbados, Dominica, Carriacou, Grenada, Union, Guadeloupe, La Desirade, Marie Galante, Martinique, Montserrat, Saba, St. Lucia, St. Vincent, Nevis, St. Kitts |
| <i>Mormopterus</i> | <i>minutus</i> | + | | Cuba |
| <i>Nyctinomops</i> | <i>laticaudatus</i> | | | Cuba |
| | <i>macrotis</i> | | | Cuba, Jamaica, Hispaniola |
| <i>Tadarida</i> | <i>brasiliensis</i> | | | Acklins, Crooked Island, Fortune Island, Middle Caicos†, Eleuthera Island, Great Exuma, Little Exuma, Long Island, New Providence†, Great Abaco, Little Abaco, Cuba, Isle of Pines, Grand Cayman, Hispaniola, Jamaica, Puerto Rico, St. John, Anguilla, St. Barthelemy, St. Eustatius, St. Martin, Antigua, Barbuda, Dominica, Guadeloupe, La Desirade, Martinique, Montserrat, Saba, St. Lucia, St. Vincent, Nevis, St. Kitts |
| MORMOOPIDAE | | | | |
| <i>Mormoops</i> | <i>blainvilliei</i> | + | | Little Exuma†, New Providence†, Great Abaco†, Cuba, Hispaniola, Ile de la Gonave†, Jamaica, Mona, Puerto Rico, Anguilla†, Antigua†, Barbuda† |

| ORDER, FAMILY, and Genus | SPECIES | ENDEMIC | EXTINCT | DISTRIBUTION († indicates extirpated from an island) |
|--------------------------|---------------------------|---------|---------|--|
| <i>Pteronotus</i> | <i>magna</i> | + | † | Cuba |
| | <i>megaloophylla</i> | | † | Andros, Great Abaco, Cuba, Hispaniola, Jamaica |
| | <i>davyi</i> | | | Dominica, Grenada, Marie Galante, Martinique |
| | <i>macleanii</i> | + | | New Providence†, Cuba, Isle of Pines, Jamaica |
| | <i>parnellii</i> | + | | New Providence†, Great Abaco†, Cuba, Isle of Pines†, Grand Cayman†, Jamaica |
| | <i>parnellii</i> | + | | Mona, Puerto Rico, Antigua† |
| | <i>portoricensis</i> | | | |
| | <i>parnellii pusillus</i> | + | | Hispaniola, Ile de la Gonave† |
| | <i>parnellii</i> | | | St. Vincent |
| | <i>rubiginosus</i> | | | |
| | <i>pristinus</i> | + | † | Cuba |
| | <i>quadridens</i> | + | | Andros†, New Providence†, Great Abaco†, Cuba, Hispaniola, Jamaica, Puerto Rico |
| | <i>sp. nov.</i> | + | † | Hispaniola |
| NATALIDAE | | | | |
| <i>Chilonatalus</i> | <i>tumidifrons</i> | + | | Andros, Cat Island†, Great Exuma†, New Providence†, Great Abaco, San Salvador |
| | <i>micropus micropus</i> | + | | Hispaniola, Jamaica, Providencia |
| | <i>micropus macer</i> | + | | Cuba, Isle of Pines, Grand Cayman† |
| <i>Natalus</i> | <i>stramineus</i> | + | | Anguilla, St. Martin, Antigua, Barbuda, Dominica, Guadeloupe, Marie Galante, Martinique, Montserrat, Saba, Nevis |
| | <i>jamaicensis</i> | + | | Jamaica |
| | <i>major</i> | + | | Hispaniola, Middle Caicos† |
| | <i>primus</i> | + | | Andros†, New Providence†, Great Abaco†, Cuba, Isle of Pines†, Grand Cayman† |
| <i>Nyctiellus</i> | <i>lepidus</i> | + | | Andros†, Cat Island, Eleuthera Island, Great Exuma†, Little Exuma, Long Island, Cuba, Isle of Pines |

(continues)

Table A9.1 (continued)

| ORDER, FAMILY, and Genus | SPECIES | ENDEMIC | EXTINCT | DISTRIBUTION († indicates extirpated from an island) |
|--------------------------|---------------------|---------|---------|--|
| NOCTILIONIDAE | | | | |
| <i>Noctilio</i> | <i>leporinus</i> | | | Great Inagua, Cuba, Isle of Pines, Hispaniola, Jamaica, Mona, Culebra, Puerto Rico, St. John, St. Thomas, Vieques, St. Croix, St. Martin, Antigua, Barbuda, Barbados, Dominica, Carriacou, Grenada, Guadeloupe, Marie Galante, Martinique, Montserrat, St. Lucia, St. Vincent, Nevis, St. Kitts |
| PHYLLOSTOMIDAE | | | | |
| <i>Ardops</i> | <i>nichollsi</i> | + | | St. Eustatius, St. Martin, Dominica, Guadeloupe, Marie Galante, Martinique, Montserrat, Saba, St. Lucia, St. Vincent, Nevis, St. Kitts |
| <i>Ariteus</i> | <i>flavescens</i> | + | | Jamaica |
| <i>Artibeus</i> | <i>jamaicensis</i> | | | Providenciales, Great Inagua, Little Inagua, Mayaguana, Cayman Brac, Little Cayman, Cuba, Isle of Pines, Grand Cayman, Hispaniola, Ile de la Gonave, Jamaica, Anegada, Culebra, Guana, Puerto Rico, St. John, St. Thomas, Tortola, Vieques, Virgin Gorda, St. Croix, Anguilla, St. Barthelemy, St. Eustatius, St. Martin, Antigua, Barbuda, Barbados, Dominica, Bequia, Carriacou, Grenada, Mustique, Union, Guadeloupe, La Desirade, Marie Galante, Martinique, Montserrat, Saba, St. Lucia, St. Vincent, Nevis, St. Kitts, Providencia, San Andres |
| <i>Brachyphylla</i> | <i>lituratus</i> | | | St. Vincent |
| | <i>anthonyi</i> | + | † | Cuba |
| | <i>schwartzi</i> | + | | Barbados, Montserrat, St. Lucia, St. Vincent, Nevis, St. Kitts |
| | <i>planirostris</i> | | | St. Vincent |
| | <i>cavernarum</i> | + | | Guana, Puerto Rico, St. John, St. Thomas, St. Croix, Anguilla, St. Barthelemy, St. Eustatius, St. Martin, Antigua, Barbuda, Barbados, Dominica, Guadeloupe, La Desirade, Marie Galante, Martinique, Montserrat, Saba, St. Lucia, St. Vincent, Nevis, St. Kitts |
| | <i>nana nana</i> | + | | Andros†, New Providence†, Cayman Brac†, Cuba, Isle of Pines, |
| | <i>nana pumila</i> | + | | Middle Caicos, Cayman Brac†, Hispaniola, Jamaica† |

| ORDER, FAMILY, and Genus | SPECIES | ENDEMIC | EXTINCT | DISTRIBUTION († indicates extirpated from an island) |
|--------------------------|---------------|---------|---------|---|
| Chiroderma | improvisum | + | | Guadeloupe, Montserrat |
| Cubanxeris | silvai | + | † | Cuba |
| Desmodus | puntajudensis | + | † | Cuba |
| Erophylla | bombifrons | + | | Hispaniola, Puerto Rico |
| | szekorni | + | | Acklins, Crooked Island, East Caicos, Middle Caicos, North Caicos, Providenciales, Andros, Cat Island, Eleuthera Island, Great Exuma, Little Exuma, Long Island, New Providence, Great Inagua, Grand Bahama, Great Abaco, Mayaguana, East Plana Cay, San Salvador, Cayman Brac, Cuba, Isle of Pines, Grand Cayman, Jamaica |
| Glossophaga | longirostris | | | Carriacou, Grenada, Union, St. Vincent |
| | soricina | | | Jamaica |
| Macrotus | waterhousii | + | | Acklins, Crooked Island, East Caicos, Middle Caicos†, North Caicos, Providenciales, Andros, Cat Island, Darby, Eleuthera Island, Great Exuma, Little Exuma, Long Island, New Providence, Great Inagua, Great Abaco, East Plana Cay, San Salvador, Cayman Brac, Little Cayman, Cuba, Isle of Pines, Grand Cayman, Hispaniola, Ile de la Gonave†, Jamaica, Navassa, Puerto Rico†, Anguilla† |
| Monophyllus | plethodon | + | | Puerto Rico†, Anguilla, St. Barthelemy, St. Martin, Antigua, Barbuda, Barbados, Dominica, Guadeloupe, Martinique, Montserrat, Saba, St. Lucia, St. Vincent, Nevis, St. Kitts |
| | redmani | + | | Acklins, Crooked Island, Middle Caicos, North Caicos, Providenciales, Andros†, New Providence†, Great Abaco†, Cayman Brac†, Cuba, Isle of Pines, Grand Cayman†, Hispaniola, Ile de la Gonave†, Jamaica, Puerto Rico |
| Phyllonycteris | aphylla | + | | Jamaica |
| | poeyi | + | | New Providence†, Great Abaco†, Cayman Brac†, Cuba, Isle of Pines, Hispaniola |
| | major | + | † | Puerto Rico |

(continues)

Table A9.1 (continued)

| ORDER, FAMILY, and Genus | SPECIES | ENDEMIC | EXTINCT | DISTRIBUTION († indicates extirpated from an island) |
|--------------------------|--------------------|---------|---------|---|
| Phyllips | falcatus | + | | Cayman Brac, Cuba, Isle of Pines†, Grand Cayman, Hispaniola |
| | silvai | + | † | Cuba |
| | vetus | + | † | Cuba |
| Stenoderma | rufum | + | | Puerto Rico, St. John, St. Thomas, Vieques, St. Croix |
| Sturnira | lilium | | | Dominica, Grenada, Martinique, St. Lucia, St. Vincent |
| | thomasi | + | | Guadeloupe, Montserrat |
| Tonettia | saurophila | | † | Jamaica |
| VESPERTILIONIDAE | | | | |
| Antrozous | pollidus | | | Cuba |
| Eptesicus | fuscus | | | Grand Bahama, Great Abaco, San Salvador, Cayman Brac, Cuba, Isle of Pines, Grand Cayman, Hispaniola, Jamaica, Puerto Rico, Dominica |
| | guadeloupensis | + | | Guadeloupe |
| Lasiurus | degelidus | + | | Jamaica |
| | insularis | + | | Cuba |
| | minor | + | | Providenciales, Andros, Cat Island, Long Island, New Providence, Great Inagua, Grand Bahama, Mayaguana, Hispaniola, Puerto Rico |
| | peifferi | + | | Cuba |
| | intermedius | | | Cuba, Isle of Pines, Hispaniola† |
| Myotis | dominicensis | + | | Dominica, Guadeloupe |
| | martiniensis | + | | Martinique, Barbados |
| | cf. austroriparius | + | † | Abaco |
| Nycticeius | cubanus | + | | Cuba |