Journal of Mammalogy, 98(4):964–985, 2017
DOI:10.1093/jmammal/gyx017
Version of Record, with fixed content and layout in compliance with Art. 8.1.3.2 ICZN.



# Biodiversity and conservation of Cuban mammals: past, present, and invasive species

RAFAEL BORROTO-PÁEZ\* AND CARLOS A. MANCINA

Sociedad Cubana de Zoología, Boyeros, CP 11900 La Habana, Cuba (RBP) Instituto de Ecología y Sistemática, Carretera de Varona No. 11835, Boyeros, CP 11900 La Habana, Cuba (CAM)

\* Correspondent: borroto@yahoo.com

Land mammals of the Caribbean Islands biodiversity hotspot have suffered a high rate of extinction since human arrival, principally in the last 500 years since colonialism began. Here, we present an extensive review and bibliography of this topic in Cuba, including details regarding the surviving endemic species of volant and terrestrial mammals and locations of species on 121 protected areas. We analyzed patterns of species richness, endemism, body mass, diet, habitat, geographic distribution of the observed richness, conservation threats, and possible causes and threats to future extinction. Cuban mammal biodiversity is comprised of 59 native species, 24 extinct species and 35 extant species, most of which are endemic to the Cuban archipelago. We compared the threats of habitat destruction and hunting, with emphasis on invasive mammal species as drivers of historical extinction in Cuba. A total of 44 mammal species have been introduced since 1509, with 33 invasive species living in the wild and exerting differing degrees of impact, principally by predation and competition. Additionally, we evaluated interactions among invasive and native mammals, emphasizing predation of feral cats upon *Solenodon cubanus*, *Capromys pilorides*, and other small endemic vertebrates as determined from analyses of scat contents. We found that black rats (*Rattus rattus*) reach densities of 147–322 individuals/ha in *Solenodon* habitat, thus likely are major competitors for food and refuges to these evolutionarily distinct and endangered Cuban mammals.

Los mamíferos terrestres del "hotspot" de las islas del Caribe han sufrido una elevada tasa de extinción después de la llegada de los humanos, principalmente en los últimos 500 años. Se realizó una extensa revisión bibliográfica, incluyendo detalles concernientes a las especies endémicas de mamíferos voladores y terrestres y su localización en 121 áreas protegidas en Cuba. Se analizó la riqueza de especies, endemismo, masa corporal, dieta, hábitat, patrones de distribución de la riqueza de especies, amenazas a la conservación y posibles causas de extinciones. La diversidad de los mamíferos cubanos está formada por 59 especies nativas, 24 fósiles y 35 vivientes hasta tiempos recientes, la mayoría de ellos endémicos del archipiélago cubano. Se compara las amenazas de la destrucción del hábitat, la caza, con énfasis en las especies invasoras como factor histórico de extinción. Un total de 44 especies de mamíferos han sido introducidas desde 1509, de las cuales 33 son invasivas al vivir en áreas naturales y producir diferentes grados de impactos, principalmente por depredación y competencia. Adicionalmente evaluamos la interacción entre mamíferos invasores y nativos, enfatizando en la depredaciones de gatos asilvestrados sobre *Solenodon cubanus*, *Capromys pilorides* y otros pequeños vertebrados endémicos, a partir del análisis del contenido de los excrementos. Se encontró que la rata negra (*Rattus rattus*) tiene altas densidades relativas de 147–322 individuos por hectárea en el hábitat del *Solenodon* y por tanto son probables competidores por alimento y sitios de refugio para esta especie, evolutivamente distintiva y en peligro.

Key words: Cuban land mammals, bats, fossil mammals, introduced mammals, hutia, extinction, Solenodon, threats, endemism

The Caribbean Islands are classified as a hotspot of world biodiversity with a high concentration of endemic and threatened genera and families (Myers et al. 2000; Smith et al. 2005).

This geographic area has experienced one of the globally highest rates of extinction in the last 500 years, with Caribbean mammals representing 37.5% of all known modern-era

extinctions (Morgan and Woods 1986; MacPhee and Marx 1997; MacPhee 2009; Turvey 2009). The Cuban archipelago is an important part of the Caribbean Islands hotspot, hosting significant biodiversity and endemism, including the greatest number of vertebrate and mammal species in the region. As with other Caribbean islands, total species richness in Cuba is not as extensive as in adjacent mainland areas, especially for terrestrial mammals, but is instead proportionately richer in endemic species.

Biodiversity conservation in Cuba is supported by 77 protected areas of "National Significance" and 134 of "Local Significance," which together cover 20.2% of the Cuban land area (CNAP 2013). Almost all species of Cuban mammals have a portion of their habitat protected by the National System of Protected Areas (SNAP). Several recent analyses have been published on the conservation of Cuban mammals, including summaries of existing legislation, protected areas, conservation status, and human threats (Mancina et al. 2007a; Borroto-Páez and Ramos 2012; Borroto-Páez et al. 2012a; Mancina 2012). These studies concluded that invasive species, habitat deterioration, and hunting are the leading factors threatening the persistence of endemic Cuban mammals. In particular, invasive species are considered the most immediate threat for Caribbean biodiversity today (Wege et al. 2010). Invasive mammals in Cuba include several (Rattus rattus [black rats], Mus musculus [house mice], Herpestes auropunctatus [small Indian mongoose], Felis catus [cats], Sus scrofa [pigs], Capra hircus [goats], and *Macaca fascicularis* [crab-eating macagues]) of the world's most invasive species (Lowe et al. 2000). These invasives in most instances arrived during European colonization and continue to prey upon and compete for resources with threatened native mammals throughout the country (Borroto-Páez 2009; Borroto-Páez 2011b; Borroto-Páez and Woods 2012b; Mancina et al. 2014).

In this review, we will reevaluate species-level biodiversity, conservation status, and threats for Cuban terrestrial mammals, including bats. We especially investigate the impacts of invasive species on the native mammal fauna and the role of invasions upon historical and recent extinctions.

#### MATERIALS AND METHODS

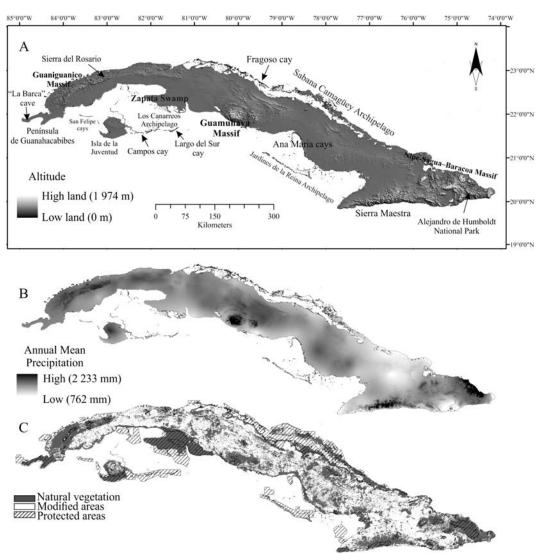
Study area.—Cuba is an archipelago (Fig. 1) with a total area of 109,884 km², including the largest island in the Caribbean Sea and more than 3,000 offshore islands and keys, which are arranged in 4 groups of islands: Los Colorados and Sabana Camagüey archipelagos in the north, and Jardines de la Reina and Los Canarreos archipelagos in the south (SHGRC 2003). The Cuban archipelago presently is forested over 27.3% of the land surface, and contains 4 mountain groups (Guaniguanico in western Cuba, Guamuhaya in the central region, and Sierra Maestra and Nipe-Sagua–Baracoa in the east). The coastline is roughly 6,400 km in length and has mangrove forests covering around 4,000 km². The country contains many wetland areas (Zapata Swamp, Rio Maximo, Delta of Rio Cauto, and Lanier Swamp being the most extensive areas) that together constitute

29% of Cuban territory. Moreover, almost 66% of the land area is underlain by karstified rocks (Gebelein 2012; CNAP 2013). All of these biomes are suitable habitats for various species of native Cuban mammals.

In this study, we analyzed in detail 2 localities. Cat scats and density of black rats were studied in the El Toldo plateau (-74°51′37″W, 20°26′33″N) of the Alejandro de Humboldt National Park (AHNP), Guantanamo province, which ranges in elevation between 700 and 850 m above sea level (masl), but higher elevations up to 1,175 masl exist in the area. El Toldo is covered by rainforest vegetation with an annual rainfall of 1,800-4,000 mm, and forms a protected area for the conservation of the almiquí (Solenodon cubanus, also referred to as Atopogale cubana, see Turvey et al. this issue, but see Sato et al. 2016), the hutias (Mesocapromys melanurus and Capromys pilorides), and other endemic vertebrates of conservation concern. The AHNP is the single most important area for biodiversity in the Caribbean Islands (CNAP 2013). Diets of feral cats were studied at a 2nd site in the Refugio de Fauna Cayo Campo (-82°18.5′1″W, 21°34′34″N), which covers an area of 213.7 km<sup>2</sup> in the Canarreos Archipelago of southern Cuba. This protected area is drier with an annual rainfall of around 1,000 mm, and is home to a native population of C. pilorides and other endemic vertebrates.

Distribution maps.—We generated distribution maps for extinct and extant native mammals using records obtained from the literature, museum databases, personal communications, and from our own field survey data collected across Cuba over a 20-year period. Point occurrences were compiled into a database of 3,086 records of all species of extinct and extant native Cuban mammals occurring in 1,227 localities, all of which were georeferenced. Geographic information system software (ArcGIS 10.2; ESRI, 2013) was used to divide a map of the Cuban archipelago into 1,360 grid cells of  $10 \times 10$ km resolution. We mapped the number of unique species that occurred in each cell considering 4 major groupings: all species, and terrestrial, volant (bat), and endangered species. The spatial limits of each category were automatically established using the "natural breaks" classification with the Jenks' optimization algorithm in ArcGIS (Brewer 2005). Data classes were based on natural groups, i.e., those that identify the group of species with most similar values that maximize the differences between classes. To assess the degree to which Cuban mammals are represented in the existing protected area system, we overlaid species occurrences onto the layer of Cuba's 121 protected areas (CNAP 2013). We then calculated the percentage of occurrences for each extant species that lies within protected areas. Separate maps were generated for extant and extinct species.

Data analysis.—We conducted an extensive bibliographic review of native and invasive Cuban mammals, and updated this information with our unpublished data and experience. We reviewed 103 management plans of Cuban protected areas, many of them updated for native mammals in the new System Plan of Protected Areas 2014–2016 (CNAP 2013), and we reviewed 86 management plans with data on invasive mammals.



**Fig. 1.**—Maps of the Cuban archipelago showing: A) digital elevation model with geographical regions and relevant localities for Cuban mammals, B) the annual mean precipitation gradient (Hijmans et al. 2005; data available at <a href="http://www.worldclim.org/">http://www.worldclim.org/</a>), and C) natural vegetation (dark) and anthropogenically modified areas (e.g., forestry, agriculture, and human settlements) based on **Estrada et al.** (2011); the map also shows the outline of National System of Protected Areas (CNAP 2013).

The management plans of protected areas with legal administration are available as unpublished manuscripts from the National Center for Protected Areas (CNAP, Spanish acronym).

We organized the information profile of each Cuban mammal species, including synonymies, status (referring to level of endemism and whether living or extinct), diet, habitats, body mass, abundance, and distribution (Appendix I). Using these data, each species was classified according to the extent of their geographic distribution in quartiles of the following classes: restricted or localized range (0.07–0.88%), moderate (0.89–2.35%), wide (2.36–4.56%), and widespread (4.57–12.6%). Although our mapping effort in some instances misrepresented poorly surveyed localities, it provided the best resolution available from current data. Based on the degree of specialization for certain types of roosts and habitats, we assigned volant and terrestrial mammals to the following classes: generalist species (G), including species that have been observed using man-made

structures as roosts for bats; cave-dwelling species (C), highly dependent on caves for diurnal habitat or roosts; tree-dwelling species (T), that use trees as habitat or roosts; and terrestrial-dwelling species (TR), that use the ground and karstic zones. Diet was used to classify them as frugivore, folivore, nectarivore, insectivore, piscivore, or hematophage.

For fossil species, ecological information was estimated from inferences of body size of living relatives and the expectation that each species' behavioral repertoire was likely similar to that of its extant relative. Within this general framework, we aimed to evaluate past extinction processes, the causal role of invasive species, and the present vulnerability of surviving native species to extinction.

Endemic Cuban mammals, their conservation status, and threats are considered, including conservation categories for mammals in the Cuban Vertebrates Red Book (Table 1; Mancina 2012). We also summarized interactions among

Table 1.—Endemic mammals (species and subspecies) in Cuba and their conservation status and threats. H, hunting; IM, invasive mammals; HD, habitat destruction; RD, extremely restricted distribution; and CC, climate changes. Invasive mammal interactions: invasive mammals sharing distribution, habitat, and refuges producing possible impacts. Invasive mammals listed in bold font have high impacts (predation and competition); invasive mammals listed in regular font have lesser impact on endemic mammals. Invasive mammals sharing distribution, but without recognized impacts on endemic mammals are not included. Status: EN, endangered; VU, vulnerable; and CR, critical endangered. Invasive mammals: Cf, Canis familiaris; Fc, Felis catus; Ha, Herpestes auropunctatus; Rr, Rattus rattus; Mm, Mus musculus; Dm, Dasyprocta mexicana; Dp, Dasyprocta punctata; Cp, Cuniculus paca; Ss, Sus scrofa; Sf, Sylvilagus floridanus; Oc, Oryctolagus cuniculus; Bt, Bos taurus; Bb, Bubalus bubalis; Ce, Chlorocebus aethiops; Mf, Macaca fascicularis; and Ma, Macaca arctoides.

Endemic Cuban mammals	Red Book of Cuban Vertebrates 2012	Threats	Invasive mammal interactions	Cause of habitat destruction
Rodentia				
Capromys pilorides		H, IM, HD	Cf, Fc, Ha, Rr, Mm, Dm, Dp, Cp, Ss, Sf, Bt, Bb, Ce, Mf, Ma	Tourism Agriculture Mining
C. p. pilorides		H, IM, HD	idem	Deforestation Urbanization Tourism
				Agriculture Mining Deforestation Urbanization
C. p. ciprianoi		H, IM, HD	Cf, Fc, Rr, Mm, Ss, Oc	Tourism
C. p. relictus		H, IM, HD	Cf, Fc, Rr	Deforestation
C. p. doceleguas		Н	Fc, Rr	Tourism
C. p. gundlachianus		Н	Cf, Fc, Rr, Mm, Ce, Ma	Tourism
Capromys garridoi <sup>a</sup>	CR?	IM, RD	Fc, Rr	Tourism
Mysateles prehensilis		H, IM HD, RD	Cf, Fc, Ha, Rr, Mm, Dm, Dp, Ap,	Deforestation
			Ss, Sf	Agriculture Tourism
M. p. prehensilis		H, HD	Cf, Fc, Ha, Rr, Mm, Dm, Dp, Ap, Ss, Sf	Deforestation Agriculture
				Tourism
M. p. gundlachi		H, HD, IM	Cf, Fc, Rr, Mm	Deforestation
M. p. meridionalis		H, IM, HD, RD	Cf, Fc, Rr, Ss, Mm	Deforestation
				Tourism
Mesocapromys angelcabrerai	CR b2a	H, IM, RD, CC	Rr	Tourism
				Climate changes
Mesocapromys auritus	CR	IM, HD, RD, CC	Rr	Mining
				Climate change
Mesocapromys nanus <sup>b</sup>	CR D; B1a	IM, HD, RD, CC	Cf, Fc, Ha, Rr, Mm, Ss	Deforestation Fire
				Agriculture Climate change
Mesocapromys sanfelipensis <sup>b</sup>	CR B2a	IM, HD, RD, CC	Cf, Fc, Rr, Rn	Fire
Mesocapromys melanurus	VU B2b(i,ii,iii)	H, IM, HD	Cf, Fc, Rr, Mm, Ss	Deforestation
	, 6 226(1,11,111)	11, 111, 112	01, 20, 211, 11111, 55	Mining
Soricomorpha	CD D11 (' '' ''') C2 (1)	IM IID DD	Cf. F. D. M. G.	Mining
Solenodon cubanus	CR B1b(i,ii,iii); C2a(1)	IM, HD, RD	Cf, Fc, Rr, Mm, Ss	Mining Deforestation
Chiroptera Natalus primus	CR B1ab(iii,v) c(iv)	IM, HD, RD, CC	Fc, Rr	Deforestacion
				Tourism
				Climate change
Chilonatalus macer		IM, HD	Fc, Rr	Deforestation Agriculture Tourism
Nycticeius cubanus		HD		Deforestation Agriculture
Lasiurus pfeifferi		HD, CC		Deforestation Agriculture Climate change
Dasypterus insularis	VU B2ab(i,iii)	HD, RD, CC		Deforestation Agriculture
Antrozous koopmani	EN B2ab(i,ii)	HD, RD, CC		Deforestation Agriculture Climate change
Mormopterus minutus	VU B1b(ii,iii)	HD, RD, CC		Agriculture Deforestation
				Climate change
Phylonypteris poeyi		IM, HD	Fc, Rr	Agriculture
1 nywnypieris poeyi		1141, 1112	rc, Mi	Deforestation
				Climate change
				Chinate change

<sup>&</sup>lt;sup>a</sup>This species was not included originally in the Cuban Vertebrate Red Book because it has a doubtful taxonomic status, known only from a single specimen. <sup>b</sup>Species possibly extinct.

invasive mammals, including a list of species sharing distributions in protected areas, offshore islands, and other habitats with endemic Cuban mammals, and the influence of human activity and economic development on the native fauna.

The top 3 threats to conservation of Cuban mammals are invasive species, habitat destruction, and hunting, as previously identified by Borroto-Páez et al. (2012a). We evaluated the cumulative increase in each of the introduced vertebrate species in Cuba (168 species, from unpublished data) and discuss key mammal introduction events. The list of introduced Cuban mammals (Appendix II) was updated from Borroto-Páez (2009, 2011b) and Borroto-Páez and Woods (2012b). We recorded all human-caused introduction events (accidental or intentional), excluding mammals brought to Cuba for zoo exhibitions if they have never lived in wild conditions. For each invasive species, we provided their introduction date, source of introduction, pathways, number of protected areas invaded, and offshore islands where information on levels of interaction and impacts are available. We defined 4 categories of introduced species following Borroto-Páez et al. (2015), consistent with their presence in Cuba: 1) invasive (INV), including those invasives restricted to limited areas (LINV); 2) established noninvasive (ENI); 3) not established (NES); and 4) transported (TRAN). These categorizations are based on an introduced species' stage in the invasion process: transport, introduction, release, establishment, or spread.

The level of interaction among introduced and native mammals was considered as high, medium, low, and none relative to their degree of overlap in distribution, habitats, and refuges; evidence of predation and competition; number of protected areas that are invaded; and links to possible extinction in past and recent times. The level of impact was evaluated following Hawkins et al. (2015), who proposed the IUCN Environmental Impact Classification for Alien Taxa (EICAT) with 7 categories: minimal concern (MC), minor (MN), moderate (MO), major (MR), massive (MV), data deficient (DD), and no alien population (NA).

We followed Duncan et al. (2003) regarding the biological concept of invasion. This definition explicitly excludes any connotation of impact to define a species as invasive and is based exclusively on ecological and biogeographical criteria: species that have been deliberately or accidentally transported by humans to a new location beyond their normal geographic range limits.

Additionally, we used trapping data to study the density of black rats in the habitat of Cuban *Solenodon*. Also, we examined scats of feral cats to infer their diet in the same *Solenodon* habitats and in an offshore island habitat.

Trapping.—We performed a rapid assessment of black rat density at the El Toldo site with live traps baited with either toasted coconut or bread with pig fat and used the removal method of Wilson et al. (1996). We set 10–16 Sherman traps at each of 3 plots near water sources for 7–11 days. Each plot contained 2 trap lines separated by 5 m with traps set every 10 m, and each plot covered an area of 750–1,200 m². Traps were pre-baited for 2 days prior to being activated to enhance trap success, and were examined 2 times during the night. All animals were removed, after transferring into a black bag and

killed by cervical dislocation using procedures listed in Sikes et al. (2016) and AVMA (2013). Trapping data were analyzed with Ecological Methodology software, using a Catch-Effort Model for Exploited Populations (Krebs 2003).

Diet.—We examined 83 scats collected from feral cats, which consisted of 43 scats collected in March 2012 from *S. cubanus* habitat in El Toldo, AHNP, and 40 scats collected in May 2011 from *C. pilorides* habitat in Cayo Campo. Scats were collected to broadly survey the diet of feral cats at El Toldo by walking a line transect for 4 h over 13 successive days around our camping place, and at Cayo Campo using a transect of 500 m on an open trail and with dusty places appropriate for the hiding of scats by cats.

Scats were softened in 95% alcohol and broken with a scalpel and small forceps to enable prey items to be visually sorted by type and species under a magnifying lamp. Bones and fragments were compared with bones of a reference collection and the results are presented in terms of frequencies of occurrence (Hervías et al. 2013).

Nomenclature.—For most bat species, we follow the systematic arrangement of Simmons (2005) except for Natalidae (Tejedor 2011). The taxonomic status of Antrozous koopmani Orr and Silva Taboada, 1960, remains unclear; it is here retained as an endemic species and distinct from A. pallidus pending further study. Although several authors have treated Phyllonycteris poeyi as a polytypic species common to Cuba and Hispaniola (e.g., Koopman 1993; Simmons 2005; Dávalos and Turvey 2012), we followed Silva Taboada (1983) in considering P. poevi a monotypic species endemic to Cuba. Simmons (2005) considered Eumops ferox as a synonym of E. glaucinus, but more recently McDonough et al. (2008) concluded that E. ferox is a distinct species restricted to the Caribbean islands and Central America. The Cuban subspecies of the common vampire bat (Desmodus rotundus) was raised to specific rank (D. puntajudensis Woloszyn and Mayo, 1974) by Suárez (2005). However, based on newly available specimens, Orihuela (2011) found that Cuban specimens fell within the range of variation observed in D. rotundus, a determination that we followed here. For the taxonomy of terrestrial mammals (capromyids and soricomorphs), we follow the last reviewers (Woods and Kilpatrick 2005; Silva Taboada et al. 2007; Mancina and Borroto-Páez 2011; Borroto-Páez et al. 2012b; Kilpatrick et al. 2012; Upham and Patterson 2015). We reject the result of Leite and Patton (2002) and Fabre et al. (2014) considering Capromyidae as part of Echimyidae because these analyses did not include all capromyid variation or lacked the statistical support to reject the reciprocal monophyly of those 2 clades.

#### RESULTS

Native mammals.—Cuban terrestrial mammals include 59 species of fossil or extant mammals, including 38 endemic species (64.4% endemism). The 24 fossil Cuban mammals are represented by 5 orders: Soricomorpha (2 species), Pilosa (5), Rodentia (7), Primates (2), and Chiroptera (8), and all fossil species are endemic to Cuba, except 2 fossil bats and 1 soricomorph also found on Hispaniola. The 35 extant species of terrestrial Cuban mammals are represented by 8 rodents,

1 soricomorph, and 26 bats. Of the extant mammals, 17 are endemic to Cuba (48.6%). Extant and extinct bats have the highest richness among the Cuban mammals with 34 species of which 14 are endemics (41.2%).

Seventeen of the living species of Cuban mammals have geographic ranges that are either widespread (9) or wide (8), 9 have moderate distributions, and 9 are range-restricted microendemics. The 11 threatened species have restricted (8), moderate (2), or wide (1) distributions; 6 of the 8 restricted species are limited to only 1 locality (Table 1). All range-restricted species are considered threatened by the Cuban Vertebrates Red Book. According to the Cuban Vertebrates Red Book, 10 species are considered threatened including 6 as Critically Endangered, 1 as Endangered, and 3 as Vulnerable (excluding *Capromys garridoi*, which is not categorized in the Cuban Red Book because of its uncertain taxonomic status; Table 2). Many invasive mammals, including those with highly invasive impacts globally, are co-distributed with endemic mammal species and in many instances share the same refuges or burrows.

Many extant and extinct Cuban mammals have (or have had) a folivorous diet, including all capromyid and echimyid rodents, megalonichid sloths, and primates. Insectivory is present in 22 bats and 3 soricomorphs. Ten species are phytophagous bats, 1 is piscivorous, and the extirpated Desmodus rotundus puntajudensis feeds on blood. A large proportion of Cuban mammals use the canopy of primary and secondary forest trees as foraging habitat and refuges. Fourteen living and extinct species (excluding bats) are tree- or ground-dwelling. Mesocapromys angelcabrerai and some populations of C. pilorides have specialized habitat requirements and are restricted to mangrove forests (i.e., Rhizophora mangle), and M. auritus is strongly linked to mangroves. Mysateles prehensilis is a strictly arboreal species. C. pilorides (sensu lato) is the capromyid species with greatest ecological plasticity, using caves, ground, trees, mangroves, and karst, among other refuge sites. Among bats, close to 60% of species are facultative or obligate cave dwellers, whereas the remainders are tree-dwelling or have generalized roosting habits. However, various habitats are or were used by Cuban mammals at one time: wet and dry forest, mangroves, scrublands, xerophytic areas, karstic areas, caves, and swamps.

The almiquí (*S. cubanus*) today is confined to only 2 regions in eastern Cuba: the National Park Alejandro de Humboldt where they have been observed and studied in the El Toldo plateau of Guantanamo province more recently (Sato et al. 2016) and the National Park Pico Cristal of Holguin province. The almiquí feeds upon arachnids, myriapods, and insects and their

grubs. Both localities are within rain forest and a thick accumulation of dead leaves under which the almiquí find refuge.

Distribution maps (Fig. 2A-D) illustrate the observed richness patterns for extant Cuban mammals. Highest-diversity areas coincide with areas of mountainous terrain, wetlands, and the coastal zone. Archipelagos contain key distributions of extant mammal species, thus are central to the conservation goals of the SNAP. However, distribution records appear to be biased by collection effort and road infrastructure (i.e., clustered effort around major cities), and no data are available for several areas of eastern Cuba. The highest and middle levels of species richness are concentrated in mountain systems (Fig. 2A). The plotted terrestrial mammal distributions show (Fig. 2B) the highest richness in the AHNP, Sierra Maestra, and Zapata Swamp. The map of bat species richness illustrates many areas without records of bats. However, several grid cells harbor 13–18 species (Fig. 2C) at localities associated with karst formations, thus containing abundant caves (e.g., "Caguanes" National Reserve or the long-term bat studies of "Sierra del Rosario" Biosphere Reserve). The eastern part of Cuba has the highest concentration of endangered Cuban mammals coexisting with populations of Solenodon and M. melanurus (Fig. 2D).

For fossil species (Fig. 3), the abundance and distribution of bone remains provides an estimate of historical levels of abundance. Pleistocene–Holocene extinct taxa such as *Boromys*, *Nesophontes*, and other extinct capromyid rodents were distributed across the country and probably were abundant, with accumulations of small bones resulting from owl pellets in some caves. Large mammals were abundant as well, e.g., *Megalocnus rodens* and other sloths have an extensive fossil record in Cuba. We estimate that 17 species (73.9%) of the 23 extinct Cuban mammals could be considered historically abundant and widely distributed based on the distribution of fossil remains. Western Cuba has the greatest number of fossil localities, followed by the central part, and an eastern region with few localities and many areas without exploratory effort (Fig. 3).

Non-native mammals.—Between 1509 and 2015, 168 Cuban vertebrates were introduced (Fig. 4). Several introduced species (e.g., black rats, cats, dogs, and pigs as the most impactful invasive mammals) with the greatest ecosystem impacts arrived soon after colonization, and 2 other high-impact introductions (brown rats and mongooses) arrived before 1900. From 1980 to 2000, several big game mammals (Equus zebra granti, Antilope cervicapa, Boselaphus tragocamelus, Taurotragus derbianus, and Ammotragus lervia) were introduced in protected areas or game reserves, here categorized as local invasives among the

**Table 2.**—Rapid estimates of density for black rats (*Rattus rattus*) in *Solenodon* habitat in Alejandro de Humboldt National Park (March 2012) by removal trapping.

Plot	Date	Area in m <sup>2</sup>	Rats/ha $\pm$ $SE$		
			Leslie regression model	Ricker semi-log regression model	
1	March 2012	1,200	313.66 ± 18.4	322.25 ± 2.9	
2	March 2012	1,200	$176.92 \pm 4.1$	$146.58 \pm 0.9$	
3	May 2010	750	$268.0 \pm 4.8$	$214.3 \pm 0.9$	

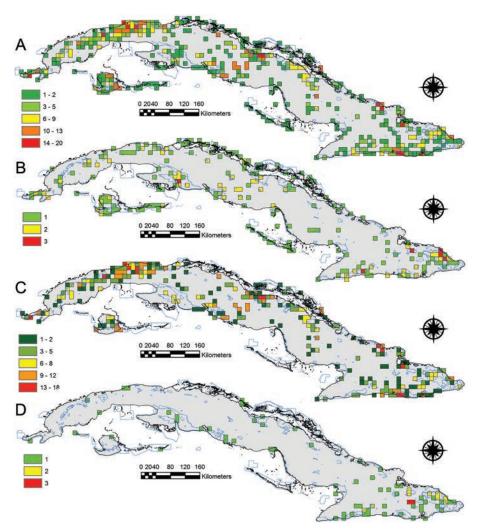


Fig. 2.—Distribution patterns of the observed richness of extant Cuban mammals: A) all 35 native species; B) 9 terrestrial species; C) 26 bat species; and D) 11 endangered species. Different colors on the map indicate the number of species per grid cell  $(10 \times 10 \text{ km})$ , with 864 point localities of species observations included.

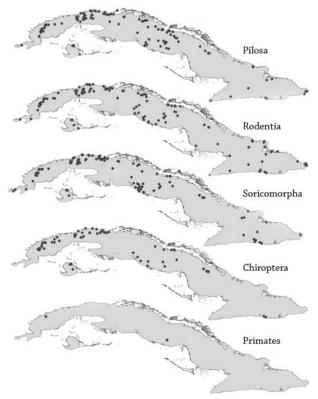
complete list of 44 introduced mammals in Cuba (Appendix II). In order of commonness, reasons for introduction were for food, hunting, colonial transportation, and protection (in the instance of the dog and horse, they were also a conquering weapon), livestock, and pets. Introductions of black rats, brown rats, and house mice were not intentional.

Introduced or invasive mammals are identified in the management plans of many (77) protected areas, and 67 offshore islands have information on the presence of at least 1 invasive mammal. The protected areas with the most introduced or invasive mammals are: Sierra del Chorillo in Camagüey (18 species), Mil Cumbres in Pinar del Río (15), La Coca in Havana (13), and Humedal de Cayo Romano and northern Camagüey (13). Eleven protected areas have at least 10 invasive mammals. Although black rats are present in almost all natural areas, and on at least 64 offshore islands, not all protected areas include it in their management plan and many other offshore islands need assessment. Only 2.1% of the islands have been assessed for presence of black rats; however, it is the most widespread and abundant invasive mammal in Cuba. Cats, dogs, mongooses,

and pigs also are widely distributed in these conservation areas. The Cuban mainland contains 32 invasive mammals, whereas the number of sympatric invasive mammals on successively smaller islands are: Isla de la Juventud (14), Romano (15), Guajaba (11), and Sabinal (9). Another 4 islands have 5–8 invasive mammal species.

For 37 introduced mammals, we evaluated their level of interaction with native mammal species. Eleven (29.7%) introduced species have a high (7) or medium (4) interaction level, based on their degree of sharing total distribution, distribution in protected areas, habitat type, and their direct impact. For the remaining 26 introduced species (72.3%), the interaction is considered as low (11) or unknown (15). However, a more general analysis considering each introduced species' level of environmental impact illustrates that 27 species (72.9%) have some type of impact: massive (7), major (4), moderate (3), minor (3), or minimal concern (7). Thirteen species are data deficient or without a population in the wild (no alien population).

Currently, species richness of all invasive mammals (33) is similar to that of native Cuban mammals (35; Fig. 5). There



**Fig. 3.**—Distribution patterns of 5 orders of fossil Cuban mammals, based on a database of 1,332 individual records and 363 localities.

is a risk that other introduced, but noninvasive mammals, will become invasive in the future.

Density of black rats.—Our rapid assessment in El Toldo found black rats ranged in density from 147 to 322 individuals/ ha within the habitat occupied by *S. cubanus* (Table 2). Three plots were located at a locality where *Solenodon* scats had been collected in the previous few days. Plot 2 had the lowest density of these 3 sites, possibly because it was disturbed by participants from our expedition.

Diet of feral cats.—In Cayo Campo, an insular ecosystem with coastal sandy vegetation, cat scats contained invertebrates (crab and insect remains) in 25% of the samples, lizards in 5%, birds in 20%, and hutias (Capromys cf. pilorides) in 52.5% of the samples. The latter item was the most frequently observed prey in the diet of feral cats (Table 3). Black rats and house mice were found in 27.5% and 12.5% of scats, respectively. The hutia population at Cayo Campo could be assigned a high level of conservation concern if the taxonomic status of this population is accepted as a species or subspecies-level taxon (Upham and Borroto-Páez this issue). C. pilorides (~2.5 kg) might represent 1 of the largest prey items taken by feral cats (1–1.5 kg) yet known globally, although the body size of cats in this instance is unknown. Interviews with the rangers that guard the key of Cayo Campo indicate that the cat population is large, but the density of these predators has never been evaluated.

In El Toldo, which has montane rainforest vegetation, our analysis of cat scats shows a greater variety of diet items: insects (23.3%), birds (2.3%), hutias (13.9%), *Solenodon* (4.7%),

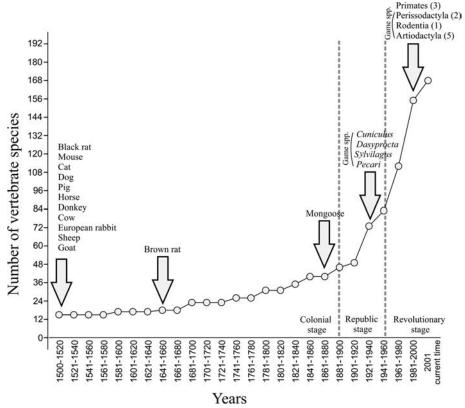
black rats (48.8%), and at least 6 different unidentified species of herpetofauna (2 amphibians, 2 lizards, and 2 small ophidians, which were separated on the basis of size) with frequencies between 2.3% and 65.1%. There was a minimum of 44 individuals in the herpetofauna, and *Anolis* lizards were found with the highest frequency (Table 3). This is the 1st reported evidence of predation on *Solenodon* by feral cats.

#### DISCUSSION

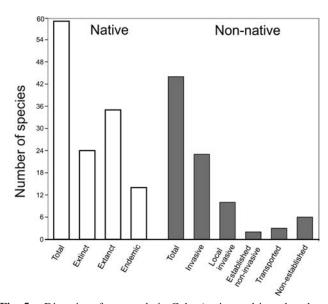
Biodiversity.—Estimates of the number of West Indian mammals have varied considerably. A recent checklist recognized 71 species of extant and extinct terrestrial mammals, excluding bats, but also 16 undescribed species (Borroto-Páez et al. 2012b), whereas another list, that included bats, tallied 99 mammal species for the region (Dávalos and Turvey 2012). Several recent reviews have attempted to simplify the nomenclature with consideration of synonymies, aiming to provide a more accurate number of fossil rodent and sloth species in Cuba (Silva Taboada et al. 2007; Mancina and Borroto-Páez 2011; Borroto-Páez et al. 2012b). These taxonomic reviews have recommended synonymy in instances where insufficient and fragmented fossil material was used for description, if fossil taxa are of similar size, form, or geographic distribution, and with consideration of the extent of morphological variation present in related extant taxa (Silva Taboada et al. 2007; Mancina and Borroto-Páez 2011; Borroto-Páez et al. 2012b). However, modern Cuban biodiversity is still being documented with the high likelihood of new taxa being detected, especially by use of molecular analyses to uncover patterns of genetic variation (Woods et al. 2001; Borroto-Páez 2002; Borroto-Páez et al. 2005; Borroto-Páez et al. 2012b; Kilpatrick et al. 2012). This includes the possibility of C. pilorides being a species complex (see Upham and Borroto-Páez this issue).

Bats represent the largest proportion of the native Cuban mammal fauna in terms of species richness and estimated abundance of individuals. Twenty-six species comprise the modern bat fauna, with another 8 species known to be extinct or extirpated from Cuba (Appendix I), making Cuba's bat fauna the richest in the West Indies with more than 45% of all species in the Caribbean region (Willig et al. 2009). The bat fauna includes 8 species endemic to Cuba, which comprise most of the bat lineages endemic to the West Indies, and also harbors vespertilionid and molossid bats with continental affinities absent from other West Indian islands. This bat diversity is favored by Cuba's relatively large surface area, its geographical proximity to North and Central America, high habitat complexity, and the abundance of roost-rich environments such as cave-bearing karst regions (Silva Taboada 1979; IGACC-ICGC 1989).

Extinctions.—Fossil evidence suggests that West Indian mammals have suffered the highest recent extinction rate of any major region in the world (Morgan and Woods 1986; MacPhee and Flemming 1999). In Cuba, at least 23 species became extinct during the Pleistocene—Holocene period (Table 1). End-Pleistocene climate change and human arrivals are 2 main factors commonly invoked to explain these high



**Fig. 4.**—Cumulative growth in 168 vertebrate introductions in Cuba. Times for introduction of important non-native mammals is shown during 3 historical stages.



**Fig. 5.**—Diversity of mammals in Cuba (native and introduced species). Data from Tables 1 and 3.

extinction rates (Morgan and Woods 1986; MacPhee 2009; Turvey 2009). Similar to other Antillean islands (see Morgan 2001), disappearance and collapse of caves, as well as changes to cave microclimates, related to flooding via rising sea levels during the Pleistocene–Holocene transition presumably affected many cave-dwelling bat populations and contributed to the extinction of species such as *Pteronotus pristinus* and *Mormoops magna* (Silva Taboada 1974). Moreover, habitat and environmental changes that occurred during this period (see

**Table 3.**—Diet of feral cats (*Felis catus*) as % of occurrence of food category (number of individual scats containing each item/total number of scats × 100) in 2 important conservation areas: *Solenodon cubanus* forested habitat and *Capromys* sp. island habitat.

Food item	Forest habitat	Island habitat			
	El Toldo, $n = 43$	Cayo Campo, $n = 40$			
	% of occurrence				
Native species					
Vegetal fiber	23.3 (10)	17.5 (7)			
Insect	23.3 (10)	7.5 (3)			
Crab		17.5 (7)			
Amphibian (size 1)	2.3(1)				
Amphibian (size 2)	2.3(1)				
Anolis lizard (size 1)	65.1 (28)	5.0(2)			
Anolis lizard (big	6.9 (3)				
size 2)					
Ophidian 1	23.3 (10)				
Ophidian 2	2.3(1)				
Bird	2.3(1)	20.0(8)			
Hutia (Capromys)	13.9 (6)	52.5 (21)			
Solenodon cubanus	4.7 (2)				
Invasive species					
Black rat	48.8 (21)	27.5 (11)			
House mouse		12.5 (5)			

Curtis et al. 2001) also likely impacted many forest-dwelling bats (e.g., *Phyllops* spp. and *Cubanycteris silvai*), and probably terrestrial mammals. However, sloths, bats, soricomorphs, and rodents survived until the mid-Holocene or even later, corresponding to the 1st human arrivals to the Antillean region, and many years after the arrival of colonialists in 1509 (MacPhee

and Flemming 1999; Turvey et al. 2007; MacPhee 2009; Turvey 2009). In Cuba, several extinct or extirpated mammals have been documented, and in some instances radiometrically dated, from archaeological sites (e.g., *Artibeus anthonyi*, *D. rotundus*, *Parocnus brownii*, *M. rodens*—MacPhee et al. 2007; MacPhee 2009; Orihuela 2012), thereby demonstrating that their populations survived up to the late Holocene.

Dogs (Canis familiaris) were first introduced by Amerindians. This species may have impacted biodiversity centuries prior to the arrival of other dogs and invasive mammals from Europe. European colonization introduced several of the most invasive mammal species and resulted in widespread transformation of the ecosystem and habitats through deforestation for agriculture, livestock grazing, and eventually urbanization. However, extinctions of Cuban mammals are not all ancient events; we have 3 small species considered as critical endangered—Mesocapromys sanfelipensis, M. nanus, and C. garridoi—whose real status of extant or extinct is uncertain. Both species of Mesocapromys could be considered extinct as the animals were overharvested, likely impacted by competition or predation from invasive mammals, last observed almost 40 years ago, and their habitats have since been fragmented or eliminated (Silva Taboada et al. 2007; Borroto-Páez 2011a). C. garridoi is known from only 1 partial individual with an uncertain locality. Each of these species requires additional effort to plan and execute field research that will identify and assess any surviving populations and confirm their actual conservation status.

Habitat destruction.—Several human activities have altered and destroyed habitats in Cuba since the start of colonialism. During the initial colonization period (1509-1902) of 392 years, the rearing of livestock, growth of agriculture (principally of sugar cane), and urbanization resulted in a reduction in forest cover from 88-92% to 54% while the human population reached 1.6 million. These enormous transformations continued during the Republican period (1903–1959). By 1959, the human population in Cuba had increased to 6 million and forest cover was reduced to 14% of its pre-colonial extent. This directly affected the habitat of all native mammals, most of which are herbivorous or use the forest canopy for refuge and subtract. Present factors affecting habitat destruction in Cuba include development of tourism, which has been the principal cause of deforestation, followed by mining to exploit mineral deposits, which threatens several endemic species. For example, the distribution of S. cubanus overlaps with several key reserves of nickel, and the presence of oil deposits in northern coastal areas could attract oil exploration and extraction, affecting the habitat of Mesocapromys auritus.

Mangrove ecosystems are a priority habitat for hutia conservation (Borroto-Páez and Mancina 2006; Borroto-Páez and Ramos 2012), and also appear to have been part of their core habitat in the past, as well given the many paleontological sites and nearby coastline. Along with mangroves, mountains, inland forests, caves, and island ecosystems remain essential areas for conservation in Cuba. The extraordinary reduction of forest cover from 88% to 92% at the moment of European arrival to 14% in 1959 (IGACC-ICGC 1989; Risco Rodríguez

1995; Funes Monzote 2008; CNAP 2013) has without doubt had a tremendous impact on Cuba's biodiversity. Although forest cover recently was estimated to have increased to 27.27% (CNAP 2013), this number includes forests plantations with non-native trees for exploitation, while natural forest is now estimated to cover 22.6% of Cuba's territory.

Many Cuban bat species are under threat from factors associated with deforestation and cave disturbance. Caves constitute vulnerable and critical roosts for Cuban bats. Sixteen species of bats use caves as day roosts, representing 61% of the total number of bat species known for the island (Silva Taboada 1979; Mancina 2011). Caves with hot chambers (termed hot caves) can in particular shelter multispecies assemblages, including high densities of phyllostomid and mormoopid bats, thus are critical habitats for the mostly cave-dwelling bat fauna. The Cuban Red List includes 4 bat species (Mancina 2012); however, at least 10 other species could be vulnerable to local extinctions due to their high specialization to hot-cave environments (Silva Taboada 1979; Mancina et al. 2007a). Several human activities threaten cave bats, including the exploitation of bat guano for fertilizer and other purposes, and there is evidence of impoverishment or loss of cave bat fauna because inappropriate management of caves (Cruz 1992). Other threats include the use of caves as storehouses and refuges, and disturbance from tourists and speleologists, especially in sensitive maternity roosts (Mancina et al. 2007a).

Hunting.—Hunting is among the principal treats for all species of hutias in Cuba, each of which has habitat under the umbrella of the Cuban System of Protected Areas; however, each protected area also exposes them to invasive mammals and illegal hunting (Borroto-Páez et al. 2012a). While there is no current evidence suggesting that hunting is a threat for S. cubanus, hutia populations are threatened by hunting. The principal hunted hutias are the large-bodied species C. pilorides, M. prehensilis, and M. melanurus. There are different reasons for hunting hutias, including subsistence consumption, commerce sale, hobby, and religious ceremonies. Methods of hunting include with dogs, guns, traps, snares, lassos, creels, and manual capture. Hunting is the principal cause for the decline or extirpation of local populations of C. pilorides and M. prehensilis. Occasional hunting of smaller-bodied hutias (Mesocapromys sp.) exists, but generally hunters mistake these animals for young individuals of C. pilorides and try to domesticate them to breed in captivity.

Cuban mammals played an important role in the diet and economy of pre-Columbian communities: *C. pilorides*, *Geocapromys columbianus*, *Boromys* (both species), and *Nesophontes micrus* are the most abundant species in midden remains. Sloths, dogs, and *Solenodon* also are present but less frequently (Pino Rodríguez 2012). Amerindian hunting targeted several species, but only for *Megalucnus rodens* or other large sloths does excessive hunting appear likely to have directly resulted in extinction, considering that their populations already were declining in the pre-Columbian era. Many Caribbean sloth species became extinct close to the 1st Amerindian arrivals (MacPhee et al. 2007; MacPhee 2009). We

discard overhunting as a singular cause of past extinction for the other small mammals in Cuba.

Tourism.—In the last 25 years, development for tourism has increased from 12,900 hotel rooms in 1990, to 37,225 rooms in 2002, and more than 50,000 rooms in 2014. Moreover, the number of annual visitors reached 3 million in 2014 (Rettinger and Wójtowicz 2014). Almost all development for tourism is based on transformation of insular and coastal ecosystems, which has reduced the available habitat for populations of several species of hutia. The fact that additional hotels are being constructed on isolated beaches (e.g., the south of Isla de la Juventud) is contributing to habitat destruction, increasing the hunting of *C. pilorides* for hobby and food, as well as spreading new invasive species such as rabbits (*Oryctolagus cuniculus*).

Invasive mammals.—With colonization came the arrival of small-sized invasive species such as black rats and house mice, along with middle-sized and larger mammals like cats, dogs, pigs, cows (Bos taurus), and horses (Equus caballus), which soon became pests with significant impacts on the island's ecosystems according to the accounts of chroniclers and historians (Fernández de Oviedo 1535; Ribera 1757; Crosby 1972, 2004; Zadik 2005). In 1514, Diego Velázquez de Cuéllar noted in a letter to his king that on Cuba there were 30,000 pigs—as Crosby (1972) translates, "more pigs than I ever saw before in my life." As is known, wild pigs have broadly negative impacts upon ecosystem structure and function (Bratton 1975; Oliver and Brisbin 1993; Taylor and Hellgren 1997).

While the majority of Cuban mammals are considered small mammals, nearly all extinct species are smaller in body size than dogs, cats, and pigs (Appendix I), with the exception of the megafaunal sloth. Body masses of Boromys torrei, B. offella, and N. micrus were similar in size or smaller (40-350 g) than rats (150-300 g), suggesting that those species, along with small hutias (400-600 g), likely were vulnerable as prey of rats, cats, dogs, and pigs. Abundant bone remains of B. torrei, B. offella, N. micrus, as well as the ~1,500 g G. columbianus have been found associated with introduced Rattus in Cuba (Guarch Delmonte 1984; Pino Rodriguez 2012), which suggests an additional role for competition from rats as well as predation. Native Cuban mammals evolved in the absence of any mammalian predators, and have a relatively low rate of reproduction and metabolism (Arends and McNab 2001), in contrast to the most of introduced Cuban mammals with a high reproductive and metabolic rates and major depredation ability.

Cats and dogs also can depredate heavier species such as *C. pilorides* in our 2 study areas of El Toldo and Cayo Campo. Rams et al. (1989) reported depredations by dogs upon Cuban *Solenodon*. We have observed the destruction of *Solenodon* burrow systems by wild dogs and pigs in the AHNP (R. Borroto-Páez, pers. obs.), as well as high rates of black rat infestation in those burrow systems. We collected dog scats containing bones of *C. pilorides* in AHNP, Zapata Swamp, and Guanahacabibes (R. Borroto-Páez, pers. obs.). According to Eberhard (1988), *Solenodon* is the largest mammalian prey species to be negatively affected by cats; however, on Cuba, cats depredate

their 2 heaviest prey known globally: *S. cubanus* (900 g) and *C. pilorides* (almost 4,000 g).

Earlier studies have observed black rats occupying abandoned *Solenodon* burrow systems, including evidence of rat predation upon mollusks and abundant rat excrements (Borroto-Páez and Begué Quiala 2011; Borroto-Páez 2013). Although we expect the presence of black rats to disturb the nesting and activity of *Solenodon*, we found no direct evidence of impact by predation, competition for food, or disease transmission in this study; however, this is a subject that requires additional urgent attention.

Among invasive mammals, cats could be considered the most serious common predators of cave bats and synanthropic bats in Cuba. Sedentary populations of feral cats are known to inhabit areas adjacent to hot caves throughout the Cuban archipelago, where bats may constitute a common food item. We have observed wing remains of several species of phyllostomid and mormoopid bats from the area surrounding hot cave openings at several localities in Cuba, including Cueva la Barca, Guanahacabibes, Pinar del Río, Cueva del Indio, Tapaste, Mayabeque, Cueva de los Majaes, Siboney, and Santiago de Cuba. Similar predatory behavior by cats has been observed in caves of Puerto Rico (Rodríguez-Durán et al. 2010). In Cayo Coco, Sabana Camagüey Archipelago, depredation by feral pigs caused the reduction of a colony of Waterhouse's leafnosed bat (Macrotus waterhousei) that inhabited a little cave (Mancina et al. 2014). Additionally, black rats are common in Cuban caves; this rodent might depredate neonates and can act as a zoonotic disease reservoir, but the direct impact of rat populations on cave bat faunas has not been studied.

Rats have broad niches, so on islands in the absence of congenerics they tend to occupy all available habitats at varying densities depending on suitability and the presence of predators (Harper et al. 2005; Russell et al. 2011; Harper and Bunbury 2015). Body size is an important life parameter related to structural niche exploitation, given that species with similar size can use the same type of refuges. Rats in the wild use many different refuges in the 3 habitat dimensions of canopy, branches, and floor; frequently, they use small holes into roof systems, rock crevices, and caves for nesting (Borroto-Páez 2013). If Nesophontes and Boromys species also formerly used these types of refuges, then rats may have quickly overlapped their niches, but with an unknown level of competitive advantage. While invasive rats are successful on oceanic islands mainly due to the paucity of other small rodents able to compete with them, on continents or large near-shore islands like Cuba, the more diverse range of functionally equivalent competitors is expected to limit the advantage of rats (Corlett 2010; King et al. 2011). However, Rattus is a conservation dilemma on big islands too, like Madagascar (Goodman 1995).

We consider the extraordinary level of perturbation caused by invasive mammals in Cuba (predation, competition for food and refuges, diseases, and transforming native habitats) after the arrival of Europeans to be a significant factor in the decline, extirpation, and extinction of several small, terrestrial Cuban mammals. Probably, the introduction of many diseases and parasites with invasive mammals had a large impact (MacPhee and Marx 1997). Within the first 50 years of colonization, 10 non-native mammals (black rats, house mice, cats, dogs, pigs, horses, cows, sheep, goats, and probably rabbits) had been introduced, released, established, and become invasive. The presence of many co-occurring invasive species also implies mutualist interactions, which may have acted in concert to worsen the total disease consequences for native mammal communities (e.g., Courchamp et al. 2003).

Invasive mammals on islands have been the cause of the extinction or extirpation of small mammal species around the world (Courchamp et al. 2003; Towns et al. 2006; Harris 2009; Varnham 2010; Banks and Hughes 2012; Harper and Bunbury 2015). On small islands, single individual predators can cause extinction (e.g., Buller 1905; Clough 1976; Vázquez-Domínguez et al. 2004), as was the case for the hutia (*Geocapromys throracatus*) of Swan Island by the presence of a single cat combined with a hurricane in the 1950s (Clough 1976). Moreover, such hyper-predation by a single individual can occur rapidly (Taborsky 1988; Diamond 1989; Courchamp et al. 2003).

Conservation.—Today, the Cuban National System of Protected Areas (SNAP) covers populations of all Cuban mammal species to protect against habitat destruction (Borroto-Páez et al. 2012a). However, this system does not fully prevent negative impacts from hunting and invasive mammals, largely as a result of incomplete information about native species for most of the SNAP management plans. We recommend environmental education involving local people to help mitigate the effects of hunting, and that more actions of invasive mammal control and eradication must be planned, especially of cats, pigs, dogs, and rats. All threatened species are located in isolated areas difficult to regularly visit, and local funding for research, assessment, and monitoring is extremely limited.

Six Cuban mammals have narrowly circumscribed distributions that pose an additional threat to their survival, with populations limited to 1 locality, offshore island, or small region (M. auritus, M. angelcabrerai, M. sanfelipensis, M. nanus, C. garridoi, and Natalus primus). Restricted distributions pose a high risk for extinction after extreme climate events like hurricanes, and in the long term from changes in sea level. These species require research effort, assessment, and monitoring, perhaps including novel relocations to extend their distributions. To date, efforts are effectively nonexistent for ex situ conservation at Cuban zoos or captive breeding of the threatened Cuban mammals.

Our knowledge of bat species richness in Cuba (Fig. 2C) illustrates large areas without information, and bat caves that have not been surveyed for several decades (Silva Taboada 1979). Upon analysis of 45 management plans for protected areas, we found that 70% lack records of bats, and recent work using ecological niche models has identified several protected areas with high potential species richness, including the presence of threatened species (Mancina and Fernández de Arcila 2013). However, several localities are known to shelter more than 13 bat species, which is more than half the overall species

richness of Cuba. These localities are associated with caverich karst formations, and include areas of long-term bat studies such as "Sierra del Rosario" Biosphere Reserve (Mancina et al. 2007b; Mancina et al. 2012), as well as localities recognized as "Important Areas for Bat Conservation" by the Latin American Network for Bat Conservation (RELCOM, www.relcomlatinoamerica.net). Recorded in these areas are several threatened species and sites of high roost concentration that support unique populations of several bat species. A highlight among these sites is "La Barca" cave, Guanahacabibes, located in the western tip of Cuba, which harbors 13 species including the only known population of *N. primus*, 1 of the world's most endangered bat species (Tejedor et al. 2004; Mancina 2012).

Conserving native Cuban mammals will require concerted, information-driven efforts toward protecting their natural habitats and roosts in karstic, inland forest, and mangrove environments across the archipelago. This work should be well integrated with the needs of local communities, including employment as protected area staff and the general promotion of environmental awareness. Strategic plans should include research and monitoring as high priorities, as well as habitat management (e.g., control of invasive species, prevention of deforestation and overhunting), to increase the likelihood that suitable habitats and viable populations of Cuban mammals will be preserved for the future.

#### ACKNOWLEDGMENTS

We thank the American Society of Mammalogists for the invitation to RBP to attend the Symposium "The Last Remaining Caribbean Mammals: Conservation Priorities and the Historical Context of Extinctions in an Island Biodiversity Hotspot," during the Annual Meeting in Jacksonville, Florida in 12–16 June 2015, organized by N. S. Upham, B. K. Lim, and B. J. Bergstrom. Thanks to N. S. Upham for proposing the symposium, including a Cuban mammalogist from the start, and finding the travel funds for him to attend the meeting. Research support was provided by Rufford Small Grants (CAM) and IDEA WILD to both authors. We are very grateful to B. A. Fabres for initial review of the language and content of the manuscript, as well as to N. S. Upham for the review of this manuscript and his suggestions.

#### LITERATURE CITED

Arends, A., and B. K. McNab. 2001. The comparative energetics of 'caviomorph' rodents. Comparative Biochemistry and Physiology, A. Comparative Physiology 130:105–122.

AVMA. 2013. AVMA Guidelines for the Euthanasia of Animals: 2013 Edition. http://www.avma.org/isuue/animal\_welfare/euthanasia.pdf. Accessed December 2014.

Banks, P. B., and N. K. Hughes. 2012. A review of the evidence for potential impacts of black rats (*Rattus rattus*) on wildlife and humans in Australia. Wildlife Research 39:78–88.

Borroto-Páez, R. 2002. Sistemática de las jutías vivientes de las Antillas (Rodentia: Capromyidae). Tesis en Opción al Grado

- Científico de Doctor en Ciencias Biológicas, Instituto de Ecología y Sistemática, CITMA, C. Habana, Cuba, 100 pp. + 30 fig. + 16 tablas + 6 anex.
- Borroto-Páez, R. 2009. Invasive mammals in Cuba: an overview. Biological Invasions 11:2279–2290.
- BORROTO-PÁEZ, R. 2011a. Las jutías perdidas o fantasmas. Pp. 108–115 in Mamíferos en Cuba (R. Borroto-Páez and C. A. Mancina, eds.). UPC Print, Vaasa, Finland.
- Borroto-Páez, R. 2011b. Los mamíferos invasores o introducidos. Pp. 220–241 in Mamíferos en Cuba (R. Borroto-Páez and C. A. Mancina, eds.). UPC Print, Vaasa, Finland.
- Borroto-Páez, R. 2013. Nidos y refugios de ratas negras (*Rattus rattus*) en Cuba (Mammalia, Rodentia). Solenodon 11:109–119.
- Borroto-Páez, R., R. Alonso Bosch, B. A. Fabres, and O. Alvarez García. 2015. Introduced amphibians and reptiles in the Cuban archipelago. Herpetological Conservation and Biology 10:985–1012.
- Borroto-Páez, R., and G. Begué Quiala. 2011. El almiquí. Pp. 64–71 in Mamíferos en Cuba (R. Borroto-Páez and C. A. Mancina, eds.). UPC Print, Vaasa, Finland.
- Borroto-Páez, R., A. González Rossel, R. Fernández de Árcila Fernández, R. Estrada Estrada, L. M. Echenique Díaz, and A. Perera Puga. 2012a. Conservation of terrestrial mammals in Cuba. Pp. 229–240 in Terrestrial mammals of the West Indies. Contributions (R. Borroto-Páez, C. A. Woods, and F. E. Sergile, eds.). Wocahoota Press and Florida Museum of Natural History, Florida.
- Borroto-Páez, R., and C. A. Mancina. 2006. Importancia del mangle rojo (*Rizophora mangle*) para la conservación de las jutías (Rodentia: Capromyidae) en Cuba. Pp. 170–177 in El Ecosistema de Manglar en el Archipiélago Cubano: Estudios y Experiencias Enfocados a su Gestión. Chapter 15 (L. Menéndez and J. M. Guzmán, eds.). Editorial Academia, La Habana, Cuba.
- Borroto-Páez, R., and C. A. Mancina (eds.). 2011. Mamiferos en Cuba. UPC Print, Vaasa, Finland.
- Borroto-Páez, R., C. A. Mancina, C. A. Woods, and C. W. Kilpatrick. 2012b. Updated checklist of endemic terrestrial mammals of the West Indies. Pp. 389–415 in Terrestrial mammals of the West Indies. Contributions (R. Borroto-Páez, C. A. Woods, and F. E. Sergile, eds.). Wocahoota Press and Florida Museum of Natural History, Florida.
- Borroto-Páez, R., AND I. RAMOS. 2012. Status of the hutias (Rodentia: Capromyidae) in Los Canarreos Archipelago, Cuba. Pp. 221–228 in Terrestrial mammals of the West Indies. Contributions (R. Borroto-Páez, C. A. Woods, and F. E. Sergile, eds.). Wocahoota Press and Florida Museum of Natural History, Florida.
- Borroto-Páez, R., and C. A. Woods. 2012a. Feeding habits of capromyid rodents. Pp. 71–92 in Terrestrial mammals of the West Indies. Contributions (R. Borroto-Páez, C. A. Woods, and F. E. Sergile, eds.). Wocahoota Press and Florida Museum of Natural History, Florida.
- Borroto-Páez, R., and C. A. Woods. 2012b. Status and impact of introduced mammals in the West Indies. Pp. 241–258 in Terrestrial mammals of the West Indies. Contributions (R. Borroto-Páez, C. A. Woods, and F. E. Sergile, eds.). Wocahoota Press and Florida Museum of Natural History, Florida.
- Borroto-Páez, R., C. A. Woods, and C. W. Kilpatrick. 2005. Sistemática de las Jutías de las Antillas (Rodentia, Capromyidae). Pp. 33–50 in Proceedings of the International Symposium "Insular Vertebrate Evolution: the Palaeontological Approach" (J. A Alcover and P. Bover, eds.). Monografies de la Societat d'Història Natural de les Balears, 12.

- Bratton, S. P. 1975. The effect of European wild boar (*Sus scrofa*) on Gray Beech Forest in the Great Smoky Mountains. Ecology 56:1356–1366.
- Brewer, C. A. 2005. Drawing better maps. ESRI Publications, Redlands, CA.
- Buller, W. L. 1905. Supplement to a history of the birds of New Zealand. Publ. by author, London, United Kingdom.
- Clough, G. C. 1976. Current status of two endangered Caribbean rodents. Biological Conservation 10:43–47.
- CNAP (CENTRO NACIONAL DE ÁREAS PROTEGIDAS). 2013. Plan del Sistema Nacional de Áreas Protegidas 2014–2020. Ministerio de Ciencias Tecnología y Medio Ambiente, La Habana, Cuba.
- CORLETT, R. T. 2010. Invasive aliens on tropical East Asian islands. Biological Conservation 19:411–423.
- COURCHAMP F., J. L. CHAPUIS, AND M. PASCAL. 2003. Mammal invaders on islands: impact, control and control impact. Biological Review 78:347–383.
- CROSBY, A. W., Jr. 1972. The Columbian exchange: biological and cultural consequences of 1492. Greenwood, Westport, Connecticut.
- Crosby, A. W., Jr. 2004. Ecological imperialism. The biological expansion of Europe, 900–1900. New edition. University Press Cambridge, Cambridge.
- CRUZ, J. de la 1992. Bioecología de las grutas de calor. Mundos Subterraneos 3:7–21.
- Curtis, J. H., M. Brenner, and D. A. Hodell. 2001. Climate change in the Circum-Caribbean (Late Pleistocene to Present) and implications for regional biogeography. Pp. 35–54 in Biogeography of the West Indies: patterns and perspectives (C. A. Woods and F. E. Sergile, eds.). CRC Press, Boca Raton, Florida.
- DÁVALOS, L. M., AND S. T. TURVEY. 2012. West Indian mammals: the old, the new, and the recently extinct. Pp. 157–202 in Bones, clones, and biomes: the history and geography of recent Neotropical mammals (B. D. Patterson and L. P. Costa, eds.). University of Chicago Press, Chicago, Illinois.
- DIAMOND, J. M. 1989. Nine hundred kiwis and a dog. Nature 338:544.
  DUNCAN, R. P., T. M. BLACKBURN, AND D. SOL. 2003. The ecology of bird introductions. Annual Review of Ecology, Evolution and Systematics 34:71–98.
- EBERHARD, T. 1988. Introduced birds and mammals and their ecological effects. Viltrevy 13:1–107.
- ESCOBAR, T. R. 1995. Isla de la Juventud. Vertebrados introducidos por causas deliberadas. Editorial Científico Técnica, Pinos Nuevos, Ciudad de La Habana, Cuba.
- ESTRADA, R., ET AL. 2011. Mapa (BD-SIG) de vegetación natural y seminatural de Cuba v.1 sobre Landsat etm 7 slc-off gap filled, circa 2011. Memorias del IV Congreso de Manejo de Ecosistemas y Biodiversidad, La Habana, Cuba.
- FABRE, P.-H., ET AL. 2014. Rodents of the Caribbean: origin and diversification of hutias unravelled by next-generation museomics. Biology Letters 10:20140266.
- Fernández de Oviedo, G. 1535. Historia general y natural de las Indias, islas y tierra-firme del mar océano. Juam Cromberger, Seville, Spain.
- Funes Monzote, R. 2008. From rainforest to cane field in Cuba: and environmental history since 1492. University of North Carolina Press, Chapel Hill, North Carolina.
- Gebelein, J. 2012. A geographic perspective of Cuban landscapes, Landscape Series 15, doi:10.1007/978-94-007-2406-8\_4. Springer Science+Business Media B.V.
- González, A., N. Manójina, and A. Hernández. 1994. Mamíferos del Archipiélago de Camagüey, Cuba. Avicennia 1:51–56.

- GOODMAN, S. M. 1995. *Rattus* on Madagascar and the dilemma of protecting the endemic rodent fauna. Conservation Biology 9:450–453.
- Guarch Delmonte, J. M. 1984. Evidencias de la existencia postcolombina de *Geocapromys* y *Heteropsomys* (Rodentia). Miscelanea Zoológica 18:1.
- HARPER, G. A., AND N. BUNBURY. 2015. Invasive rats on tropical islands: their population biology and impacts on native species. Global Ecology and Conservation 3:607–627.
- HARPER, G. A., K. J. M. DICKINSON, AND P. J. SEDDON. 2005. Habitat use by three rat species (*Rattus* spp.) on Stewart Island/Rakiura, New Zealand. New Zealand Journal of Ecology 29:251–260.
- HARRIS, D. B. 2009. Review of negative effects of introduced rodents on small mammals on islands. Biological Invasions 11:1611–1630.
- HAWKINS, C. L., ET AL. 2015. Framework and guidelines for implementing the proposed IUCN Environmental Impact Classification for Alien Taxa (EICAT). Diversity and Distribution 21:1360–1363. doi:10.1111/ddi.12379.
- Hervías, S., et al. 2013. Assessing the impact of introduced cats on island biodiversity by combining dietary and movement analysis. Journal of Zoology 292:39–47.
- HIMANS, R. J., S. E. CAMERON, J. L. PARRA, P. G. JONES, AND A. JARVIS. 2005. Very high resolution interpolated climate surfaces for global land areas. International Journal of Climatology 25:1965–1978.
- IGACC-ICGC. 1989. Nuevo Atlas Nacional de Cuba. Ediciones Alber, España, Spain.
- JIMÉNEZ-VÁZQUEZ, O., M. M. CONDIS, AND E. GARCÍA-CANCIO. 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.
- KILPATRICK, C. W., R. BORROTO-PÁEZ, AND C. A. WOODS. 2012. Phylogenetic relationships of recent capromyid rodents: a review and analyses of karyological, biochemical and molecular data. Pp. 51–70 in Terrestrial mammals of the West Indies. Contributions (R. Borroto-Páez, C. A. Woods, and F. E. Sergile, eds.). Wocahoota Press and Florida Museum of Natural History, Florida.
- KING, C. M., S. FOSTER, AND S. MILLER. 2011. Invasive European rats in Britain and New Zealand: same species, different outcomes. Journal of Zoology 285:172–179.
- Koopman, K. F. 1993. Order Chiroptera. Pp. 137–241 in Mammals species of the world, a taxonomic and geographic reference (D. E. Wilson and D. M. Reeder, eds.). Smithsonian Institution Press, Washington, D.C.
- Krebs, C. J. 2003. Ecological methodology. Addison-Wesley Educational Publishers, Inc., Menlo Park, California.
- Leite, Y. L. R., and J. L. Patton. 2002. Evolution of South American spiny rats (Rodentia, Echimyidae): the starphylogeny hypothesis revisited. Molecular Phylogenetics and Evolution 25:455–464.
- Lowe, S., M. Browne, S. Boudjelas, and M. De Poorter. 2000. 100 of the World's Worst Invasive Alien Species A selection from the Global Invasive Species Database. Published by The Invasive Species Specialist Group (ISSG) a specialist group of the Species Survival Commission (SSC) of the World Conservation Union (IUCN). First published as special lift-out in Aliens 12, December 2000. Updated and reprinted version: November 2004.
- MACPHEE, R. D. E. 2009. Insulae infortunatae: establishing a chronology for late quaternary mammal extinctions in the West Indies.Pp. 169–193 in American megafaunal extinctions at the end of the pleistocene (G. Haynes, ed.). Springer, Heidelberg.
- MacPhee, R. D. E., and C. Flemming. 1999. Requiem aeternum: the last five hundred years of mammalian species extinctions. Pp.

- 333–372 in Extinctions in near time: causes, contexts, and consequences (R. D. E. MacPhee, ed.). Kluwer Academic/Plenum Publishers, New York.
- MacPhee, R. D. E., M. ITURRALDE-VINENT, AND E. GAFFNEY. 2003. Domo de Zaza, an Early Miocene vertebrate locality in south-central Cuba, with notes on the tectonic evolution of Puerto Rico and Mona Passage. American Museum Novitates 3394:1–42.
- MacPhee, R. D. E., M. A. Iturralde-Vinent, and O. Jiménez-Vázquez. 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: human, hyperdisease, and first contact extinctions. Pp. 169–217 in Natural change and human impact in Madagascar (S. M. Goodman and B. D. Patterson, eds.). Smithsonian Institution Press, Washington, D.C.
- MANCINA, C. A. 2011. Introducción a los murciélagos. Pp. 123–133 in Mamíferos en Cuba (R. Borroto-Páez and C. A. Mancina, eds.). UPC Print, Vasa, Finland.
- MANCINA, C. A. 2012. Mamíferos. Pp. 268–274 in Libro Rojo de los vertebrados de Cuba (H. González, L. Rodríguez, A. Rodríguez, C. A. Mancina, and I. Ramos, eds.). Editorial Academia, La Habana, Cuba.
- MANCINA, C. A., AND R. BORROTO-PÁEZ. 2011. Lista taxonómica comentada de los mamíferos autóctonos de Cuba. Pp. 258–265 in Mamíferos en Cuba (R. Borroto-Páez and C. A. Mancina, eds.). UPC Print, Vaasa, Finland.
- Mancina, C. A., R. Borroto-Páez, A. Hernández Muñoz, and E. Hernández Pérez. 2014. Mamíferos Terrestres del Archipiélago Sabana-Camagüey, Cuba: sinopsis y comentarios. Pp. 339–359 in Fauna terrestre del Archipiélago Sabana-Camagüey, Cuba (D. Rodriguez Batista, A. Arias Barreto, and E. Ruiz Rojas, eds.). Editorial Científico Técnica, La Habana, Cuba.
- MANCINA, C. A., L. ECHENIQUE, A. TEJEDOR, L. GARCÍA, A. DANIEL, AND M. ORTEGA. 2007a. Endemics under threat: an assessment of the conservation status of Cuban bats. Hystrix 18:3–15.
- Mancina, C. A., and R. Fernández de Arcila. 2013. Estudio preliminar de la distribución potencial de los murciélagos en Cuba como herramienta para la conservación. Pp. 165–174 in Plan del Sistema Nacional de Áreas Protegidas 2014–2020 (Centro Nacional de Áreas Protegidas, ed.). Ministerio de Ciencias Tecnología y Medio Ambiente, La Habana, Cuba.
- Mancina, C. A., L. García, and B. W. Miller. 2012. Wing morphology, echolocation, and resource partitioning in syntopic Cuban mormoopid bats. Journal of Mammalogy 93:1308–1317.
- Mancina, C. A., E. García Tió, R. Borroto-Páez, H. M. Díaz, and F. A. Cervantes. 2015. Taxonomic identity of invasive rabbits in Cuba: first record of Eastern Cottontail, *Sylvilagus floridanus* (Mammalia: Lagomorpha). Checklist 11: 1–7, Article 1820.
- Mancina, C. A., L. García, and R. Capote. 2007b. Habitat use by phyllostomid bat assemblages in secondary forests of the "Sierra del Rosario" Biosphere Reserve, Cuba. Acta Chiropterologica 9:203–218.
- McDonough, M. M., L. K. Ammerman, R. M. Timm, H. H. Genoways, P. A. Larsen, and R. J. Baker. 2008. Speciation within bonneted bats (genus *Eumops*): the complexity of morphological, mitochondrial, and nuclear data sets in systematic. Journal of Mammalogy 89:1306–1315.
- Morgan, G. S. 1991. Neotropical Chiroptera from the Pliocene and Pleistocene of Florida. Bulletin of the American Museum of Natural History 206:176–213.

- Morgan, G. S. 2001. Patterns of extinction in West Indian bats. Pp. 369–408 in Biogeography of the West Indies: patterns and perspectives (C. A. Woods and F. E. Sergile, eds.). CRC Press, Boca Raton, Florida.
- Morgan, G. S., and C. A. Woods. 1986. Extinction and the zoogeography of West Indian land mammals. Biological Journal of the Linnean Society 28:167–203.
- Myers, N., R. A., Mittermeier, C. G., Mittermeier, G. A. B. da Fonseca, and J. Kent, 2000. Biodiversity hotspots for conservation priorities. Nature 203:853–858.
- Nowak, R. M. 1999. Walker's mammals of the world. Vol. 1 and 2. John Hopkins University Press, Baltimore, Maryland.
- OLIVER, W. L. R., AND I. L. BRISBIN. 1993. Introduced and feral pigs: problems, policy and priorities. Pp. 179–191 in Pig, peccaries and hippos: status survey and action plan (W. L. R. Oliver, ed.). IUCN, Gland, Switzerland.
- ORIHUELA, J. 2011. Skull variation of the vampire bat *Desmodus rotundus* (Chiroptera: Phyllostomidae): taxonomic implications for the Cuban fossil vampire bat *Desmodus puntajudensis*. Chiroptera Neotropical 17:863–876.
- Orihuela, J. 2012. Late Holocene Fauna from a Cave Deposit in Western Cuba: post-Columbian occurrence of the vampire bat *Desmodus rotundus* (Phyllostomidae: Desmodontinae). Caribbean Journal of Science 46:297–312.
- Paula de Couto, C. 1967. Pleistocene edentates of the West Indies. American Museum Novitates 2304:1–55.
- PINO RODRÍGUEZ, M. 2012. Association of Cuban terrestrial mammals with aborigines cultural evidences. Pp. 357–362 in Terrestrial mammals of the West Indies. Contributions (R. Borroto-Páez, C. A. Woods, and F. E. Sergile, eds.). Wocahoota Press and Florida Museum of Natural History, Florida.
- Rams, A., R. M. Abreu, and J. de la Cruz. 1989. Almiquí (*Solenodon cubanus*) depredado por perros jíbaros (*Canis familiaris*). Garciana 21:1–2.
- RETTINGER, R., AND M. WÓJTOWICZ. 2014. Regional differences in the development of tourism in Cuba. Pp. 136–154 in Environmental and socio-economic transformation in developing areas as the effect of globalization (M. Wójtowicz and A. Winiarcyk-Razniak, eds.). Wydawnictwo Naukowe, Pedagogical University of Cracow, Kraków, Poland.
- REYES PÉREZ, D., AND R. BORROTO-PÁEZ. 2016. Vertebrados terrestres autóctonos e introducidos en Cayo Caimán del Faro, archipiélago de Sabana-Camagüey, Villa Clara, Cuba. Poeyana 503:73–78.
- RIBERA, N. J. de. 1757. Descripción de la Isla de Cuba. Editorial de Ciencias Sociales, La Habana, Cuba.
- Risco Rodríguez, E. del. 1995. Los bosques de Cuba: su historia y características. Editorial Científico-Técnica, La Habana, Cuba.
- RODRÍGUEZ-DURÁN, A., J. PÉREZ, M. A. MONTALBAN, AND J. M. SANDOVAL. 2010. Predation by free-roaming cats on an insular population of bats. Acta Chiropterologica 12:359–362.
- Russell, J. C., D. Ringler, A. Trombini, and M. Le Corre. 2011. The Island Syndrome and population dynamics of introduced rats. Oecologia 167:667–676.
- SATO, J. J., ET AL. 2016. Molecular phylogenetic analysis of nuclear genes suggest a Cenozoic over-water dispersal origin for the Cuban Solenodon. Scientific Report 6:31173
- Servicio Hidrográfico y Geodésico de la República de Cuba (SHGRC). 2003. Derrotero de las costas de Cuba. Fascículos P1100 y P1101.
- Sikes, R. S., et al. 2016. 2016 Guidelines of the American Society of Mammalogists for the use of wild mammals in research and education. Journal of Mammalogy 97: 663–688.

- 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 *Mormooops megalophylla*. Acta Zoologica Cracoviensia 19:33–73.
- SILVA TABOADA, G. 1979. Murciélagos de Cuba. Editorial Academia, La Habana, Cuba.
- Silva Taboada, G. 1983. Interrelaciones en el subgénero *Phyllonycteris* (Mammalia: Chiroptera: Phyllostomidae). Ciencias Biológicas 10:117–121.
- SILVA TABOADA, G., W. SUÁREZ DUQUE, AND S. DÍAZ FRANCO. 2007. Compendio de los mamíferos terrestres autóctonos de Cuba vivientes y extinguidos. Museo Nacional de Historia Natural, La Habana, Cuba
- SIMMONS, N. B. 2005. Order Chiroptera. Pp. 312–529 in Mammal species of the world: a taxonomic and geographic reference (D. E. Wilson and D. M. Reeder, eds.). John Hopkins University Press, Baltimore, Maryland.
- SMITH, M. L., ET AL. 2005. Caribbean Islands. Pp. 112–118 in Hotspots revisited: Earth's biologically richest and most endangered terrestrial ecoregions (R. A. Mittermeier, P. R. Gil, M. Hoffman, J. Pilgrim, T. Brooks, C. G. Mittermeier, J. Lamoreux, and G. A. B. da Fonseca, eds.). CEMEX, Mexico City.
- SUÁREZ, W. 2005. Taxonomic status of the Cuban Vampire Bat (Chiroptera: Phyllostomidae: Desmodontinae: *Desmodus*). Caribbean Journal of Science 41:761–767.
- Taborsky, M. 1988. Kiwis and dog predation: observations in Waitangi State Forest. Notornis 35:197–202.
- Taylor, R. B., and E. C. Hellgren. 1997. Effect of feral hogs in the western South Texas Plains. Southwestern Naturalist 42:33–39.
- Tejedor, A. 2011. Systematics of funnel-eared bats (Chiroptera: Natalidae). Bulletin of the American Museum of Natural History 353:1–140.
- Tejedor, A., G. Silva Taboada, and D. Rodríguez-Hernández. 2004. Discovery of extant *Natalus major* (Chiroptera: Natalidae) in Cuba. Mammalian Biology 69:153–162.
- Towns, D. R., I. A. E. Atkinson, and C. H. Daugherty. 2006. Have the harmful effects of introduced rats on islands been exaggerated? Biological Invasions 8:863–891.
- Turvey, S. T. 2009. Holocene mammal extinctions. Pp. 41–61 in Holocene extinctions (S. T. Turvey, ed.). Oxford University Press, Oxford, United Kingdom.
- Turvey, S. T., R. J. Kennerley, J. M. Nuñez-Miño, and R. P. Young. this issue. The last survivors: current status and conservation of the non-volant land mammals of the insular Caribbean. Journal of Mammalogy
- Turvey, S. T., J. R. Oliver, Y. Narganes Storde, and P. Rye. 2007. Late Holocene extinction of Puerto Rican native land mammals. Biology Letters 3:193–196.
- UPHAM, N. S., AND R. BORROTO-PÁEZ. this issue. Molecular phylogeography of endangered Cuban hutias in the context of their insular Caribbean radiation.
- UPHAM, N., AND B. D. PATTERSON. 2015. Evolution of caviomorph rodents: a complete phylogeny and timetree for living genera. Pp. 63–120 in Biology of caviomorph rodents: diversity and evolution (A. I. Vassallo and D. Antenucci, eds.). SAREM Series A, Buenos Aires, Argentina.
- Valdés, A., and O. H. Garrido. 1978. Presencia de *Rattus* (Rodentia: Muridae) en cayos de Cuba. Miscelanea Zoológica 7:2–3.
- VARNHAM, K. J. 2010. Invasive rats on Tropical Islands: their history, ecology, impacts and eradication. RSPB Research Report No. 41. Royal Society for the Protection of Birds, United Kingdom.

- VARONA, L. S. 1974. Catálogo de los Mamíferos Vivientes y extinguidos de las Antillas. Editorial Academia de Ciencias de Cuba, La Habana, Cuba.
- Vázquez-Domínguez, E., G. Ceballos, and J. Cruzado. 2004. Extirpation of an insular subspecies by a single introduced cat: the case of the endemic deer mouse *Peromyscus guardia* on Estanque Island, Mexico. Orvx 38:347–350.
- Velazco, P. M., et al. 2013. Quaternary bat diversity in the Dominican Republic. American Museum Novitates 3779:1–20.
- WEGE, D. C., D. RYAN, N. VARTY, V. ANADÓN-IRIZARRY, AND A. PÉREZ-LEROUX. 2010. Hotspot de biodiversidad. Islas del Caribe. Critical Ecosystem Partnership Fund (CEPF).
- WILLIG, M. R., S. J. Presley, C. P. Bloch, and H. H. Genoways. 2009. Macroecology of Caribbean bats: effects of area, elevation, latitude, and hurricane-induced disturbance. Pp. 216–264 in Island bats (T. H. Fleming and P. A. Racey, eds.). University of Chicago Press, Chicago, Illinois.

- WILSON, D. E., F. RUSSELL COLE, J. D. NICHOLS, R. RUDRAN, AND M. S. FOSTER. 1996. Measuring and monitoring biological diversity. Standard methods for mammals. Smithsonian Institution Press, Washington, D.C.
- Woods, C. A., R. Borroto-Páez, and C. W. Kilpatrick. 2001. Insular patterns and radiations of West Indian rodents. Pp. 335–353 in Biogeography of the West Indies (C. A Woods and F. E. Sergile, eds.). 2nd ed. CRC Press, Boca de Raton, Florida.
- Woods, C. A., and C. W. Kilpatrick. 2005. Infraorder Hystricognathi. Pp. 1538–1600 in Mammal species of the world: a taxonomic and geographic record (D. E. Wilson and D. M. Reeder, eds.). 3rd ed. Johns Hopkins University Press, Baltimore, Maryland.
- Zadik, B. J. 2005. The Iberian Pig in Spain and the Americas at the time of Columbus. Thesis for the degree of Master of Arts in Latin American Studies, University of California, Berkeley.

Editor for Special Feature was Leslie N. Carraway.

#### APPENDIX I

List of recent and extinct mammals of Cuba. Sources for criteria: distribution (Silva Taboada et al. 2007; Mancina and Borroto-Páez 2011; Borroto-Páez et al. 2012a, 2012b); EED, Estimated extinction date; A, Amerindian; HO, Holocene, MI, Miocene; PL, Pleistocene (Guarch Delmonte 1984; Macphee and Flemming 1999; MacPhee et al. 2003; Jiménez-Vázquez et al. 2005; MacPhee et al. 2007; Silva Taboada et al. 2007; MacPhee 2009; Orihuela 2012); diet (Silva Taboada 1979; Borroto-Páez and Woods 2012a); mean mass and estimation (Paula de Couto 1967; Nowak 1999; Borroto-Páez 2002; MacPhee et al. 2003; Borroto-Páez et al. 2005; Silva Taboada et al. 2007; MacPhee 2009; Borroto-Páez and Mancina 2011). Habitat: G, generalist species, included species that have been observed using man-made structures as roosts for bats; C, cave-dwelling, highly dependent of caves as diurnal habitat or roosts; T, tree-dwelling, species that using trees as habitat or roosts; and TR, terrestrial-dwelling, that use the ground and karstic zones as refuges.

Taxon	Status	EED	Diet	Habits	Mean mass in g (N) or estimation of fossil body size	Abundance (population or fossil remains)	Distribution (numbers of pro- tected area for extant, number of localities as extinct, or both)
Rodentia Echimyidae Heteropsomyinae							
Boromys offella Miller, 1916	Endemic/Extinct	After 1509	Folivore	T, TR	~350	Abundant	Cuba, Isla de la Juventud and Archipiélago Sabana (87)
Borromys torrei Allen 1917 Capromyidae Capromyinae	Endemic/Extinct	After 1509	Folivore	T, TR	~150	Abundant	Cuba and Isla de la Juventud (67)
Capromys garridoi Varona, 1970°	Endemic/Living?		Folivore	T (mangrove)	~2,000	Very rare	Type locality in unnamed islet in Cayo Largo del Sur (1)
Capromys pilorides pilorides (Say, 1822)	Endemic/Living		Folivore	T, TR	3,676.5 (71)	Widespread	Cuba (81, 88)
Capromys pilorides relictus Allen, 1911	Endemic/Living		Folivore	T	3,061.8 (16)	Rare	North Isla de la Juventud
Capromys pilorides ciprianoi Borroto- Páez, Camacho and Ramos, 1992	Endemic/Living		Folivore	T, TR	4,254.1 (59)	Widespread	South Isla de la Juventud
Capromys pilorides doceleguas Varona 1980	Endemic/Living		Folivore	T	~3,000	Widespread	Archipelago Jardines de la Reina
Capromys pilorides gundlachianus Varona 1983	Endemic/Living		Folivore	T	~3,000	Widespread	Part of Archipelago Sabana-Camagüey
Macrocapromys acevedo Arredondo 1958 <sup>c</sup>	Endemic/Extinct	A	Folivore	T, TR	~4,000	Common	Some localities around Cuba (28)
Macrocapromys latus (Varona and Arredondo 1979) <sup>c</sup>	Endemic/Extinct	НО	Folivore	T, TR	~4,000	Rare	Localities in La Habana and Villa Clara (8)
Geocapromys columbianus (Chapman, 1892)	Endemic/Extinct	After 1509	Folivore	TR	~1,500	Abundant	Cuba, Isla de la Juventud, and Archipelago Sabana (116)
Mesocapromys angel- cabrerai (Varona, 1979)	Endemic/Living		Folivore	T (mangrove)	483.0 (24)	Restricted	Cayo Salinas, Cayos de Ana Maria, South Ciego de Ávila (1)
Mesocapromys auritus (Varona, 1970)	Endemic/Living		Almost Folivore	T (man- grove), TR	632.8 (14)	Restricted	Cayo Fragoso, Archipelago Sabana-Camagüey, North Villa Clara (1)
Mesocapromys kra- glievichi (Varona and Arredondo, 1979) <sup>c</sup>	Endemic/Extinct	НО	Folivore	T, TR		Rare	Only from La Habana (12)
Mesocapromys mela- nurus (Poey, 1865)	Endemic/Living		Folivore	T, TR	1,231.4 (45)	Common	Eastern Cuba (16)
Mesocapromys nanus (G. M. Allen 1917)	Endemic/Possible Extinct	1951	Folivore	T, TR	~400–450	Restricted	Zapata Swamp (2, 25)

# APPENDIX I. Continued

Taxon	Status	EED	Diet	Habits	Mean mass in g (N) or estimation of fossil body size	Abundance (population or fossil remains)	Distribution (numbers of pro- tected area for extant, number of localities as extinct, or both)
Mesocapromys san- felipensis (Varona, 1970)	Endemic/Possible extinct	1978	Folivore	T (man- grove), TR	~550	Restricted	Cayo Juan García, Cayos de San Felipe, South of Pinar del Rio (1)
Mysateles prehensilis prehensilis (Poeppig, 1824)	Endemic/Living		Folivore	Т	1,799.4 (118)	Widespread	Western to Central Cuba up to Ciego de Ávila province (43, 27)
Mysateles prehensilis gundlachi (Chapman, 1901)	Endemic/Living		Folivore	Т	1,660.5 (42)	Restricted	North Isla de la Juventud
Mysateles prehensilis meridionalis (Varona, 1986)	Endemic/Living	1980s	Folivore	Т	~	Restricted	Southwestern Isla de la Juventud
Isolobodontinae	Endemic/Living						
Zazamys veroni- cae MacPhee and Iturralde-Vinent, 1995 Soricomorpha Solenodontidae	Endemic/Extinct	MI	Folivore	?		Rare	Only from type locality in Domo de Zaza (1)
Solenodon cubanus Peters, 1861	Endemic/Living		Invertebrates	TR (litter borrowing)	730–900	Moderated	Today in 2 localities in eastern Cuba (Alejandro de Humboldt National Park and Pico Cristal National Park. Western and central localities in the past (4, 54)
Solenodon arre- dondoi Morgan and Ottenwalder, 1993) Nesophontidae	Endemic/Extinct	A	Invertebrates	TR	~1,000	Rare	Only from 5 localities in western Cuba (7)
Nesophontes micrus Allen 1917	West Indies Endemic/ Extinct	After 1509	Invertebrates	TR	40–50	Abundant	Cuba, Cayo Guillermo, Isla de la Juventud, and Hispaniola (100)
Pilosa						C	
Megalonychidae  Acratocnus antillensis (Matthew, 1931)	Endemic/Extinct	НО	Folivore	T	~100 kg	Common Common	Many localities around Cuba (50)
Neocnus gliriformes (Matthew, 1931)	Endemic/Extinct	A	Folivore	T	~10 kg	Common	Many localities around Cuba (64)
Megalocnus rodens Leidy, 1868	Endemic/Extinct	A	Folivore	TR	~ 200 kg	Common	Many localities around Cuba (121)
Parocnus browni (Matthew, 1931)	Endemic/Extinct	A	Folivore	TR	~ 200 kg	Common	Many localities around Cuba (79)
Imagocnus zazae Macphee and Iturralde-Vinent, 1994 Chiroptera Noctilionidae	Endemic/Extinct	MI	Folivore	?	~150 kg	Rare	Only from type locality in Domo de Zaza in Sancti Spiritus, Central Cuba (1)
Noctilio leporinus mastivus (Vahl, 1797)	No Endemic/Living		Piscivore	T, C	~80	Moderated	Cuba, Isla de la Juventud, and Archipelgo Sabana- Camaguey (7, 3)
Phyllostomidae  Macrotus waterhousei  minor Gundlach in  Peters, 1865	West Indies Endemic/ Living			G	12–18	Widespread	Cuba and Cayman Islands (31, 29 extinct)
Desmodus rotun- dus puntajudensis Woloszyn and Mayo, 1974	Endemic/Extinct	A	hematophage	С	~30	Rare	Cuba (5)
Brachyphylla nana Miller, 1902	West Indies endemic/ Living		Frugivore/ Nectarivore.	С	28–41	Widespread	Greater Antilles.(26, 39)

APPENDIX I. Continued

Taxon	Status	EED	Diet	Habits	Mean mass in g (N) or estimation of fossil body size	Abundance (population or fossil remains)	Distribution (numbers of pro- tected area for extant, number of localities as extinct, or both)
Phyllonycteris poeyi Gundlach, 1861	Endemic/Living		Frugivore/ Nectarivore	С	17–25	Widespread	Cuba and Isla de la Juventud. (27, 35)
Erophylla sezekorni sezekorni Gundlach in Peters, 1861	West indies Endemic/ Living		Nectarivore/ Frugivore	С	14–17	Wide	Cuba and Isla de la Juventud 18, 11)
Monophylus redmani clinedapus Miller, 1900	West Indies Endemic/ Living		Nectarivore/ Insectivore	С	9–12	Wide	Cuba and Isla de la Juventud (21, 19)
Artibeus jamaicensis parvipes Rehn, 1902	West indies Endemic/ Living		Frugivore	G	33–54	Widespread	Cuba and Archipelago Sabana-Camaguey, Cayman Island and Bahamas (40, 37)
Artibeus anthonyi Woloszyn and Silva Taboada, 1977	Endemic/Extinct	НО			~50		Eleven localities around Cuba (11)
Phyllops falcatus fal- catus (Gray, 1839)	West Indies Endemic/ Living		Frugivore	T	15–27	Moderated	Cuba, and Archipelago Sabana-Camagüey, Hispaniola, and Cayman Islands (9, 22)
Phyllops vetus Anthony, 1917	Endemic/Extinct	НО	Frugivore	T?	~20	Rare	Four localities, in Cuba, 2 in western and 2 eastern Cuba, and 1 in Isla de la Juventud (5)
Phyllops silvai Suárez and Díaz-Franco, 2003	Endemic/Extinct	НО	Frugivore	T?	~20	Rare	Only from type locality in El Abron cave, Western Cuba (1)
Cubanycteris silvai Mancina and García, 2005 Mormoopidae	Endemic/Extinct	НО	Frugivore	T?	~30	Rare	Only from type locality in GEDA cave, Western Cuba (1)
Mormoops blaninville Leach, 1821	West Indies/Endemic Living		Insectivore	С	6–11	Wide	Greater Antilles. Around Cuba and Archipelago Sabana-Camaguey (21, 11)
Mormoops megalo- phylla (Peters, 1865)	No Endemic/Extirpated	A	Insectivore	C	~15	Rare	Deposits from Western and central Cuba (5)
Mormoops magna Silva Taboada, 1974 <sup>a</sup>	Endemic/Extinct	НО	Insectivore	С	~20	Rare	Cuevas Blancas and "Los Masones" cave, Western and central Cuba (2)
Pteronotus macleayi macleayi (Gray, 1839)	West Indies Endemic/ Living		Insectivore	С	4–8	Wide	Cuba and Jamaica (18, 6)
Pteronotus qua- dridens quadridens (Gundlach, 1840)	Endemic/Living		Insectivore	С	3–6	Widespread	Cuba (23, 5)
Pteronotus parnelli parnelli (Gray, 18430	West Indies Endemic/ Living		Insectivore	C	9–15	Wide	Cuba (20, 10)
Pteronotus pristinus Silva Taboada, 1974 <sup>b</sup>	Endemic/Extinct	НО		С	~10	Rare	Only in 2 localities Jaguey and Los Masones, caves, cen- tral Cuba (2)
Natalidae Nyctiellus lepidus (Gervais, 1837)	West indies Endemic/ Living		Insectivore	С	2–3	Wide	Cuba, Isla de la Juventud, and Bahamas (18, 6)
Chilonatalus macer (Miller, 1914)	Endemic/Living	U		C	2–4	Moderated	Cuba (16, 7)
Natalus primus Anthony, 1919	Endemic/Living		Insectivore	С	7–13	Restricted	La Barca cave, Guanahacabibes Western Cuba (1, 14)

## APPENDIX I. Continued

Taxon	Status	EED	Diet	Habits	Mean mass in g (N) or estimation of fossil body size	Abundance (population or fossil remains)	Distribution (numbers of pro- tected area for extant, number of localities as extinct, or both)
Vespertilionidae  Eptesicus fuscus detertreus (Gervais, 1837)	West Indies Endemic/ Living		Insectivore	G	13–19	Widespread	Cuba, Cayman Islands, Bahamas, and some keys in northern Cuba (23, 8)
Eptesicus fuscus petersoni Silva	Endemic/Living		Insectivore	G	13–19	Widespread	Isla de la Juventud (2)
Taboada, 1974  Lasiurus pfeiffer (Gundlach, 1862)	Endemic/Living		Insectivore	T	12–18	Moderated	Cuba, Romano, Sabinal, and Las Brujas (8, 1)
Nycticeius cubanus (Gundlach, 1862)	Endemic/Living		Insectivore	G	5–7	Moderated	Western Cuba (2)
Antrozous koop- mani Orr and Silva Taboada, 1960	Endemic/Living		Insectivore	G?	~20	Restricted	Few localities (4) in western, central and eastern Cuba (3, 10)
Dasypterus insularis Hall and Jones, 1961 Molossidae	Endemic/Living		Insectivore	Т	20–30	Restricted	Three localities in western, 1 central, and 2 in eastern Cuba; presumably extirpate in Hispaniola (1, 6)
Molosus molosus tropidorhynchus Gray, 1839	West Indies Endemic/ Living		Insectivore	G	7–15	Wide	Cuba, Isla de la Juventud, and Cayman Islands (8, 1)
Nyctinomops macrotis (Gray, 1840)	No Endemic/Living		Insectivore	G	17–24	Moderated	Southwest of North America, north of Argentina, Cuba, Jamaica, and Hispaniola (3, 3)
Eumops ferox (Gundlach, 1862)	No Endemic/Living		Insectivore	G	30–45	Moderated	Central Mexico to Central America, Cuba, and Jamaica (3, 0)
Tadaria brasiliensis muscula (Gundlach in Peters, 1862)	West Indies Endemic/ Living			G	6–11	Widespread	Cuba and Isla de la Juventud (15, 6)
Mormopterus minutus (Miller, 1899)	Endemic/Living		Insectivore	T	5–8	Moderated	Central and eastern Cuba (3, 0)
Nyctinomops laticau- datus yucatanicus (Miller, 1902) Primates Pitheciidae	No Endemic/Living		Insectivore	Т	8–13	Restricted	Central America to South America and Cuba (1, 0)
Paralouatta marianae MacPhee, Iturralde- Vinent, and Gaffney, 2003	Endemic/Extinct	MI	Folivore	Т	8–10 kg	Rare	Only from type locality in Domo de Zaza in Sancti Spiritus (1)
Paralouatta varonai Rivero de la Calle and Arredondo, 1991	Endemic/Extinct	НО	Folivore	T	8–10 kg	Rare	Only from 2 localities in Sierra de Galera, Pinar del Rio (2)

<sup>&</sup>lt;sup>a</sup>Recently 2 humeri presumably assigned to *M. magna* were recovered in a fossil cave deposit from Dominican Republic extending its distribution range in 1,200 km from Cuba (Velazco et al. 2013).

<sup>&</sup>lt;sup>b</sup>Two mandibles from a fossil deposit in Florida were referred to "*Pteronotus* cf. *P. pristinus*" by Morgan (1991), however, this identification was tentative. <sup>c</sup>Species in need of taxonomic review.

### APPENDIX II

Introduced mammals in Cuba. Categories: INV, invasive; LINV, invasive locally; ENI, established noninvasive; TRAN, transported; and NES, not established. Offshore islands sources: Varona 1974; Valdés and Garrido 1978; González et al. 1994; Escobar 1995; Borroto-Páez 2009, 2011b; Borroto-Páez and Woods 2012b; Mancina et al. 2014; Mancina et al. 2015; Reyes Pérez and Borroto-Páez (2016). ?, uncertain records. Level of impact: MV, massive; MR, major; MO, moderate; MN, minor; MC, minimal concern; DD data deficient; NA, no alien population.

Introduced mammals and categories	Introduction date	Source of introduction	Pathway	No. of protected areas	Islands and keys (total)	Level of interac- tion with native mammals	Level of impact
Canis familiaris INV	1509	Canary Islands, Spain	Weapon Hunting Pet	45	Ballenato del Medio, Blanco del Norte, Caguanes, Caimán del Faro, Campo, Cantiles, Coco del Norte, Conuco, Cruz, Cuba, Español Adentro, Guajaba, Isla de la Juventud, Las Brujas, Largo del Sur, Las Brujas, La Vaca, Mono, Romano, Sabinal, Santa María. (21)	High	MV
Felis catus INV	1509	Canary Islands, Spain	Pet	40	Caimán del Faro, Cantiles, Coco, Conuco, Cruz, Cuba, Ensenacho, Español Adentro, Francés, Guajaba, Isla de la Juventud, Juan García, Las Brujas, Largo del Sur, Las Brujas, Majá 1, Mégano Grande, Romano, Sabinal, Santa María. (21)	High	MV
Herpestes auropuncta- tus INV	1882	Jamaica	Biological control	41	Cuba, Romano, Sabinal. (3)	High	MV
Rattus rattus INV	1493	Spain, Canary Islands	Accidental	85	Aguada (Cayos de Piedra), Algodón Grande, Algodoncito, Anclita, Avalos, Ballenato del Medio, Blanco (del Norte), Blanco del Sur, Caguanes, Caimán del Faro, Campo, Cantiles, Caoba, Cobo, Coco del Norte, Coco del Sur, Coco grande (Cayos de San Felipe), Coco Chico (Cayos de San Felipe), Conuco, Cruz, Cuba, Cueva, Diego Pérez, Ernest Thaelmann, Ensenacho, Español Adentro, Fábrica, Fragoso, Francés, Guajaba, Guillermo, Hicacos, Iguana (o Cayo de Piedra), Isla de la Juventud, Juan García (Cayos de San Felipe), La Cucana (Cayos de San Felipe), La Loma, La Sagra, Las Brujas, La Vaca, Largo del Sur, Lucas, Los Majaes (Majá 1, Majá del Medio and Majá 3), Matías, Mégano Grande, Pajonal, Palma, Paredón Grande, Pasaje, Peraza, Ratones, Rico, Romano, Rosario, Real (cayos de San Felipe), Salinas (Cayos de Ana María), Sinvergiuenza, Santa María, Sijú	High	MV
Rattus norvegicus INV	1560–1600	Spain	Accidental	25	(Cayos de San Felipe), Venado. (64) Cuba, Isla de la Juventud,	High	MV
Mus musculus INV	1510–1530	Spain	Accidental	35	Juan García, Largo del Sur. (4) Caimán del Faro, Campo, Cantiles, Cayos de Piedra (Aguada y Salinas), Coco del Norte, Cuba, Guajaba, Guillermo, Isla de la Juventud, Jutía, Largo del Sur, Romano, Sabinal, Santa María. (15)	High	MV
Dasyprocta punctata INV	1930	Mexico	Hunting	2	Western Cuba	Low	МО
Dasyprocta mexicana INV	1930	Mexico	Hunting	2	Western Cuba	Low	МО
Cuniculus paca INV Cavia porcellus LINV	1930 ?	Mexico Peru	Hunting Food Research Pet	2	Western Cuba Cuba	Low None	MO MC
Meriones unguiculatus TRAN	~1980s	?	Research Pet		Cuba	None	NA
Mesocricetus auratus TRAN	~1980s	?	Research Pet		Cuba	None	NA

APPENDIX II. Continued

Introduced mammals and categories	Introduction date	Source of introduction	Pathway	No. of protected areas	Islands and keys (total)	Level of interac- tion with native mammals	Level of impact
Cricetus cricetus TRAN	~1980s	?	Research Pet		Cuba	None	NA
Sciurus granatensis LINV	~1940	United States	Zoo	1	Cuba	None	MC
Hydrochoerus hydro- chaeris INV	1970s 2009	Venezuela	Food Hunting	1	Cuba	Low	MC
Oryctolagus cuniculus <sup>a</sup> INV	1880	Canary Islands	Food Hunting	?	Cuba, Isla de la Juventud, Romano? (3)	Low	MC
Sylvilagus floridanus INV	~1930?	United States	Hunting	?	Cuba	Low	MC
Sus scrofa INV	1509	Canary Islands	Food	32	Coco, Cuba, Guajaba, Isla de la Juventud, Romano, Sabinal. (6)	High	MV
Odocoileus virginianus INV	1850	United States and Mexico	Hunting Food	36	Cuba, Guajaba, Isla de la Juventud, Romano, Sabinal. (5)	Low	MC
Cervus elaphus NES	1930	United States	Hunting				
Bos taurus INV	1509	Canary Islands	Food	48	Coco, Cuba, Guajaba, Isla de la Juventud, Romano, Sabinal. (6)	Low	MC
Bubalus bubalis INV	~1985	Viet Nam	Food	5	Cuba	Low	MN
Ovis aries INV	1509	Canary Isalnds	Food	20	Cuba, Ensenacho, Francés, Guajaba, Isla de la Juventud, Romano. (6)	Low	MN
Ovis musimon LINV	1976	Canada	Food Hunting	1	Isla de la Juventud	None	DD
Capra hircus INV	1509	Canary Islands	Food	18	Cuba, Isla de la Juventud, Romano. (3)	Low	MN
Ammotragus lervia LINV	~1980s	?	Hunting	1	Cuba	None	DD
Tayassu pecari NES	~1930	Possibly Mexico	Hunting				
Pecari tejacu NES	~1930	Possibly Mexico	Hunting				
Lama glama NES	1840 1856	Peru	Transport				
Camelus dromedarius ENI	1832 1856	Canary Islands	Transport		Cuba	None	NA
Dama dama LINV	1979	Canada	Hunting	1	Isla de la Juventud	None	DD
Equus caballus INV	1509	Spain, Canary Islands	Weapon Transport	36	Coco, Cuba, Guajaba, Isla de la Juventud, Romano, Sabinal. (6)	None	MC
Equus asinus ENI	~1600s	Spain	Transport	1	Cuba	None	NA
Equus hemionus LINV	1990	?	Transport	1	Cuba	None	DD
Equus zebra granti LINV	~1980s	?	Hunting	1	Cuba	None	DD
Antilope cervicapra LINV	1985	Canada	Hunting	2	Guajaba, Romano. (2)	None	DD
Boselaphus tragoca- melus LINV	1985	Canada	Hunting	2	Cuba, Romano. (2)	None	DD
Taurotragus derbianus LINV	~1990s	Canada	Hunting	1	Cuba	None	DD
Chlorocebus aethiops INV	1983	St Kitts and Nevis	Research	3	Cuba, Cantiles, Romano. (3)	Medium	MR
Macaca nemestrina INV	1986	Viet Nam	Research	1	Cantiles	Medium	MR
Macaca fascicularis INV	1986	Viet Nam	Research	1	Campo	Medium	MR
Macaca arctoides INV	1986	Viet Nam	Research	1	Guajaba	Medium	MR
Macaca mullata NES Armadillo (unidentified) NES	1946 1939	United States Possibly Mexico	Research Hunting				

<sup>&</sup>lt;sup>a</sup>The report of *Oryctolagus cuniculus* as invasive mammals, with a permanent population in the wild, must be reconfirmed. Previous reports in Cuba could be assigned to *Sylvilagus floridanus* (Mancina et al. 2015). Records from Cayo Romano (González et al. 1994) must be reviewed and confirmed, whereas in Isla de la Juventud rabbits are present from recent introduction by hotel constructors during the 2000s.