

Taxonomic status and conservation relevance of the raccoons (*Procyon* spp.) of the West Indies

Kristofer M. Helgen^{1,2*} and Don E. Wilson³

¹ Mammal Department, Museum of Comparative Zoology, Harvard University, Cambridge, MA 02138, U.S.A.

² Department of Environmental Biology, University of Adelaide, Adelaide 5005, Australia

³ Division of Mammals, National Museum of Natural History, Smithsonian Institution, Washington, DC 20560, U.S.A.

(Accepted 10 April 2002)

Abstract

Raccoons *Procyon* spp. from New Providence Island in the Bahamas and from Barbados and Guadeloupe in the Lesser Antilles have traditionally been recognized as distinctive species endemic to their respective islands. All three of these 'species' currently possess official conservation status of high concern. Bahamian and Guadeloupean raccoons are recognized as endangered species by the World Conservation Union (IUCN), which also considers the Barbados raccoon to be a recently extinct West Indian mammal. However, historical, biogeographic, genetic, and morphological evidence demonstrate that all three West Indian raccoon populations are the result of human-sponsored introductions from the eastern U.S.A. that have occurred in the past few centuries. Accordingly, these animals should not be considered either conservation priorities or recent losses of biodiversity in the Caribbean. Instead, they may actually represent ecological threats to the insular ecosystems on their respective islands. Procyonid conservation goals must be re-examined and updated accordingly.

Key words: Bahamas, Barbados, Guadeloupe, *Procyon gloveralleni*, *Procyon maynardi*, *Procyon minor*

INTRODUCTION

Raccoons, genus *Procyon*, have a wide distribution, spanning the Americas from central Canada to southern Amazonia. More than 50 forms of raccoon have been named from across this large geographic area, many of which possess uncertain taxonomic status. The most complete taxonomic review of the genus to date was provided by Goldman (1950), who revised representatives of *Procyon* from North America, Central America and the West Indies. In total, Goldman recognized seven species: the Northern raccoon *P. lotor* of North America and Central America, the Crab-eating raccoon *P. cancrivorus* of Central and South America, and five additional insular species (Table 1). All subsequent authoritative taxonomic and geographic compendia for mammals have followed Goldman's arrangement (e.g. Lotze & Anderson, 1979; E. R. Hall, 1981; Wozencraft, 1993; Nowak, 1999; Wilson & Cole, 2000; Macdonald, 2001). However, raccoons have been widely introduced to many areas of the world where they are not native, often very successfully (Lever, 1985), and some recent authors have noted in passing that some or all insular raccoons could be introduced populations and

not endemic species (Wozencraft, 1989; Corbet & Hill, 1991; McKenna & Bell, 1997; MacPhee & Flemming, 1999). Nevertheless, the notion that West Indian raccoons represent distinctive species that dispersed naturally to their respective islands remains well-ingrained in the literature (e.g. Simpson, 1956; MacPhee & Fleagle, 1991; Macdonald, 1993, 2001; Bininda-Emonds, Gittleman & Purvis, 1999). In this paper we discuss the status of these raccoon populations based on historical accounts and our study of all available museum specimens of West Indian raccoons.

HISTORICAL BACKGROUND

One of the earliest accounts of *Procyon* in the West Indies is Sloane's (1725) description of raccoons from Jamaica. During his visit he noted that 'the raccoons are commonly here in the mountains, and live in hollow fiddlewood trees, from whence they make paths to go to seek sugar canes, which is their chief if only sustenance'. Interestingly, no evidence other than Sloane's account suggests that wild raccoons have ever inhabited Jamaica; no museum specimens originate from the island, and no further observations of wild raccoons have been noted. As Goldman (1950) suggested, the record is probably erroneous. Sloane may have mistaken some other kind

*All correspondence to: K. M. Helgen, South Australian Museum, North Terrace, Adelaide, SA 5000, Australia.
E-mail: kristofer.helgen@adelaide.edu.au

Table 1. Goldman's (1950) classification of raccoons

<i>P. lotor</i>	Mainland North and Central America
<i>P. cancrivorus</i>	Mainland South and Central America
<i>P. pygmaeus</i>	Cozumel Island off eastern Mexico
<i>P. insularis</i>	Tres Marias Island (western Mexico)
<i>P. maynardi</i>	New Providence Island (Bahamas)
<i>P. minor</i>	Guadeloupe (Lesser Antilles)
<i>P. gloveralleni</i>	Barbados (Lesser Antilles)

of animal for a raccoon (see MacPhee & Fleagle, 1991), or perhaps his observations were actually made on Barbados, an island he visited on the same voyage. Raccoons were certainly present on Barbados as early as the late 17th century (R. Hall, 1764). However, Browne (1789) described the transport of pet raccoons to Jamaica, and it is not impossible that similarly transported raccoons had established a feral population by the time of Sloane's visit. Whatever the origin or identity of Sloane's 'raccoons', there seem to be no raccoons on Jamaica today.

In 1837, based on two specimens obtained from a menagerie in Louisiana, Wiegmann (1837) described a new species of raccoon he named *Procyon brachyurus*. Wiegmann's raccoons supposedly originated from somewhere in the West Indies, and he hesitantly gave the type locality of *brachyurus* as 'Antillae?' The current whereabouts of these two specimens are unknown; they may not have been preserved. Hershkovitz (1966) discussed Wiegmann's account, concluding that it could not be applied with certainty to any of the raccoons later described from the West Indies. *Procyon brachyurus* has never been used as a scientific name since (but see E. R. Hall, 1981).

The first raccoon from the West Indies to be formally described from a known locality was *P. maynardi*, from New Providence Island in the Bahamas (Bangs, 1898). Miller (1911) later named the raccoon population from Guadeloupe as a new species, *P. minor*. Both of these raccoons were said to differ from mainland *P. lotor*, chiefly in their smaller body size. By the time of Miller's paper, description of insular raccoons as distinct species had become a taxonomic trend; in addition to Bangs' *P. maynardi*, Merriam (1898, 1901) had described *P. insularis* from the Tres Marias off the western coast of Mexico and *P. pygmaeus* from Isla Cozumel, east of the Yucatan Peninsula. Nevertheless, Allen (1911) expressed scepticism about the taxonomic validity of the New Providence and Guadeloupe raccoons, writing:

It is doubtful what significance may be attached to the recent discovery of a small race of raccoon in New Providence (Bahamas) and in Guadeloupe (Windward Islands). A third raccoon is known from Barbados, but its identity is uncertain. Some have supposed that the silent 'dogs' ('perros mudos') mentioned by the early Spanish explorers as kept by the natives of Haiti were really these raccoons, but such a possibility seems extremely remote. Feilden and others assume with some confidence that the raccoon on Barbados might readily have drifted thither from South America with some of the wreckage of trees and flotsam that is constantly borne to the windward

shores of that island by the easterly currents of air and sea. On the other hand, it may have readily been introduced during the last one hundred years by the European invader.

Although raccoons from Barbados had never been formally described, Allen (1911) and Feilden (1890) knew of their existence from historical accounts (Hughes, 1750; R. Hall, 1764; Schomburgk, 1848; Chester, 1869). Allen (1911) referred to the Barbados raccoon as '*P. cancrivorus?*', assuming a potential South American origin. However, when Nelson & Goldman (1930) formally described *Procyon gloveralleni* from Barbados, they recognized its close relationship to North American *P. lotor*, not *P. cancrivorus*. The Barbados raccoon was last sighted in 1964 (Lazell, 1972), and is now generally regarded as extinct (Glatston, 1994).

The presence (or former presence) of three supposedly distinct species of raccoon from widespread locations in the West Indies (Fig. 1), all closely related to *P. lotor*, presents a biogeographic conundrum. The native Bahamian fauna includes only one other non-volant mammal, the hutia *Geocapromys ingrahami*. Guadeloupe and Barbados have no native non-volant mammals except for their supposedly endemic raccoons (Varona, 1974), although Barbados may have supported an undescribed rice rat *Oryzomys* in the recent past (Marsh, 1984). Excluding Amerindian dogs from Holocene deposits (Arredondo & Varona, 1974; MacPhee & Fleagle, 1991), mammalian carnivores have no deep presence in the Caribbean, either palaeontological or archaeological (Arredondo, 1976; Olson, 1978). Furthermore, the bat faunas of these islands are primarily derived from South America or the Greater Antilles rather than North America, where one must look for the insular raccoons' affinities. This strange biogeography is a problem that has been recognized for some time. Goldman (1950: 31) wrote, 'How the particular West Indian islands now inhabited were reached by raccoons, and why these animals do not occur on many other islands of the archipelago where conditions seem similarly suitable are interesting subjects for speculation.'

In the Bahamas, raccoons are found today on Grand Bahama Island and New Providence Island. Although the New Providence population is considered a distinct species, that of Grand Bahama, known to have been introduced from Florida in 1932–33 (Sherman, 1954), is not. However, after a visit to the Bahamas in 1784, the German naturalist Johann Schöpf (Schöpf, in Morrison, 1911; McKinley, 1959) discussed the introduction of raccoons to New Providence as well, writing:

Of wild quadrupeds, there are but two species, properly only one, indigenous to these islands. The Raccoon is found only on Providence Island, of which it is no more originally a native than the rats and mice brought in by ships. From one or more tame pairs of these droll beasts, brought over by the curious from the main-land, and afterwards escaped by chance in the woods, the race has amazingly increased, to the great vexation and damage of the inhabitants, who can scarcely protect their house-fowls from these stealthy thieves.

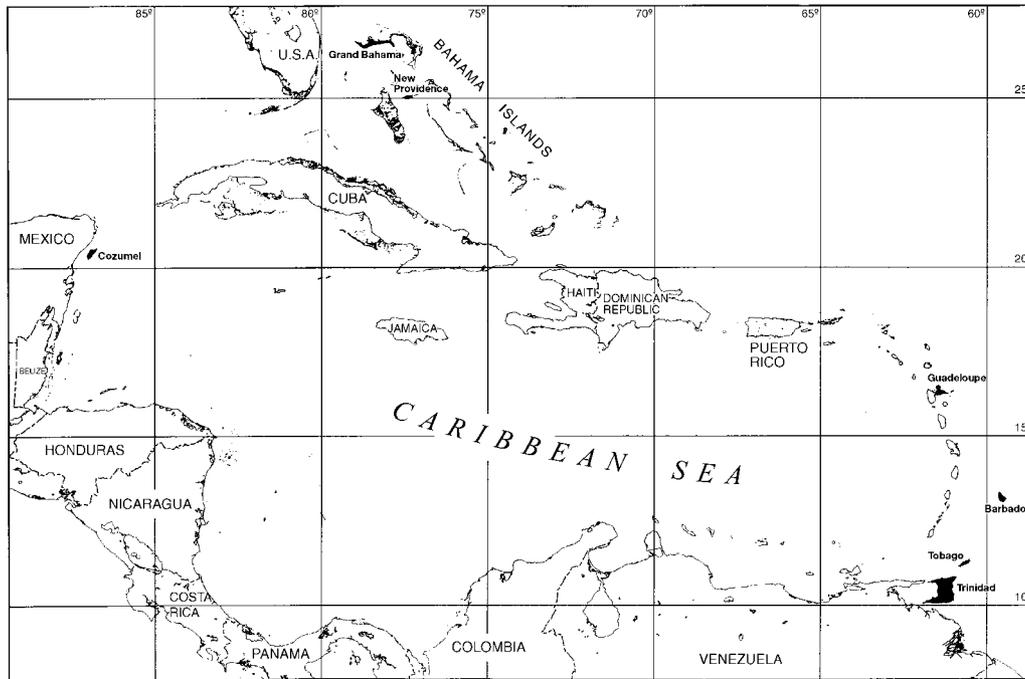


Fig. 1. Map of the West Indies, showing the locations (in black) of insular raccoons in the region. *Procyon lotor* has been introduced on Grand Bahama, New Providence, Guadeloupe, and Barbados. *Procyon cancrivorus* has also been introduced on Guadeloupe. *Procyon cancrivorus* probably occurs naturally on Trinidad and Tobago, as does *P. pygmaeus* on Cozumel.

Although Bangs (1898) justified the description of *P. maynardi* by noting that ‘there is no tradition among the inhabitants of Nassau that the raccoon was ever introduced upon the island’, Miller (1905) observed that his own Bahamian informants actually believed that the animals were introduced. In light of these sources, McKinley (1959) noted that *P. maynardi* is almost certainly not a native West Indian mammal.

Several other authors have also refuted the native status of Bahamian raccoons. After examining specimens of *maynardi* not available to Goldman (1950), Koopman, Hecht & Ledecy-Janacek (1957) concluded that the skin and skull traits used to separate the species from *P. lotor* did not withstand scrutiny in larger series. Olson & Pregill (1982), Morgan & Woods (1986) and Morgan (1989) considered *P. maynardi*, absent from Bahamian fossil and subfossil deposits, as nothing more than a recent introduction, the last author explicitly noting that ‘the raccoon . . . is often listed as a native Bahamian mammal, but it is clearly a recent human introduction based on its absence from palaeontological and Amerindian archaeological sites in the Bahamas’.

Several lines of evidence point to a recent introduction for raccoons on Guadeloupe as well. As in the Bahamas, there is no palaeontological or archaeological record for raccoons in the Lesser Antilles (Olson, 1978, 1983), and although we have not discovered any account describing the raccoon’s introduction to Guadeloupe, it seems noteworthy that the first published mention of the animal may be as late as its formal description (Miller, 1911; although the type specimen was collected no later than 1886). Evidence strongly suggesting a recent introduction for Guadeloupean raccoons comes from DNA-sequence

data and karyotype comparisons (Pons *et al.*, 1999), which demonstrate that *P. minor* is genetically indistinguishable from *P. lotor* from the east coast of North America. We also note that raccoon introductions to Guadeloupe represent more than a singular event, as *P. cancrivorus* from South America has also been introduced to the island in the last few years (Glatston, 1994).

On the grounds of geographic distance alone, the Barbados raccoon is the least likely of all the West Indian raccoons to have colonized its home naturally. *Procyon cancrivorus* of South America is found on Trinidad and Tobago to the south (specimens at AMNH, MCZ, USNM), and if this species occurred on Barbados, it could reasonably be suggested to have arrived by sweepstakes dispersal (cf. Allen, 1911), as the fauna of the southern Lesser Antilles is largely derived from the South American continent. However, the presence of an animal closely related to North American *P. lotor* on Barbados is undoubtedly unnatural. The mention of Barbados raccoons in historical accounts as early as 1679 and 1682 (R. Hall, 1764; Denham, 1987) provides no support for their supposed native status, as the same accounts also mention monkeys, presumably the introduced African green monkeys *Chlorocebus sabaeus* that still inhabit the island (but see Schomburgk, 1848). Earlier, Ligon (1657) mentioned neither of these animals, writing in his detailed review of the Barbadian fauna and flora that ‘there are no kind of wild beasts in the island’. According to Denham (1987), raccoons and monkeys became part of an extensive assemblage of feral Barbadian mammals that included dogs, cats, mongooses *Herpestes javanicus*, horses, asses, pigs, cattle, goats, ‘African black-bellied sheep’, camels (now extinct), and commensal rodents (*Mus musculus*,

Rattus rattus and *R. norvegicus*). Introduction of non-native mammals to Barbados was clearly not a rare phenomenon.

As noted above, the sentiment among mammalogists is that West Indian raccoons may not be valid species. This viewpoint has not received acceptance because a paper explicitly discussing their status has not been produced (Wozencraft (1993) noted ‘... *gloveralleni*, *maynardi*, and *minor* may be conspecific with *lotor*; however, primary systematic works supporting these views are lacking’). This paper is an attempt to fill that void. To investigate the taxonomic status of West Indian raccoons above and beyond the evidence already summarized, all available museum specimens of these raccoons were assembled to study their morphological affinities. Glatston (1994) observed that the taxonomic status of these raccoons is of primary conservation importance, and that any definitive account of insular raccoon taxonomy ‘will undoubtedly have some impact on future policy’. This is also a topic addressed below.

METHODS AND MATERIALS

The skins and skulls of West Indian raccoons (including all relevant type specimens) in the collections of the United States National Museum of Natural History (USNM) in Washington, DC, the Museum of Comparative Zoology (MCZ) in Cambridge, Massachusetts, the American Museum of Natural History (AMNH) in New York, and the Yale Peabody Museum of Natural History (YPM) in New Haven, Connecticut were examined. Specimens were qualitatively compared directly against large series of raccoons from mainland North, Central, and South America (at USNM, AMNH, and MCZ), to assess the morphological distinctiveness of each insular population, and to examine potential affinities between insular and mainland populations.

Specimens examined are listed in the Appendix, accompanied where available by useful collection information extracted from specimen labels, field notebooks, and museum accession catalogues.

RESULTS

Raccoons from New Providence Island, Bahamas

The holotype of *P. maynardi* (MCZ 7750) is a broken skull and study skin of an immature male. With only this unfortunate comparative material at his disposal, Bangs (1898) described *maynardi*, writing ‘the small size of the specimen, together with the peculiarities of the unbroken part of the skull, are sufficient to distinguish the animal as a distinct island form’ (1898: 92).

Ten raccoon specimens were located from New Providence in museum collections (Appendix). Goldman (1950: 76) examined only three of these, and diagnosed *maynardi* by its narrow palatal shelf and light dentition. Although he noted similarities between Bahamian and Florida raccoons, Goldman maintained that

‘the differential characters [of *maynardi*]...warrant its recognition as a different species’.

Examination of all 10 specimens reveals that the diagnostic characters used by Bangs and Goldman clearly represent individual variation. There seem to be no trenchant differences between skulls of *maynardi* and skulls of raccoons from the south-eastern U.S.A. Like the subspecies *varius*, *solutus* and *elucus* (of the south-eastern U.S.A.) and the many described forms of raccoon from the Florida Keys, adult skulls of *maynardi* possess a heightened frontal region with minimal development of postorbital processes and a noticeable depression in the braincase at the fronto-parietal suture. They also resemble *P. lotor* from the south-eastern U.S.A. in their relatively light dentition, gracile zygomatic arches and dentary, and slightly-hooked coronoid process of the mandible. An interesting feature of Bahamian raccoon skulls is the high frequency of an extraneous basioccipital foramen. We have observed this unusual skull character at low frequencies in the skulls of most procyonids, but it is common only in raccoons from Florida, the Florida Keys, the Bahamas, and Guadeloupe (as well as in some populations of raccoons from California and Central America, which Bahamian raccoon skulls otherwise do not closely resemble). Skins of *maynardi* bear a closer resemblance to raccoons from mainland U.S.A. than to those from the outer Florida Keys, which are characteristically light-coloured. We conclude that *P. maynardi* is morphologically indistinguishable from *P. lotor*, supporting similar conclusions reached by Koopman *et al.* (1957) and Lazell (1981). It is currently impossible to ally the New Providence population with any one of the raccoon subspecies of the eastern U.S.A., because the many recognized forms are not well marked and can be discriminated only on the basis of geographic provenance. Interestingly, because the name *maynardi* pre-dates the scientific names of many mainland raccoons, it may well be the earliest available name for a subspecies of *P. lotor*. Thus, with further revision, *maynardi* may be retained as a valid name not for an endemic Bahamian raccoon but for a mainland subspecies historically transported to the Bahamas.

Raccoons from Guadeloupe

The holotype of the Guadeloupe raccoon (USNM 38417/15481) is a juvenile skull and poorly prepared study skin. As with *P. maynardi*, this scanty type material is all that Miller (1911) had available when he described *minor* as a new species. Goldman (1950) examined one additional specimen, also immature. We have examined four specimens, including one adult (Appendix). These agree with *maynardi* and raccoons from the south-eastern U.S.A. in the same cranial features as discussed above. Goldman’s (1950) description of pelage and cranial traits in two immature specimens do not justify the separation of *P. minor* from *P. lotor* at any level, and it is likely he maintained the species primarily on geographic grounds. As with *P. maynardi*, we conclude that *P. minor* is assuredly conspecific with *P. lotor*. Two of the skulls exhibit an

extraneous basioccipital foramen (situated immediately anterior to the foramen magnum) as noted above.

We further note that the adult specimen from Guadeloupe is similar in size to raccoons from the southeastern U.S.A. Too much attention has been paid to the purported small size of West Indian raccoons (each of which was originally described based on a single immature holotype), as this difference appears less real in our material than previously supposed (and cf. Schomburgk, 1848), and because the rapid dimensional change of recently introduced species on small islands is a well-documented phenomenon (e.g. Ashton & Zuckerman, 1951; Case & Schwaner, 1993; Yom-Tov, Yom-Tov & Moller, 1999).

Raccoons from Barbados

The type material of *P. gloveralleni* is a juvenile male skin and skull (MCZ 18951). Nelson & Goldman (1930) wrote that 'such scanty material affords an unsatisfactory basis for a new species'; this did not, however, discourage them from naming one. They correctly observed that 'the general form of the skull ... shows alliance to other West Indian and Florida raccoons, rather than to those of the Middle [=Central] American mainland' (Nelson & Goldman, 1930: 454). Despite this, Goldman (1950) and Hall (1981) suggested a possible relationship between raccoons from Central America and Barbados.

One of the most distinctive features of the holotype of *gloveralleni* as described by Nelson & Goldman (1930: 454) is the absence of first premolars in every quadrant of the jaw; they also noted that 'the crown of the upper carnassial [is] longer than broad, a condition unusual [in raccoons]'. Two unsexed adult specimens from Barbados, collected in c. 1867, were discovered on display at USNM after *gloveralleni* was described (Appendix). The skins of these specimens are badly preserved, but both skulls are largely intact. None of the unusual traits of the young holotype characterize these specimens, each of which has anterior premolars present in both jaws. Goldman's (1950) measurements for the upper fourth premolars of these specimens demonstrate that length and breadth of this tooth are roughly equal for both. While the occiput and zygomatic arches of USNM 267380 are damaged, the skull of USNM 267381 is almost fully intact. The large postorbital processes of this latter specimen approach the size of those seen in some Central American representatives of *P. lotor*, such as *P. l. pumilus* of Panama. However, its more moderate dentition, inflated auditory bullae, posteriorly deflected postorbital processes, and hooklike coronoid process of the mandible suggest an affinity with the raccoons of Georgia and Florida rather than Central America, in line with Nelson & Goldman's (1930) initial observations. Lack of first premolars is an abnormality observed elsewhere only in raccoons from coastal Georgia (Goldman, 1950), and we suggest the Florida/Georgia region as a probable point of origin for the raccoon population formerly present on Barbados. Lazell (1981),

who examined one additional skull of *gloveralleni* (in a museum on Barbados), arrived at a similar conclusion.

DISCUSSION

We conclude that raccoons from Guadeloupe, Barbados and the Bahamas are not morphologically distinguishable from the North American raccoon *P. lotor*, leaving no avenue open to argue that these are Caribbean endemics. Thus, classification of *P. maynardi* and *P. minor* as endangered species with high conservation priority (Putney, 1980; Glatston, 1994; Baillie & Groombridge, 1996) is not warranted, and recognizing *P. gloveralleni* as a recently extinct West Indian species, as many authors have done (e.g. Cole, Reeder & Wilson, 1994; Glatston, 1994; Simmons & Associates, 2000) is also taxonomically unjustified, and adds to the confusion associated with accurate assessments of mammalian extinctions in the modern era (MacPhee & Marx, 1997; MacPhee & Flemming, 1999). The implications of this change in status are potentially large. For example, as a result of its purported endemic status (Pinchon, 1971; Benito-Espinal, 1976), the Guadeloupean raccoon has been used as a flagship species by local conservationists in Guadeloupe and was chosen as the emblematic species of the 'Parc National de Guadeloupe' (Pons *et al.*, 1999). However, given their alien origins, granting protected status or other positive attention to Caribbean raccoons could be counter-productive from a conservation standpoint. Although Pons *et al.* (1999) held that 'in Guadeloupe the raccoon [sic] does not raise important management problems, either with insular fauna or with human activities,' it is important to note that raccoons have the potential for negative environmental impact and could be sources of ecological duress to their respective insular ecosystems. Raccoons have been widely implicated in predation on native ground-nesting birds and eggs (Hartman, Gaston & Easton, 1997; Hartman & Eastman, 1999; Erwin, Truitt & Jimenez, 2001), and on nests of endangered sea turtles (Ratnaswamy *et al.*, 1997; Ratnaswamy & Warren, 1998; Foley *et al.*, 2000), both of which are present on Guadeloupe, Barbados, and in the Bahamas. In discussing similarly introduced raccoon populations in the Queen Charlotte Islands of Canada, Hartman *et al.* (1997) warned that 'raccoon predation represents a conservation threat of international significance' because of their capacity for devastating native populations of endangered birds. Raccoons can also act to facilitate the spread of epizootic disease in populations of native wildlife (Page, Swihart & Kazacos, 1999), and are well-known as vectors for dangerous human diseases (Dobson, 2000; Murray, 2000) and as agricultural pests (Goldman, 1950; Conover, 1998). Because they are extinct, questions regarding the environmental impact of raccoons on Barbados are largely irrelevant from a current conservation standpoint. However, raccoon impact on the insular environments of New Providence, Grand Bahama, and Guadeloupe is a topic of genuine conservation concern worthy of immediate research.

Taxonomic confusion in the genus *Procyon* has been longstanding, and conservation priorities within the genus have unfortunately remained obscure as a result. We hope this report will initiate new discussions regarding current goals in procyonid conservation. For instance, we suggest that any conservation attention or effort currently devoted to insular raccoons would be best focused on the raccoons of Isla Cozumel, Mexico (*Procyon pygmaeus*), which are critically endangered, and (unlike West Indian raccoons) morphologically distinctive.

Acknowledgements

This study was supported by the Smithsonian Institution, the National Science Foundation (REU DBI-9820303), and the Museum of Comparative Zoology at Harvard University. We are thankful to N. Campeau, L. Gordon, A. Gardner, B. Shepherd, R. Fisher, D. Cole, A. Biewener, T. McFadden, M. Rutzmoser, J. Harrison, J. Chupasko, E. Brothers, R. Voss, C. Norris, H. Angarita, K. Zyskowski, and M. Sangrey for helpful discussion, access to specimens, and other assistance. We additionally thank R. Medellin for his helpful review of our manuscript.

REFERENCES

- Allen, G. M. (1911). Mammals of the West Indies. *Bull. Mus. Comp. Zool.* **54**: 175–263.
- Arredondo, O. (1976). The great predatory birds of the Pleistocene of Cuba. *Smithson. Contrib. Paleontol.* **27**: 169–187.
- Arredondo, O. & Varona, L. S. (1974). Nuevos género y especie de mamífero (Carnivora: Canidae) del Cuaternario de Cuba. *Poeyana* **131**: 1–12.
- Ashton, E. H. & Zuckerman, S. (1951). The influence of geographic isolation on the skull of the green monkey (*Cercopithecus aethiops sabaesus*) IV. *Proc. R. Soc. Lond. B Biol. Sci.* **138**: 354–374.
- Baillie, J. & Groombridge, B. (Eds) (1996). *1996 IUCN red list of threatened animals*. Gland, Switzerland: IUCN (World Conservation Union).
- Bangs, O. (1898). A new raccoon from Nassau Island, Bahamas. *Proc. Biol. Soc. Wash.* **12**: 91–92.
- Benito-Espinal, E. (1976). *La faune 1: Reptiles, mammifères, amphibiens Antilles d'hier et d'aujourd'hui 2*. Fort de France, Martinique: E. Desormeaux.
- Bininda-Emonds, O. R. P., Gittleman, J. L. & Purvis, A. (1999). Building large trees by combining phylogenetic information: a complete phylogeny of the extant Carnivora (Mammalia). *Biol. Rev.* **74**: 143–175.
- Browne, P. (1789). *The civil and natural history of Jamaica*. 2nd edn. London: B. White.
- Case, T. J. & Schwaner, T. D. (1993). Island mainland body size differences in Australian varanid lizards. *Oecologia (Berl.)* **94**: 102–109.
- Chester, G. J. (1869). *Transatlantic sketches in the West Indies, South Atlantic, Canada, and the U.S.A.* London: Smith, Elder, and Co.
- Cole, F. R., Reeder, D. M. & Wilson, D. E. (1994). A synopsis of distribution patterns and the conservation of mammal species. *J. Mammal.* **75**: 266–276.
- Conover, M. R. (1998). Perceptions of American agricultural producers about wildlife on their farms and ranches. *Wildl. Soc. Bull.* **26**: 597–604.
- Corbet, G. B. & Hill, J. E. (1991). *A world list of mammalian species*. 3rd edn. London: British Museum (Natural History).
- Denham, W. W. (1987). *West Indian green monkeys: problems in historical biogeography. Contributions to Primatology* **24**. Basel: Karger.
- Dobson, A. (2000). Raccoon rabies in space and time. *Proc. Natl. Acad. Sci. U.S.A.* **97**: 14041–14043.
- Erwin, R. M., Truitt, B. R. & Jimenez, J. E. (2001). Ground-nesting waterbirds and mammalian carnivores in the Virginia barrier island region: running out of options. *J. Coast. Res.* **17**: 292–296.
- Feilden, H. W. (1890). Notes on the terrestrial mammals of Barbados. *Zoologist (Ser. 3)* **14**: 52–55.
- Foley, A. M., Peck, S. A., Harman, G. R. & Richardson, L. W. (2000). Loggerhead turtle (*Caretta caretta*) nesting habitat on low-relief mangrove islands in southwest Florida and consequences to hatchling sex ratios. *Herpetologica* **56**: 433–445.
- Glatston, A. R. (Ed.) (1994). *The red panda, olingos, coatis, raccoons, and their relatives: status survey and conservation action plan for procyonids and ailurids*. Gland, Switzerland: IUCN (World Conservation Union).
- Goldman, E. A. (1950). Raccoons of North and Middle America. *N. Am. Fauna* **60**: 1–153.
- Hall, E. R. (1981). *The mammals of North America* **1 & 2**. 2nd edn. New York: John Wiley.
- Hall, R. (1764). *Acts passed in the island of Barbados 1643–1762*. London: Printed for the author.
- Hartman, L. H. & Eastman, D. S. (1999). Distribution of introduced raccoons *Procyon lotor* on the Queen Charlotte Islands: implications for burrow-nesting seabirds. *Biol. Conserv.* **88**: 1–13.
- Hartman, L. H., Gaston, A. J. & Eastman, D. S. (1997). Raccoon predation in ancient murrelets in East Limestone Island, British Columbia. *J. Wildl. Manag.* **61**: 377–388.
- Hershkovitz, P. (1966). On the status of *Procyon brachyurus* Wiegmann and *P. obscurus* Wiegmann. *Bull. Zool. Nomencl.* **22**: 338.
- Hughes, G. (1750). *The natural history of Barbados*. London: Printed for the author.
- Koopman, K. F., Hecht, M. K. & Ledecy-Janacek, E. (1957). Notes on the mammals of the Bahamas with special reference to the bats. *J. Mammal.* **38**: 164–174.
- Lazell, J. D. Jr (1972). Raccoon relatives. *Man and nature* September 1972: 11–15.
- Lazell, J. D. Jr (1981). Field and taxonomic studies of tropical American raccoons. *Nat. Geogr. Soc. Res. Rep.* **13**: 381–385.
- Lever, C. (1985). *Naturalized mammals of the world*. Essex: Longman House.
- Ligon, R. (1657). *A true and exact history of the island of Barbados*. London: Privately printed.
- Lotze, J.-H. & Anderson, S. (1979). *Procyon lotor*. *Mamm. Species* **119**: 1–8.
- Macdonald, D. W. (1993). *The velvet claw: a natural history of the carnivores*. London: British Broadcasting Company.
- Macdonald, D. W. (Ed.) (2001). *The new encyclopedia of mammals*. Oxford: Oxford University Press.
- MacPhee, R. D. E. & Fleagle, J. G. (1991). Postcranial remains of *Xenothrix mcgregori* (Primates, Xenotrichidae) and other Late Quaternary mammals from Long Mile Cave, Jamaica. *Bull. Am. Mus. nat. Hist.* **206**: 287–321.
- MacPhee, R. D. E. & Flemming, C. (1999). Requiem aeternam: the last five hundred years of mammalian species extinctions. In *Extinctions in near time: causes, contexts, and consequences*: 333–372. MacPhee, R. D. E. (Ed.). New York: Kluwer Academic/Plenum.
- MacPhee, R. D. E. & Marx, P. A. (1997). The 40,000-year plague: humans, hyperdisease, and first-contact extinctions. In *Natural change and human impact in Madagascar*: 169–217.

- Goodman, S. M. & Patterson, B. D. (Eds). Washington: Smithsonian Institution Press.
- Marsh, R. E. (1984). Evidence does not support the existence of a Bajan mouse. *J. Barbados Mus. Hist. Soc.* **37**: 159–60.
- McKenna, M. C. & Bell, S. K. (1997). *Classification of mammals above the species level*. New York: Columbia University Press.
- McKinley, D. (1959). Historical note on the Bahama raccoon. *J. Mammal.* **40**: 248–249.
- Merriam, C. H. (1898). Mammals of Tres Marias Islands off western Mexico. *Proc. Biol. Soc. Wash.* **12**: 13–19.
- Merriam, C. H. (1901). Six new mammals from Cozumel Island, Yucatan. *Proc. Biol. Soc. Wash.* **14**: 99–104.
- Miller, G. S. Jr (1905). Mammals of the Bahama Islands. In *The Bahama Islands*: 373–384. Shattuck, G. B. (Ed.). Baltimore: Johns Hopkins Press.
- Miller, G. S. Jr (1911). Descriptions of two new raccoons. *Proc. Biol. Soc. Wash.* **24**: 3–6.
- Morgan, G. S. (1989). Fossil Chiroptera and Rodentia from the Bahamas, and the historical geography of the Bahamian mammal fauna. In *Biogeography of the West Indies: past, present, and future*: 685–740. Woods, C. A. (Ed.). Gainesville, FL: Sandhill Crane Press.
- Morgan, G. S. & Woods, C. A. (1986). Extinction and the zoogeography of West Indian land mammals. *Biol. J. Linn. Soc.* **28**: 167–203.
- Morrison, A. J. (transl., Ed.) (1911). *Travels in the Confederation [1783–1784] from the German of Johann David Schöpfung 2*. Philadelphia: W. J. Campbell.
- Murray, W. J. (2000). The epidemiology of a case of raccoon roundworm infection. *Proc. Vertebr. Pest. Conf.* **19**: 118–120.
- Nelson, E. W. & Goldman, E. A. (1930). Six new raccoons of the *Procyon lotor* group. *J. Mammal.* **11**: 453–459.
- Nowak, R. M. (1999). *Walker's mammals of the world 1 & 2*. 6th edn. Baltimore: Johns Hopkins University Press.
- Olson, S. L. (1978). A paleontological perspective of West Indian birds and mammals. *Acad. Nat. Sci. Phil. Spec. Publ.* **13**: 99–117.
- Olson, S. L. (1983). Biological archeology in the West Indies. *Fla Anthropol.* **35**: 162–168.
- Olson, S. L. & Pregill, G. K. (1982). Introduction to the paleontology of Bahaman vertebrates. *Smithson. Contrib. Paleobiol.* **48**: 1–7.
- Page, L. K., Swihart, R. K. & Kazacos, K. R. (1999). Implications of raccoon latrines in the epizootiology of baylisascariasis. *J. Wildl. Dis.* **35**: 474–480.
- Pinchon, R. (1971). *D'autres aspects de la nature aux Antilles*. Fort de France, Martinique: Ozanne.
- Pons, J.-M., Volobouev, V., Ducroz, J. F., Tillier, A. & Reudet, D. (1999). Is the Guadeloupean racoon [sic] (*Procyon minor*) really an endemic species? New insights from molecular and chromosomal analyses. *J. Zool. Syst. Evol. Res.* **37**: 101–108.
- Putney, A. D. (1980). *Survey of conservation priorities in the Lesser Antilles: preliminary data atlas, Guadeloupe*. St Croix, U.S. Virgin Islands: Eastern Caribbean Natural Area Management Program.
- Ratnaswamy, M. J. & Warren, R. J. (1998). Removing raccoons to protect sea turtle nests: are there implications for ecosystem management? *Wildl. Soc. Bull.* **26**: 846–850.
- Ratnaswamy, M. J., Warren, R. J., Kramer, M. T. & Adam, M. D. (1997). Comparisons of lethal and nonlethal techniques to reduce raccoon depredation of sea turtle nests. *J. Wildl. Manage.* **61**: 368–376.
- Schomburgk, R. H. (1848). *The history of Barbados; comprising a geographical and statistical description of the island; a sketch of the historical events since the settlement; and an account of geology and natural productions*. London: Longman, Brown, Green & Longmans.
- Sherman, H. B. (1954). Raccoons of the Bahama Islands. *J. Mammal.* **35**: 126.
- Simmons and Associates (2000). *First National Report to the Conference of Parties to the Convention on Biological Diversity*. Barbados: Ministry of Environment, Energy, and Natural Resources.
- Simpson, G. G. (1956). Zoogeography of West Indian land mammals. *Am. Mus. Novit.* **1759**: 1–28.
- Sloane, H. (1725). *A voyage to the islands Madera, Barbados, Nieves, St. Christopher's, and Jamaica with the natural history of the herbs and trees, four-footed beasts, insects, reptiles, etc., of the last of these islands 2*. London: British Museum.
- Varona, L. S. (1974). *Catálogo de los mamíferos vivientes y extinguidos de las Antillas*. Havana: Instituto de Zoología, Academia de Ciencias de Cuba.
- Wiegmann, A. F. A. (1837). Über die gattung. *Procyon*. *Arch. Naturgesch.* **1**: 353–372.
- Wilson, D. E. & Cole, F. R. (2000). *Common names of mammals of the world*. Washington, DC: Smithsonian Institution Press.
- Wozencraft, W. C. (1989). Classification of the Recent Carnivora. In *Carnivore behavior, ecology, and evolution 1*: 569–593. Gittleman, J. L. (Ed.). Ithaca, NY: Cornell University Press.
- Wozencraft, W. C. (1993). Order Carnivora. In *Mammal species of the world*: 279–348. 2nd edn. Wilson, D. E. & Reeder, D. R. (Eds). Washington: Smithsonian Institution Press.
- Yom-Tov, Y., Yom-Tov, S. & Moller, H. (1999). Competition, coexistence, and adaptation amongst rodent invaders to Pacific and New Zealand islands. *J. Biogeogr.* **26**: 947–958.

**APPENDIX. MUSEUM SPECIMENS EXAMINED OF
INSULAR RACCOONS *PROCYON LOTOR***

New Providence Island (Bahamas)

AMNH 17998, skin and skull, young adult, unsexed, from Nassau (25°05'N, 77°21'W), collected February 1902. USNM 121905, skin and skull, adult male, no specific locality, collected 23 June 1903. MCZ B7750, holotype of *P. maynardi*, skin and skull, immature male from Nassau, collected August 1897. MCZ 11766, skin and skull, sub-adult female, from Nassau, collected 1915. MCZ 29433–29435, 29962–29963, 34282 skins and skulls, adults and sub-adults, from Nassau, collected 1933–34.

Guadeloupe

USNM 38417/15481, holotype of *P. minor*, skin and skull, juvenile male, from Pointe-à-Pitre (16°14'N, 61°32'W),

collected before 26 June 1886. MCZ 15939, skin and skull, unsexed sub-adult, no specific locality, collected 1914. MCZ 51075, skin and skull, male sub-adult, from Matouba (16°03'N, 61°42'W), collected 17 August 1961. YPM 14224, skin and skull, adult female, from Pointe-à-Rifflet (16°20'N, 61°48'W), collected 16 June 1973.

Barbados

MCZ 18591, holotype of *P. gloveralleni*, skin and skull, juvenile male, no specific locality, collected 1920. USNM 267380, skin and skull, unsexed adult, no specific locality, no other information. USNM 267381, skin and skull, unsexed adult, no specific locality, no other information.