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MOLECULAR CONFIRMATION OF THE ORIGIN AND INVASIVE STATUS OF WEST INDIAN RACCOONS

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Raccoons occur on a number of islands in the Bahamas and the Lesser Antilles in the West Indies. Zooarcheological studies have long suggested that these animals are not native to the West Indies. Originally, Caribbean populations were described as endemic insular species *Procyon maynardi* (Bahamas), *P. minor* (Guadeloupe), and *P. gloveralleni* (Barbados), a classification that was recognized throughout much of the 20th century. More recently, studies of qualitative morphology and a review of historical publications and documents have been used to bolster arguments that these populations of raccoons are not unique species worthy of special conservation attention, but invasive populations of the North American raccoon (*P. lotor*) introduced in recent centuries. Raccoons in the Bahamas and the French Antilles appear to be spreading onto other islands with human assistance, but the population on Barbados is now apparently extinct. We present evidence from the mitochondrial control region, including sequence data from the extinct population on Barbados generated using ancient DNA protocols, indicating that all 3 major insular populations of West Indian raccoons are conspecific with *P. lotor* and probably originated via recent translocations from eastern North America. Like nonnative populations of raccoons that have been established elsewhere (e.g., in Alaska, Japan, and Europe), the raccoons of the West Indies deserve no special taxonomic recognition or conservation status. They may be destructive to native wildlife on West Indian islands where they have been introduced, particularly if their spread to and across other islands continues.

Key words: ancient DNA, Carnivora, conservation, invasive species, island biogeography, taxonomy

This is a cautionary tale involving island endemics, invasive aliens, premature descriptions, and the need for solid systematic studies in making conservation decisions. In a previous paper (Helgen and Wilson 2003), we documented that the 3 recently recognized ''species'' of raccoons from the Caribbean (Wozencraft 1993) are each the result of introductions of the widespread North American species, *Procyon lotor* (Fig. 1). Modern molecular methods allow for an unprecedented level of discrimination in determining the origin of introduced populations. Building on the genetic study by Pons et al. (1999), we used DNA sequencing to further establish the provenance of populations of raccoons from the Bahamas, Guadeloupe, and Barbados.

In the latter part of the 19th century, Charles Johnson Maynard, a nationally known ornithologist respected for his research, particularly on the vocal organs of birds, travelled from his home in Newton, Massachusetts, to the Bahamas in search of natural history specimens. He noted the abundance of raccoons on New Providence Island, and brought back live animals in 1897, which he showed to Outram Bangs, Curator of Mammals at the Museum of Comparative Zoology at Harvard University. Bangs subsequently arranged for the collection of a specimen, an immature male with the posterior part of the skull smashed, which became the type specimen of *Procyon maynardi* Bangs, 1898 (Helgen and McFadden 2001).

Had Bangs been aware of the journals of Johann David Schöpf, he would have realized that Bahamian raccoons were the result of an introduction, rather than a naturally occurring, undescribed species. Schöpf was born in 1752 in the German

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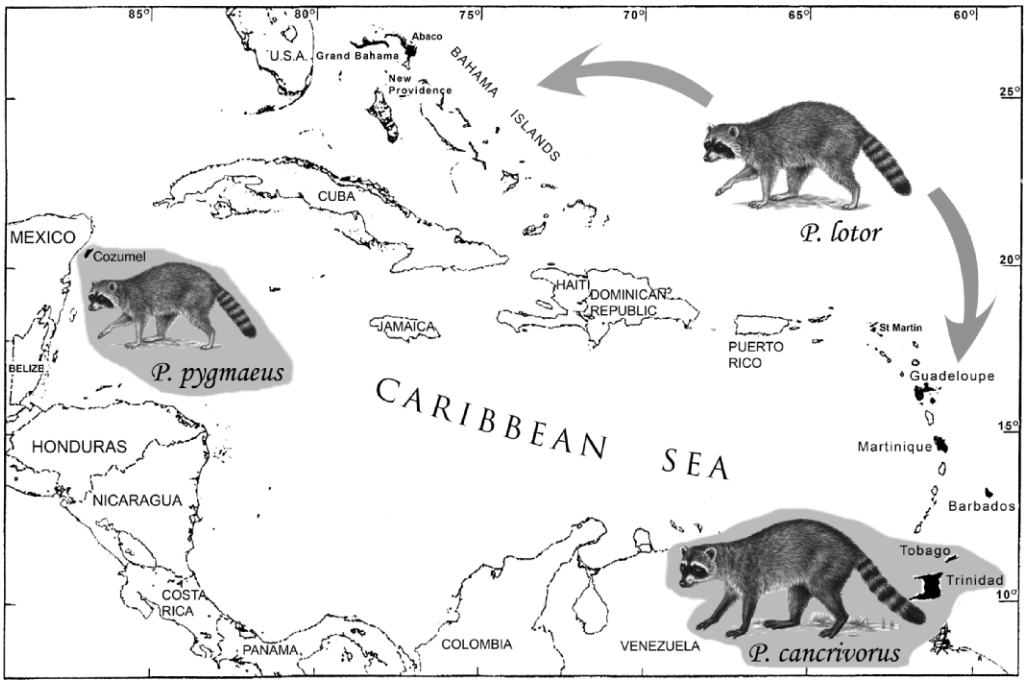

FIG. 1.—Map of the West Indies, showing the distribution of raccoons on islands throughout the region. The North American raccoon (*Procyon lotor*) occurs throughout the mainland of North and Central America and has been introduced in the Bahamas (New Providence, Grand Bahama, and Abaco), St. Martin, Guadeloupe and surrounding islands, Martinique, and formerly Barbados and perhaps Jamaica. The crab-eating raccoon (*Procyon cancrivorus*) occurs throughout mainland South America and also (probably naturally) on Trinidad and Tobago. The Cozumel raccoon (*Procyon pygmaeus*), a small insular species immediately related to *P. lotor* but recognized nominally here as by Helgen and Wilson (2005), is found only on the oceanic island of Cozumel. Drawings borrowed from Reid (1997).

principality of Bayreuth. Educated as a physician and natural scientist, he arrived in New York in 1777 as chief surgeon of the Ansbach troops in the service of George III. Schöpf travelled widely in the southeastern United States and in the Bahamas, where he documented the increasing population of raccoons on New Providence Island, and clearly identified their presence as the result of an introduction from the mainland. After returning to Europe that same year (1784), Schöpf died in 1800 while serving as president of the United Medical Colleges of Ansbach and Bayreuth. The German edition of his book was published in Erlangen in 1788, but an English translation by Alfred J. Morrison appeared only in 1911, well after Bangs described the animals as new (Bangs 1898; Morrison 1911).

A subsequent introduction of raccoons to Grand Bahama Island occurred in 1932 or 1933, when a Mr. Jack Morris turned loose a pair that had been brought from the Florida mainland. According to Senior Commissioner Herman Pyfrom, as of 1952 "... the raccoons have multiplied immensely and ... they are now scattered over the entire island ..." (Sherman 1954:126). Raccoons are still present on the island today.

In 1911, Gerritt S. Miller, Jr., Curator of Mammals at the United States National Museum in Washington, described *Procyon minor* from the Lesser Antillean island of Guadeloupe (Miller 1911). The holotype and only specimen was once again an immature male, collected at Pointe-à-Pitre by L. Guesde. Miller, a careful worker and diligent observer of slight morphological differences, noted that *P. minor* was characterized by "size and general appearance as in the other small members of the genus ... ." He added "the color indicates no special peculiarities ... ," and "the skull is too young to furnish a satisfactory basis for comparison." Nevertheless, he concluded with "Although represented by a single rather unsatisfactory specimen this animal shows such marked characters that I have no hesitation in regarding it as a distinct species." Little is known about the origin or timing of the introduction to Guadeloupe (Helgen and Wilson 2002). Allen (1911:221) speculated that raccoons had possibly been "... introduced by the French in the early days" and Lorvelec et al. (2007) discussed the possibility of raccoons being imported from Canada or South Carolina in the early to mid-19th century. Interestingly enough, the animals are viewed with such affection on Guadeloupe that their change in status from island endemic to invasive alien has had no apparent effects (Fig. 2).

Helgen and Wilson (2002) documented the introduction of raccoons to Barbados in some detail. Barbados served as 1 leg of a triangular trade route involving the eastern seaboard British Colonies of North America and West African slave ports. Raccoons were introduced sometime between 1650 and 1680 (Helgen and Wilson 2002). In 1867, a Reverend Barnett collected 2 specimens and sent them to the Smithsonian, where they were put on display (Goldman 1950).

Glover M. Allen (1911) knew of the presence of raccoons on Barbados, and he speculatively and erroneously referred to them as "*Procyon ? cancrivorus*" (see also Tate 1939:201). Through Allen's efforts, Sir Francis Watts collected a juvenile male in 1920, and later sent it to Allen at the Museum of

Comparative Zoology (Helgen and McFadden 2001). This is the holotype of *Procyon gloveralleni*, later described by Nelson and Goldman (1930). Nelson and Goldman were unaware of Barnett's 2 additional mounted specimens from Barbados, on exhibit at the time (Goldman 1950; Helgen and Wilson 2002, 2003), so this made the 3rd new species of raccoon named from Caribbean islands on the basis of a single immature specimen.

Today, taxonomists usually recognize only 3 species of raccoons—the North American raccoon (*Procyon lotor*) of North and Central America; the Cozumel raccoon (*P. pygmaeus*), a closely related insular endemic restricted to the Mexican island of Cozumel; and the more distantly related crab-eating raccoon (*P. cancrivorus*) of Central and South America (Helgen and Wilson 2005; Wozencraft 2005). Having affirmed that all 3 previously recognized West Indian insular ''species'' (Fig. 1) were the result of introductions of the widespread species *P. lotor* (Helgen and Wilson 2002, 2003), we sought to determine the origin of the populations in greater detail. The promise of using modern methods of DNA analysis led us to assemble tissue samples from a variety of sources, including museum specimens and freshly collected material from different islands in the Bahamas and Barbados that, according to historical publications and documents, are supposedly the result of separate raccoon introductions.

Fig. 2.—Raccoons in Guadeloupe (left) are favorite animals exhibited in the Parc des Mamelles (Parc Zoologique et Botanique) and used as symbols for the island's national park (right).

Methods and Materials

Study areas.—The 3 taxonomically described populations of Caribbean raccoons are from New Providence (Bahamas), Guadeloupe, and Barbados (Fig. 1). We visited each of these islands in May–June 2004, in order to establish the current status of these insular populations, as well as to obtain additional specimens and tissue samples (Table 1). In the Bahamas we collected voucher specimens and tissue samples from New Providence and Abaco islands. In Guadeloupe we did not obtain specimens of raccoons, and relied on previously collected museum specimens (Helgen and Wilson 2002, 2003) and previously published molecular sequences (Pons et al. 1999; Table 2) for our analyses. From Barbados, we attempted to obtain DNA from 1 skin sample from the only museum specimen remaining on the island (Fig. 3), and we also attempted to extract DNA from the turbinal bones of 2 museum specimens previously collected in Barbados and deposited at the National Museum of Natural History (USNM 267380 and USNM 267381—see Helgen and Wilson 2002, 2003). However, we were only successful in amplifying and sequencing 1 of the museum bone samples (USNM 267380; Table 1). Our newly sequenced mainland tissue samples came from the states of Georgia, South Carolina, and Virginia, in the southeastern United States (Table 1).

Extraction, amplification, and analysis of mitochondrial DNA.—Tissue samples were obtained from 2 raccoons from

Table 1.—Sampling localities, haplotype designation, and GenBank accession numbers of raccoon samples sequenced for this study. PL numbers designate samples stored in the laboratory of Michael L. Kennedy (University of Memphis, Memphis, Tennessee); NDM numbers designate samples from the tissue collection of Nancy D. Moncrief (Virginia Museum of Natural History, Martinsville, Virginia); and USNM numbers designate samples at the United States National Museum of Natural History, Smithsonian Institution, Washington, D.C.

Locality	Specific locality	Specimen no.	Haplotype	GenBank accession no.
Bahamas	Bahamas—Abaco	USNM 597652	*BAH1*	EU021073
Bahamas	Bahamas—Abaco	USNM 597653	*BAH1*	EU021073
Bahamas	Bahamas—New Providence	USNM 597654	*BAH2*	EU021074
Bahamas	Bahamas—New Providence	USNM 597655	*BAH2*	EU021074
Barbados	''Barbados''	USNM 267380	*BAR1*	EU021075
Virginia	Barrier Islands	NDM 2900	*V5*	EU021077
Virginia	Barrier Islands	NDM 3859	*V4*	EU021076
Georgia	Chatham—Ossabaw Island	PL1350	*GA/SC1*	EU021078
Georgia	Chatham—Ossabaw Island	PL1351	*GA2*	EU021081
Georgia	Chatham—Ossabaw Island	PL1352	*GA2*	EU021081
Georgia	Chatham—Ossabaw Island	PL1353	*GA2*	EU021081
South Carolina	Aiken—Savannah River Plant	PL1355	*SC2*	EU021079
South Carolina	Aiken—Savannah River Plant	PL1356	*SC3*	EU021080
South Carolina	Aiken—Savannah River Plant	PL1357	*SC2*	EU021079
South Carolina	Aiken—Savannah River Plant	PL1358	*SC3*	EU021080
South Carolina	Aiken—Savannah River Plant	PL1359	*GA/SC1*	EU021078

TABLE 2.—Sampling localities, haplotype designation, and GenBank accession numbers of raccoons used by Pons et al. (1999) and also in this study.

Locality	Sample size	Specific locality, if known	Haplotype	GenBank accession no.
Guadeloupe	3		*G*	AF08174
Virginia	1		*V1*	AF08175
Virginia	1		*V2*	AF08176
Virginia	1		*V3*	AF08178
Maryland	1	Greenbelt	*M*	AF08179
Illinois	3	Kane	*I*	AF08180
Quebec	2	Chaudiere-Appalache	*Q1*	AF08181
Quebec	1	Chaudiere-Appalache	*Q2*	AF08182
Arizona	3	NW Tucson	*A*	AF08183

Abaco and 2 from New Providence in the Bahamas (the type locality of "*P. maynardi*") and stored in ethanol (95%) at −70°C. Eleven additional tissue samples were obtained from 3 different localities from the southeastern United States including Georgia ($n = 4$), South Carolina ($n = 5$), and Virginia ($n = 2$; Table 1). Total genomic DNA was extracted from tissue samples using the tissue protocol of the QIAGEN DNeasy DNA extraction kit (Qiagen Inc., Valencia, California). In order to compare our results with previously published sequences from raccoons throughout the United States and Canada, we amplified approximately 450 base pairs (bp) of the left domain of the mitochondrial DNA control region with universal primers L15910 and H16498 (Kocher et al. 1989) as in Pons et al. (1999). We also attempted to extract DNA from the turbinal bones of 2 museum specimens following protocols for sampling ancient DNA that minimize damage to museum specimens established by Wisely et al. (2004). DNA extractions and polymerase chain reactions for the 2 museum samples were conducted in a separate facility specifically designed for DNA extraction of ancient samples. Because our amplifications with the larger universal primers did not work for the museum specimens, we also designed 2 internal primers—Proc L 5′-TCATCGAAAATAATCTGTTAAAATGAA-3′ and Proc H 5′-CGGAGCGAGAAGAGGTACAC-3′, that amplify a shorter 392-bp fragment of the mitochondrial control region of raccoons. For both primer sets the polymerase chain reactions were performed in a volume of 25 μl with 1.0 unit of AmpliTaq Gold (Applied Biosystems, Foster City, California), 1× polymerase chain reaction buffer, 0.2 mM each deoxynucleoside triphosphate, 0.6 μM each primer, 3 mM $MgCl_2$ and 20 μg bovine serum albumin. A 10-min denaturation at 95°C was used followed by 35 cycles of 94°C for 1 min, 53°C for 1 min, and 72°C for 1 min, and finally a 10-min elongation step at 72°C. Polymerase chain reaction products were cleaned using Qiaquick polymerase chain reaction purification columns (Qiagen Inc.) and sequenced in both directions using the BigDye Terminator V3.1 Cycle Sequencing kit (Applied Biosystems) according to manufacturer's recommendations. Reactions were purified via centrifugation through Sephadex columns (Amersham Biosciences, Piscataway, New Jersey). Sequences were run on an ABI Prism 3100 Genetic Analyzer (Applied Biosystems) and edited and aligned in Sequencher 4.1 (Gene Codes Corporation, Inc., Ann Arbor, Michigan). Sequence data have been submitted to GenBank (accession numbers EU021073–EU021081; Table 1).

FIG. 3.—The raccoon population in Barbados is extinct. This mounted skin, on display in the Barbados Museum, Bridgetown, is 1 of only 5 known museum specimens from the island (others are at BMNH, MCZ, and USNM).

Levels of genetic diversity within populations (Table 3) were evaluated using control region sequences by estimating the mean number of pairwise differences along with nucleotide and gene diversity (Nei 1987; Tajima 1983). We used TCS version 1.18 (Clement et al. 2000) to generate a haplotype network and to assess the intraspecific phylogeny of the mitochondrial control region haplotypes of raccoons collected for this study and from the study of Pons et al. (1999). This method uses parsimony (as defined by Templeton et al. [1992]) to construct pairwise distances (number of mutational steps) between all haplotypes until the probability exceeds 95%. The matrix just above this cutoff point represents the maximum number of mutational steps justified by the 95% parsimony criterion. This method is particularly appropriate for population-level analysis because it does not involve many of the assumptions of phylogenetic reconstruction methods. For instance, it does not assume that the ancestral sequence is missing and does not require bifurcating relationships (Gentile et al. 2002). The TCS program then connects the haplotypes based on these criteria into a network with the number of mutational steps indicated on the lines connecting haplotypes. On the basis of coalescent theory, this program also identifies the haplotype that has the highest probability of representing the outgroup haplotype among the collection of samples (Castelloe and Templeton 1994; Donnelly and Tavaré 1986).

Table 3.—Estimates of mitochondrial DNA control region sequence divergence between haplotypes from the Bahamas and Barbados and continental raccoons. Absolute values of number of all substitutions are given above the diagonal; Kimura-2-parameter distances are provided in percentages (%) below the diagonal.

	BAH1	*BAH2*	*BAR1*	*G*	*V1*	*V2*	*V3*	*V4*	*V5*	*M*	*GASC1*	*SC2*	*SC3*	*GA2*	*I*	*Q1*	*Q2*	*A*
BAH1	0	4	8	12	7	12	13	11	3	14	2	4	11	4	6	3	9	12
BAH2	1.4	0	6	12	7	12	13	11	3	14	2	4	11	4	6	3	9	13
BAR1	6.4	4.8	0	1	5	1	1	2	5	1	6	4	1	6	5	6	5	7
G	4.3	4.3	0.7	0	7	2	3	3	9	4	10	8	1	10	6	11	5	13
V1	2.5	2.5	4.2	2.5	0	5	6	6	6	7	5	5	6	7	1	6	6	10
V2	4.3	4.3	0.7	0.7	1.8	0	1	3	9	2	10	8	1	10	6	11	5	13
V3	4.6	4.6	0.7	1.0	2.1	0.3	0	4	10	3	11	9	2	11	7	12	6	14
V4	3.9	3.9	1.5	1.0	2.1	1.0	1.4	0	8	5	9	7	2	9	5	10	4	12
V5	1.0	1.0	3.8	3.2	2.1	3.2	3.5	2.8	0	11	1	1	8	1	5	2	6	10
M	5.0	5.0	0.7	1.4	2.5	0.7	1.0	1.7	3.9	0	12	10	3	12	8	13	7	15
GASC1	0.7	0.7	4.8	3.5	1.7	3.6	3.9	3.1	0.3	4.2	0	2	9	2	4	1	7	11
SC2	1.4	1.4	3.1	2.8	1.8	2.8	3.2	2.4	0.3	3.5	0.7	0	7	2	4	3	5	9
SC3	3.9	3.9	0.7	0.3	2.1	0.3	0.7	0.7	2.8	1.0	3.2	2.4	0	9	5	10	4	12
GA2	1.4	1.4	4.4	3.5	2.5	3.6	3.9	3.1	0.3	4.2	0.7	0.7	3.1	0	6	3	7	11
I	2.1	2.1	4.1	2.1	0.3	2.1	2.4	1.7	1.7	2.8	1.4	1.4	1.7	2.1	0	5	5	9
Q1	1.0	1.0	4.8	3.9	2.1	3.9	4.3	3.5	0.7	4.6	0.3	1.0	3.5	1.0	1.7	0	8	12
Q2	3.1	3.1	3.4	1.7	2.1	1.7	2.1	1.4	2.1	2.4	2.4	1.7	1.4	2.4	1.7	2.8	0	12
A	4.2	4.6	5.9	4.6	3.5	4.7	5.0	4.2	3.5	5.3	3.9	3.1	4.2	3.9	3.1	4.2	4.2	0

Museum specimens discussed herein are deposited in the Natural History Museum, London, United Kingdom (BMNH); the Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts (MCZ); and the United States National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM).

Results

Geography.—On the basis of published accounts and museum material, we have previously noted the occurrence of raccoons on 2 islands in the Bahamas (New Providence and Grand Bahama) and on Guadeloupe. Although extinct today, populations of raccoons were also present until the late 20th century on Barbados, and possibly also on Jamaica during the 18th century (Helgen and Wilson 2002, 2003).

We have documented in detail the historical evidence for the introduction of raccoons to these islands (Helgen and Wilson 2002). Raccoons were introduced to Barbados sometime between 1650 and 1679, and persisted there until about 1970 (Helgen and Wilson 2002; Fig. 3). Raccoons were probably introduced to New Providence in the early 18th century (Schöpf, in Morrison 1911), and they may have been introduced to Jamaica, where they do not occur today, around the same time (Browne 1789; MacPhee and Fleagle 1991; Sloane 1725). As noted earlier, the introduction of raccoons to Grand Bahama Island occurred in 1932–1933, with a pair of raccoons from Florida released on the island (McKinley 1959; Sherman 1954). Raccoons were probably introduced to Guadeloupe in the 19th century, and were definitely established there before 1886 (Helgen and Wilson 2002; Miller 1911). More recently, Breuil (2003:260) suggested that a historical reference to the killing of an animal ''which belongs to the genus *Felis*'' in Guadeloupe in 1840 mistakenly refers to a raccoon, but we regard this as highly unlikely, and suggest instead that the referral of the animal to *Felis* indicates that it was likely a feral cat, not a raccoon.

Here we note that raccoons are now found on a number of additional West Indian islands. First, we learned during our work in the Bahamas that in recent years, raccoons have been introduced to the island of Abaco (apparently from Grand Bahama Island, immediately adjacent to Abaco), where they have been rapidly spreading across the island, from north (Little Abaco) to south (Great Abaco). As far as we are aware, our specimens from Abaco constitute the 1st vouchered record of occurrence of raccoons on this island. Second, raccoons are now rather widespread in the French Antilles, where they occur beyond Guadeloupe on the nearby islands of Marie-Galante and La Désirade, and farther afield to Martinique and Saint-Martín—all French overseas possessions (Bon Saint Côme and Tanasi 1994; Breuil 2003; Laurent 2006; Lorvelec et al. 2001). The presence of raccoons on Martinique dates back at least half a century, perhaps longer. Raccoons have been present on Martinique since at least 1954 (Bon Saint Côme and Tanasi 1994), where according to Lorvelec et al. (2001:13) they are firmly established. Raccoons may have been present in Martinique several decades earlier than 1954, because Matthew (1919) made mention of a ''Martinique raccoon,'' although we suspect based on Matthew's comments that this was a *lapsus* for the Guadeloupe raccoon, at the time recently described by Miller (1911). However, other Antillean introductions date to recent years (Lorvelec et al. 2001). Raccoons were probably introduced to St. Martin around 1985, since which time the population has progressively increased (Lorvelec et al. 2001). Glatston (1994) stated that the crab-eating raccoon (*P. cancrivorus*) also has been introduced to Guadeloupe in recent decades, an assertion that we have repeated (Helgen and Wilson 2003), but we have been unable to find any evidence to support this claim.

In summary, introduced populations of *P. lotor* apparently occur today on at least 3 islands in the Bahamas (New

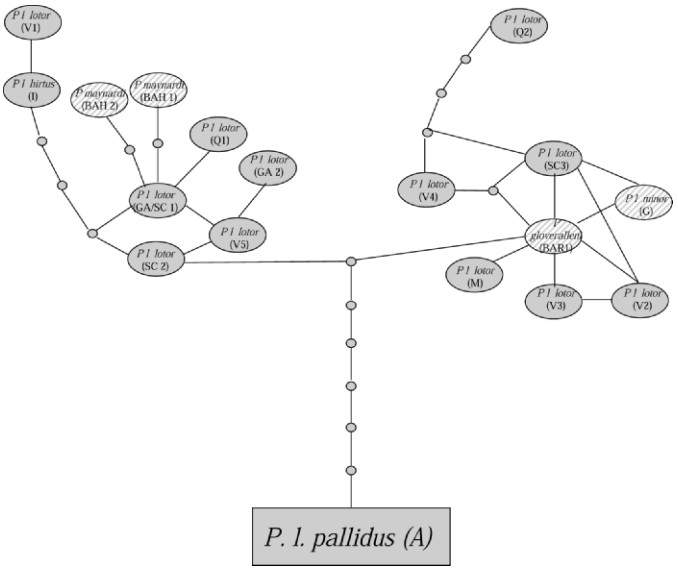

Fig. 4.—Statistical parsimony (TCS) network of control region haplotypes. Each line connecting a circle/oval/square indicates 1 base pair substitution and each substitution is indicated for each step. Small circles denote hypothetical internodes. Note that the haplotype with the highest outgroup probability in TCS is *Procyon lotor pallidus* (*A*) from Arizona, displayed as a square, whereas other haplotypes are displayed as ovals. West Indian haplotypes are denoted by slanted lines; all others are shown in solid shading. Localities and haplotypes are specified in brackets (BAH, Bahamas; BAR, Barbados; SC, South Carolina; GA, Georgia: Q, Quebec; V, Virginia; I, Illinois; M, Maryland; A, Arizona; G, Guadeloupe).

Providence, Grand Bahama, and Abaco) and on at least 5 islands in the French Antilles (Guadeloupe, Marie-Galante, La Désirade, Martinique, and Saint-Martín). The spread of raccoons to many of these islands has occurred in recent decades or years.

Morphology.—In an earlier study, we explored qualitative morphological affinities between West Indian and other populations of raccoons on the basis of museum specimens, leading to the suggestion that West Indian populations are morphologically indistinguishable from *P. lotor* and in particular resemble specimens of *P. lotor* from the southeastern United States (Helgen and Wilson 2003).

We also noted that, despite previous assertions that West Indian raccoons represent size-dwarfed populations (Allen 1911; Bangs 1898; Goldman 1950; Miller 1911; Zeveloff 2003), the few specimens available suggest that there is probably no true size difference between raccoon populations from the West Indies and the eastern United States (Helgen and Wilson 2002). Here we bring a few more measurements of body mass to bear on this point. A body mass of 4.1 kg has been reported for a raccoon from Barbados (Helgen and Wilson 2002; Schomburgk 1848), and a mass of 3.9 kg for an adult from New Providence (Helgen and Wilson 2002). More recently, Morin (2003) noted that raccoons from Guadeloupe may reach weights up to 15 kg (although we suspect that this could well be based on captive raccoons at the Parc Zoologique et Botanique). The range of body masses established for West Indian raccoons (3.9–15 kg) corresponds to that established for *P. lotor* from across its North American range (Goldman 1950; Nowak 1999). We suspect that the idea of smaller insular raccoons derived from the original descriptions of all 3 purported Caribbean species, all of which were based on immature specimens.

Genetics.—Pons et al. (1999) previously demonstrated that control region sequences from 3 Guadeloupe raccoons nested among haplotypes of *P. lotor* from eastern North America. We build on their study by reporting the 1st genetic analyses involving the other major populations of West Indian raccoons—those from Barbados (based on a museum specimen) and the Bahamas (based on fresh tissues). As noted above, we successfully obtained mitochondrial DNA from the turbinal bones of only 1 specimen of a raccoon from Barbados (USNM 267380); other specimens that we had access to (USNM 267381 and a mount at the Barbados Museum) failed to amplify.

Our genetic sampling of North American *P. lotor* included samples collected in the southeastern United States (Georgia and South Carolina), east-central United States (Virginia and Maryland), midwestern United States (Illinois), western United States (Arizona), and Canada (Quebec). The most divergent haplotype was from Arizona (*P. lotor pallidus*), whereas the remainder of central and eastern North American haplotypes clustered into 2 divergent groups, with samples from Virginia, South Carolina, and Quebec sorting within both haplotype clusters (Fig. 4). This indicates that genetic variation in *P. lotor* is broadly correlated with geography, but it also suggests that there is extensive gene flow between regional populations—results generally concordant with earlier genetic analyses drawing from other analytical techniques (Beck and Kennedy 1980; Dew and Kennedy 1980; Hamilton and Kennedy 1987; Kennedy and Lindsay 1984; White et al. 1998). It is not unexpected that raccoons should exhibit little regional genetic structure, especially in eastern North America, given that the species is geographically widespread, maintains high local population densities in some areas, is capable of long-distance individual dispersal events, and has been widely translocated by humans within the eastern United States (Beck and Kennedy 1980; Dew and Kennedy 1980; Frantz et al. 2005; Gehrt and Fritzell 1998; Hamilton and Kennedy 1987; Kennedy and Lindsay 1984; Mosillo et al. 1999; Nielsen and Nielsen 2007; Randa and Yunger 2006; Sherfy and Chapman 1980; Smith et al. 2005; Wright 1977).

Two different haplotypes sampled from the Bahamas (from New Providence and Abaco, respectively—the latter from animals introduced from Florida to Grand Bahama about 70 years ago, and only recently established on Abaco) cluster with samples from the southeastern United States (Georgia, South Carolina, and Virginia) and Quebec, and more distantly with other haplotypes from Virginia and Illinois. Different haplotypes from raccoons from Barbados and Guadeloupe cluster with another group of haplotypes that includes samples from the east-central United States (Maryland, Virginia, and South Carolina), and more distantly, from eastern Canada (Quebec).

Historical accounts document at least 3 independent introductions of *P. lotor* to Caribbean islands. The earliest was from an unrecorded source population to Barbados in the mid-17th

century (see Helgen and Wilson 2002). The 2nd was the establishment of raccoons on New Providence Island, probably in the early 18th century, via ''one or more tame pairs of these droll beasts, brought by the curious from the mainland'' (Schöpf, in Morrison 1911). The 3rd was a pair of raccoons from mainland Florida introduced to Grand Bahama Island in 1932–1933. The source population of the population of raccoons in the French Antilles is unknown. Goldman (1950) highlighted morphological resemblances between the raccoons from the Bahamas and Guadeloupe, allowing for the possibility that the latter insular population was derived secondarily from the former.

The presence of 4 different haplotypes of *P. lotor* in the West Indies, each from a different island, is compatible with the historical record's documentation of at least 3 independent introductions of raccoons in these archipelagos. Because we suggest that each of these translocation events was more likely to be the result of the establishment of very few animals (e.g., as described by Sherman [1954]) and occurred in the past few hundred years, we imagine that the 4 haplotypes that have been detected to date likely represent 4 independent initial translocation events from mainland North America. Whatever the actual number of events, the distribution of particularly divergent haplotypes on New Providence and on Guadeloupe render it extremely improbable that the French Antillean population was derived from a secondary translocation from the Bahamas.

Discussion

West Indian raccoons are unknown in the subfossil record of the Bahamas or the Lesser Antilles (Allen 1911; Drewett 1991, 2000; Matthew 1919; Morgan 1989; Morgan and Woods 1986; Olson 1978, 1983; Olson and Pregill 1982; Steadman et al. 1984), are not morphologically distinctive relative to North American *P. lotor* (Helgen and Wilson 2002, 2003), are known to have been introduced on their respective islands of occurrence (Helgen and Wilson 2002; Schöpf, in Morrison 1911; Sherman 1954), and are shown by molecular analyses to be nested genetically within continental populations of *P. lotor* (Pons et al. 1999; present study). There is no avenue open for recognizing these nominal taxa as distinct species endemic to their respective islands, as some have continued to do (Laurent 2006; Morin 2003; Zeveloff 2003). Instead, the remaining tasks are to assess from where these populations of raccoons were originally introduced, what impacts they have on West Indian ecosystems, and how they should best be managed.

Considerably more extensive genetic sampling will be needed to effectively unravel the phylogeographic patterns of variation in *P. lotor* across its extensive range (cf. Helgen and Wilson 2005), but results from the molecular dataset presented here are concordant with our earlier morphology-based assessment (Helgen and Wilson 2003) in suggesting that West Indian raccoons were most likely introduced from source populations in the eastern United States. On purely geographic grounds, this would seem to be the most straightforward explanation as well. Although previous interpretations of the native status of Caribbean raccoons were perhaps based on the perception that these animals were unlikely to have been introduced multiple times throughout the Caribbean (Bangs 1898; Miller 1911), the historical record demonstrates that raccoons were introduced to the West Indies on at least 3 independent occasions from mainland North America. The presence of at least 4 different haplotypes of *P. lotor* in the West Indies suggests to us that the actual number of independent introductions was probably even greater.

Examination of our molecular data reconfirms a point that we have previously made on the basis of historical and anatomical research. Although most recent authors have regarded *P. maynardi*, *P. minor*, and *P. gloveralleni* as endemic insular species in need of conservation attention, these insular populations instead represent introduced *P. lotor* (Helgen and Wilson 2002, 2003). These nonnative populations do not deserve taxonomic recognition or conservation attention, and should be regarded in the same way as introduced populations of raccoons in other regions where they are established as invasive species, including in Alaska, Japan, and Europe (e.g., Abe et al. 2005; Frantz et al. 2005; Long 2003; Okabe and Agetsuma 2007; Schrader and Hennon 2005). Populations of raccoons in the Bahamas and the French Antilles can truly be regarded as ''invasive'' species in that they are nonnative, are spreading to new islands, and have been identified as threats to native wildlife. In the Caribbean, raccoons have been identified as a potential or actual threat to iguanas (Hayes et al. 2004; Laurent 2006), sea turtles (e.g., Barton and Roth 2007; Engeman et al. 2005; Garmestani and Percival 2005; Ratnaswamy and Warren 1998), and ground-nesting birds, particularly the Bahama parrot (*Amazona leucocephala bahamensis*), a Bahamian endemic found only on the islands of Abaco and Inagua (Hayes 2006; although the species nests on the ground only on Abaco—S. Buckner, in litt.). Raccoons also are considered agricultural pests on some islands (Goldman 1950; Helgen and Wilson 2002, 2003; Lorvelec et al. 2001; Schöpf, in Morrison 1911). The Bahamas now recognizes the raccoon as an invasive species, rather than a conservation priority, and steps are being taken to manage populations or attempt its eradication on Bahamian islands (Bahamas Environment Science and Technology Commission 2003). The same cannot be said in Guadeloupe, where the raccoon remains a popular animal and the symbol of the Parc National de la Guadeloupe (see Fig. 2)—that is, still held up as a ''flagship'' species and the largest ''native'' terrestrial mammal (Morin 2003). This popularity may explain its continuing spread to other French possessions in the Caribbean, increasing its invasive potential in an archipelago without native mammalian carnivores.

Introduction of invasive organisms into an ecosystem or removal of engrained species from an ecosystem can fundamentally and unpredictably transform the ecological dynamics of the system, complicating removal or control of problematic elements (Courchamp et al. 2003; Helgen 2004; Rodriguez 2006; Roemer et al. 2002; Urban et al. 2007). A particularly relevant example comes from coastal Florida, where raccoons prey on sea turtle eggs (Engeman et al. 2005; Garmestani and Percival 2005). In some areas, removal of raccoons from beach areas, an undertaking aimed at reducing predation on sea turtle

nests, actually had the opposite effect (Barton 2005; Pennisi 2006). On these same beaches, raccoons eat ghost crabs, which also prey on sea turtle nests. When released from raccoon predation, ghost crabs may take a greater overall toll on sea turtle eggs than when raccoons were present (Barton 2005; Pennisi 2006). Barring the potential for similar dynamics in West Indian ecosystems, which invite detailed study, we encourage the active control, if not eradication, of all extant West Indian populations of *P. lotor*. Certainly there is no need to elevate them as worthy targets of conservation attention.

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