

Fossil vertebrates from Antigua, Lesser Antilles: Evidence for late Holocene human-caused extinctions in the West Indies

(anthropology/island biogeography/vertebrate paleontology)

DAVID W. STEADMAN*, GREGORY K. PREGILL†, AND STORRS L. OLSON*

*National Museum of Natural History, Smithsonian Institution, Washington, DC 20560; and †Natural History Museum, P.O. Box 1390, San Diego, CA 92112

Communicated by Jared M. Diamond, March 30, 1984

ABSTRACT Vertebrate remains recovered from a limestone fissure filling on Antigua, Lesser Antilles, are associated with radiocarbon dates ranging from 4300 to 2500 yr B.P., contemporaneous with the earliest aboriginal human occupation of the island. Nine taxa of lizards, snakes, birds, bats, and rodents (one-third of the total number of species represented as fossils) are either completely extinct or have never been recorded historically from Antigua. These extinctions came long after any major climatic changes of the Pleistocene and are best attributed to human-caused environmental degradation in the past 3500 yr. Such unnatural influences have probably altered patterns of distribution and species diversity throughout the West Indies, thus rendering unreliable the data traditionally used in ecological and biogeographic studies that consider only the historically known fauna.

Episodes of vertebrate extinction are well documented for continental areas in the Quaternary Period, although the relative role of man versus climate in these extinctions is still the subject of considerable debate (1). In North America, the arrival of humans coincided with terminal Pleistocene climatic changes, and extinctions are concentrated near the Pleistocene/Holocene boundary (2), making it difficult to separate the effects of the two processes. In the West Indies, the extinction or reduction in range of many vertebrates has been thought to be associated with climatic changes at the end of the Pleistocene (3), although a number of extinct taxa found in archeological sites are known to have persisted longer (4, 5). Man did not arrive in the West Indies until well after the end of the Pleistocene—about 4500 yr B.P. to perhaps 7000 yr B.P. in the case of the Greater Antilles (6), and 3700 yr B.P. in the Lesser Antilles (7). It should, therefore, be possible to sort out the effects of man versus climate in the West Indies, just as in the case of other islands where the fossil record has clearly demonstrated a direct correlation between the extinction of vertebrates and human colonization—e.g., Madagascar (8), New Zealand (9), Hawaii (10), and Galapagos (unpublished data).

We now present paleontological evidence that documents the loss within the past 3500 yr of 14 species of small vertebrates from the island of Antigua, Lesser Antilles (Fig. 1), presumably as a result of habitat destruction and predation by man and introduced mammals. Some of these species are totally extinct, whereas others still survive elsewhere in the Antilles. These findings raise serious doubts about the validity of biogeographical studies in the West Indies that rely solely on modern, but unnatural, patterns of distribution.

In 1980 and 1983 we excavated fossiliferous sediment from a limestone fissure filling at a site known as Burma Quarry in northern Antigua (Fig. 2). This fissure consisted of a narrow vertical crevice bisected by a wide horizontal chamber. The

fissure was in an active working face of the quarry and was presumably but a remnant of a larger cave or crevice that had been quarried away. Five stratigraphically concordant radiocarbon ages range from 2560 ± 70 yr B.P. in the upper vertical unit to 4300 ± 150 yr B.P. in the lower vertical unit (Table 1). Contemporaneity of man with the extinct fauna is demonstrated by the presence of shell remains of molluscan food items and several lithic artifacts, including a blade from the horizontal portion of the fissure associated with a radiocarbon age of 3695 ± 100 yr B.P. The first Amerindians on Antigua (the "Archaic" culture) are believed to have arrived during the time interval represented at the Burma Quarry site. Of the 24 Archaic sites known on Antigua, the only reliable radiocarbon age, aside from those for Burma Quarry, is 3725 ± 90 yr B.P. for the Jolly Beach site on the west-central coast (7).

The Burma Quarry sediments contained nine species of vertebrates that were unrecorded in the historic period on Antigua and three others that became extinct in the historic period (Table 2). The nine prehistorically extinct species make up 33% of the total number of species in the fossil fauna, which itself, of course, is only a subset of the late Holocene fauna of Antigua; other extinct taxa would be expected with a more complete fossil sample. Species recovered as fossils from Burma Quarry that are still extant on Antigua include the frog *Eleutherodactylus johnstonei*; the lizards *Thecadactylus rapicauda* and *Anolis bimaculatus leachi*; the snake *Typhlops monastus*; the birds *Calidris* spp., *Zenaidura aurita*, *Columbina passerina*, *Orthorhynchus cristatus*, cf. *Tyrannus dominicensis*, *Margarops fuscatus*, and *Loxigilla noctis*; and the bats *Brachyphylla cavernarum*, *Natalus stramineus*, *Tadarida brasiliensis*, and *Molossus molossus*.

Whereas artifacts and marine mollusks used as food probably were washed into the fissure from the surrounding ground surface, the majority of vertebrates from Burma Quarry are quite small species that appear to have been concentrated as prey remains of an owl, possibly an undescribed form of barn owl (*Tyto*). Bones of two species of *Tyto* have been found on Barbuda (unpublished observation), an island on the same bank as Antigua (Fig. 1), although no such owls are known historically from Antigua or elsewhere in the northern Lesser Antilles, nor were remains of large owls found in Burma Quarry.

Among the extinct taxa from Burma Quarry, the bat *Phyllostictis major* was previously known only from Quaternary deposits in Puerto Rico (11) and the lizard *Leiocephalus cuneus* only from the late Quaternary (Pleistocene?) of Barbuda (13). The Burma Quarry deposits show that these species, heretofore often assumed to have died out in the Pleistocene, still existed up to ≈3500 yr ago. No boid snakes occur anywhere in the Leeward Islands today; the indeterminate boid from Burma Quarry may be allied to Greater Antillean forms. The trembler (*Cinlocerthia ruficauda*) is a medium-sized passerine bird restricted to Lesser Antillean islands to the northwest and south of Antigua. Its absence

The publication costs of this article were defrayed in part by page charge payment. This article must therefore be hereby marked "advertisement" in accordance with 18 U.S.C. §1734 solely to indicate this fact.

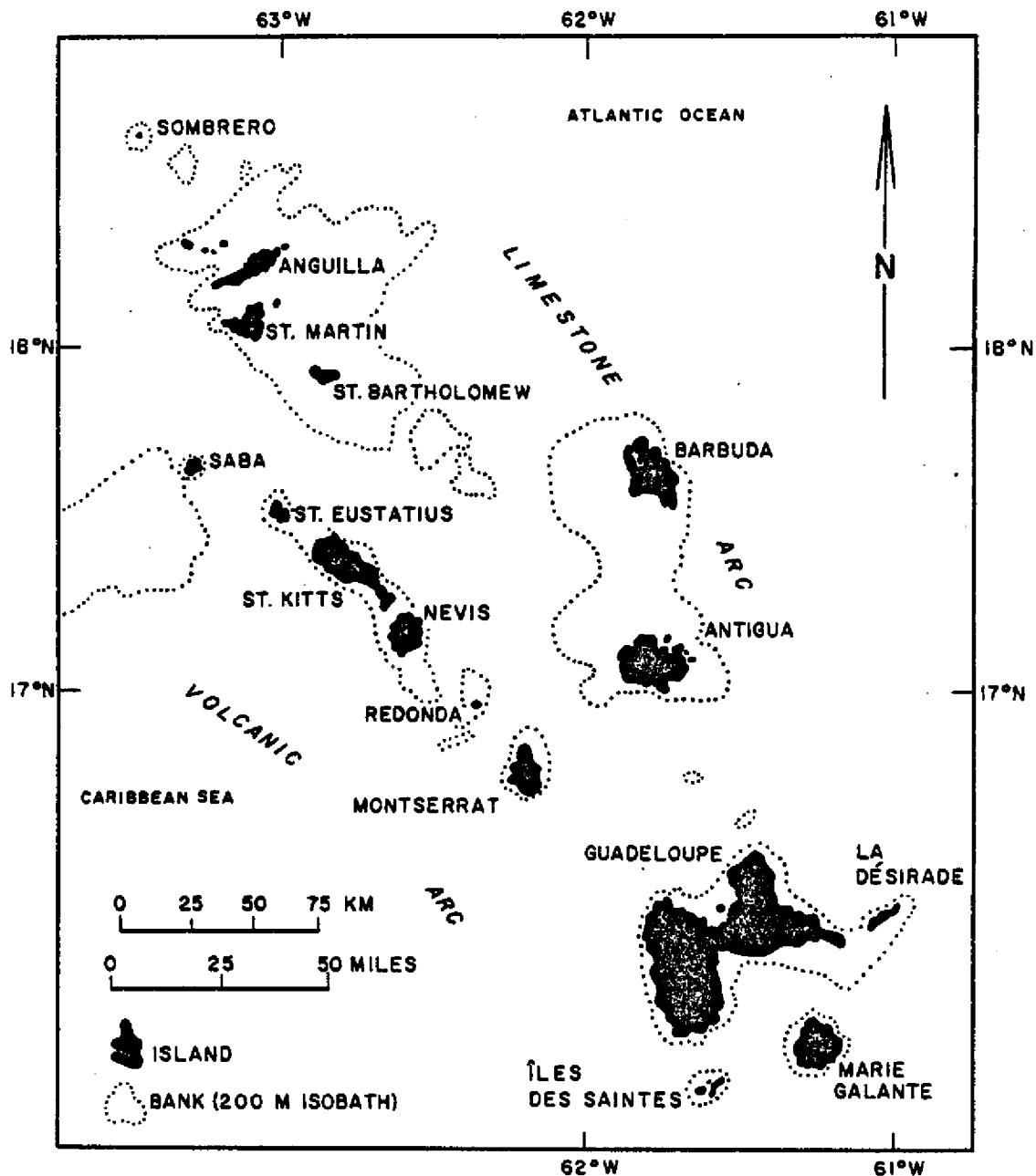


FIG. 1. The northern Lesser Antilles.

from Antigua and Barbuda would be inexplicable without a fossil record showing that tremblers were indeed present, at least on Antigua, in the recent past.

The Burma Quarry fossils provide the first Lesser Antillean records for the bats *Pteronotus parnellii* and *Mormoops blainvillei*, and the yellow-breasted crake *Porzana flaviventer*, all known in the West Indies today only from the Greater Antilles. Thus, the paleontological record shows that the faunal distinctions between the Greater and Lesser Antilles, while undeniable, are perhaps less marked than would be apparent from modern distributions alone.

Porzana flaviventer requires bodies of fresh water with lush emergent vegetation. Although no such habitats exist on Antigua today, their disappearance within the past 3500 yr may be due to siltation from agricultural erosion. Because the three species of bats lost from Antigua all would have roosted in caves (14), their extinction could be related to a decrease in available food through forest destruction, but not

to the loss of roosting sites. *Pteronotus parnellii* and *Mormoops blainvillei* are insectivorous, whereas *Phyllonycteris poeyi*, the living counterpart of *Phyllonycteris major*, feeds mainly on nectar and plant material (14). The extinct species of cricetid rodent (*Oryzomyini* sp.) is very common at Burma Quarry, as well as in later archeological sites. Although such rice rats frequently appear to have been used as food by Amerindians in the northern Lesser Antilles (15), the extinction of these rodents may not have occurred until the introduction of Old World rats (*Rattus*) in historic times. Native rodents in Galapagos (16) and Fernando de Noronha (17) also seem to have been unable to coexist with Old World rats.

Additional extinct vertebrates have been recorded from archeological sites on Antigua that postdate the Archaic culture. Indian Creek and Mill Reef are two large ceramic cultural sites (Fig. 2), the former ranging in age from 1915 ± 80 yr B.P. to 845 ± 80 yr B.P. (6), and the latter from approxi-

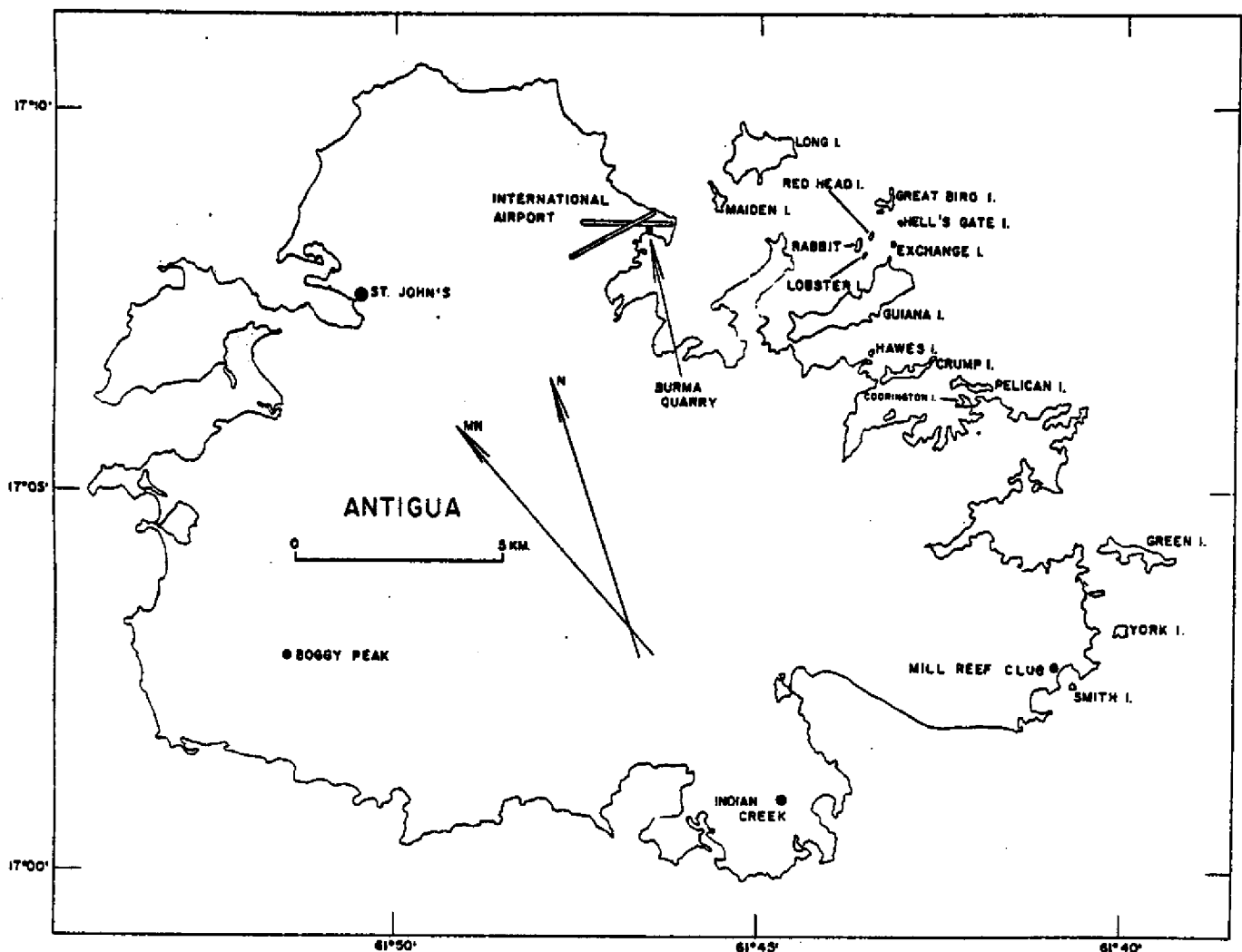


FIG. 2. Antigua and its satellite islands.

mately 1450 to 800 yr B.P. (12). Bones from these two sites add several other taxa to the fauna of Antigua (Table 2). Certain of these species, however, such as the agouti (*Dasyprocta aguti*), were introduced to Antigua from South America by Amerindians, and others, such as the boa (*Boa constrictor*) and parrot (*Amazona* sp.), may also have been brought by man from other islands in the Antilles. Bones of manatee (*Trichechus manatus*) and flamingo (*Phoenicop-*

Table 1. Radiocarbon ages from Burma Quarry, Antigua

Laboratory no.	Age, yr B.P.	Strata dated	Material dated
SI-4621	2560 ± 70	Upper vertical unit (0–1 m, 1–1.7 m, 2–2.8 m)	Charcoal
SI-4618	3515 ± 60	Horizontal unit, east side (0–1 m)	Charcoal
SI-4619	3330 ± 50	Horizontal unit, east side (1–2 m, 3–3.8 m)	Charcoal
SI-4624	3695 ± 100	Horizontal unit, west side (0–1 m, 1–2 m)	Charcoal (small sample; diluted)
A-3282	4300 ± 150	Lower vertical unit (0–1 m)	Charcoal

SI, Smithsonian Institution Radiation Biology Laboratory; A, University of Arizona Laboratory of Isotope Geochronology.

terus ruber) do not necessarily indicate resident populations, although neither has been recorded from Antigua, even as a vagrant, in historic times. The only extinctions of indigenous populations documented by the ceramic archeological sites are those of the rice rat and the gallinule *Porphyryla martinica*, the latter's habitat requirements being similar to those of *Porzana flaviventer*.

Chronology alone makes a strong case for suspecting man's involvement in prehistoric extinctions on Antigua. This is strengthened by the occurrence of extinct vertebrates in archeological sites, often represented by bones that are charred or broken in a manner indicative of human consumption. These Late Quaternary extinctions are not confined to large edible vertebrates, however, but include small species of lizards, snakes, birds, and bats, showing that habitat perturbations and introduced predators also greatly affected the composition of the fauna.

Although the forests of Antigua were described as being very lush when English colonists settled in the early 1600s (18), native trees were soon felled for timber, and nearly the entire island was cleared for agriculture that stressed exotic plants such as sugar cane and cotton. No lowland area on the island is in native vegetation today, and only certain hillsides have second-growth forest, usually heavily mixed with exotic fruit trees. European colonists also introduced rats, cats, dogs, goats, and other mammals, all of which combined to alter the natural flora and fauna. Around 1900, the mongoose was brought in to control introduced rats (19). This experi-

Table 2. Extinct vertebrates from Antigua

Taxa extinct on Antigua	Burma Quarry	Indian Creek	Mill Reef	Historic record or specimen
Reptiles				
<i>Leiocephalus cuneus</i> (curly-tailed lizard)*	X			
<i>Ameiva griswoldi</i> (ground lizard)	X		X	X
<i>Alsophis antillensis</i> (ground snake)	X		X	X
cf. <i>Boa constrictor</i> (boa constrictor)		X		
cf. Boidae, genus uncertain (unknown boid snake)*	X			
Birds				
<i>Puffinus lherminieri</i> (Audubon's shearwater)	X	X	X	
<i>Porzana flaviventer</i> (yellow-breasted crane)	X			
<i>Porphyryla martinica</i> (purple gallinule)		X	X	
<i>Phoenicopterus ruber</i> (greater flamingo)			X	
<i>Amazona</i> sp. (?)* (parrot)		X	X	
<i>Athene cucularia</i> (burrowing owl)	X			X
<i>Cinclocerthia ruficuuda</i> (trembler)	X			
Mammals				
<i>Pteronotus parnellii</i> (bat)	X			
<i>Mormoops blainvillei</i> (bat)	X			
<i>Phyllonycteris major</i> (bat)*	X			
<i>Oryzomyini</i> sp. (rice rat)*	X	X	X	
<i>Trichechus manatus</i> (manatee)			X [†]	

Identifications from Burma Quarry and Indian Creek are our own. Those from Mill Reef are from ref. 12.

*Totally extinct taxon.

[†]Taxon identified from Hawkes Bill Bay site, not Mill Reef (see ref. 12).

ment failed, and instead the mongooses depleted native populations of animals. Human predation alone could account for the loss of shearwaters, flamingos, and manatees, with the two birds being especially vulnerable on their nesting grounds.

As a result of the above disturbances, certain organisms are known to have become extinct on Antigua during the historic period. An endemic subspecies of butterfly, *Papilio polydamas antiquus*, is known only from a painting made in 1770 (20); the burrowing owl *Athene cucularia* disappeared in the late 1800s (21); and the lizard *Ameiva griswoldi* and snake *Alsophis antillensis* have been effectively eliminated from Antigua in this century by mongooses, and now persist only on outlying islets. Many of the extinct vertebrates known from Antigua only from prehistoric sites may actually have died out in early historic times before being recorded by naturalists. The loss of the curly-tailed lizard, parrot, trembler, and perhaps the bats may be related to the destruction of forest and its replacement by alien plants.

It is increasingly evident that most modern insular biotas are merely remnants of what would have been present under pre-human conditions. If Antigua is at all representative, then the endemic or localized distributions that characterize many insular species may actually be more a consequence of

recent habitat degradation than such factors as niche partitioning and competition, which are now popularly assumed to regulate the kind and number of species on islands under natural conditions (22). Even the distinction between major faunal realms such as the Greater and Lesser Antilles may have been artificially enhanced by recent man-caused extinctions. It no longer seems realistic to attempt to interpret insular faunas in terms of such elusive theoretical constructs as species packing, trophic guilds, and faunal saturation (23, 24) when these faunas are actually only arbitrary remnants of natural assemblages that have been variously altered by man. Without a comprehensive assessment of the effects of human disturbance, studies of the distribution and diversity of insular organisms will have limited bearing on understanding natural processes.

We thank R. I. Crombie, J. P. Dean, H. F. James, D. Nicholson, and J. A. Sammon for assistance in the field. For radiocarbon ages, we thank R. Stuckenrath, A. Long, and T. Linick. We are grateful for identifications of specimens provided by R. H. Eyde (plants), W. W. Fitzhugh (artifacts), F. V. Grady (certain bats), K. F. Koopman (*Phyllonycteris major*), R. B. Manning (crustaceans), and J. Rosewater (mollusks). E. M. Paige drew Figs. 1 and 2, the latter based on D. R. Watters' original. We are also grateful to J. M. Diamond for helpful comments on the manuscript. This research was supported by funds generously donated to the Division of Birds, Smithsonian Institution by Mrs. Alexander Wetmore, by the Smithsonian's Scholarly Studies Program, and by the National Science Foundation (Grant DEB-8207347 to G.K.P.). We appreciate the cooperation of officials of the government of Antigua and of the Antigua-based U.S. Satellite Tracking Station.

- Martin, P. S. & Klein, R. G., eds. (1984) *Quaternary Extinctions* (Univ. of Arizona Press, Tucson, AZ), in press.
- Meltzer, D. J. & Mead, J. I. (1983) *Quat. Res. (N.Y.)* 19, 130-135.
- Pregill, G. K. & Olson, S. L. (1981) *Annu. Rev. Ecol. Syst.* 12, 75-98.
- Olson, S. L. (1978) *Philadelphia Acad. Nat. Sci. Spec. Pub.* 13, 99-117.
- Olson, S. L. & Pregill, G. K. (1978) *Smithson. Contrib. Paleobiol.* 48, 1-7.
- Rouse, I. & Allaire, L. (1978) in *Chronologies in New World Archaeology*, eds. Taylor, R. E. & Meighan, C. W. (Academic, New York).
- Davis, D. D. (1982) *Carib. J. Sci.* 17, 107-122.
- Tattersall, I. (1982) *The Primates of Madagascar* (Columbia Univ. Press, New York).
- Cassells, R. (1984) in *Quaternary Extinctions*, eds. Martin, P. S. & Klein, R. G. (Univ. of Arizona Press, Tucson, AZ), in press.
- Olson, S. L. & James, H. F. (1982) *Smithson. Contrib. Zool.* 365, 1-59.
- Anthony, H. E. (1918) *Mem. Am. Mus. Nat. Hist.* n.s. 2 (2), 333-435.
- Wing, E. S., Hoffman, C. A. & Ray, C. E. (1968) *Carib. J. Sci.* 8, 123-139.
- Etheridge, R. (1964) *Bull. Fla. State Mus. Biol. Sci.* 9, 43-75.
- Silva Taboada, G. (1979) *Los Murcielagos de Cuba* (Editorial Academia, Havana, Cuba).
- Steadman, D. W., Watters, D. R., Reitz, E. J. & Pregill, G. K. (1984) *Ann. Carnegie Mus.* 53, 1-29.
- Steadman, D. W. & Ray, C. E. (1982) *Smithson. Contrib. Paleobiol.* 51, 1-23.
- Olson, S. L. (1981) *Natl. Geog. Soc. Res. Rep.* 13, 481-492.
- Harris, D. R. (1965) *Univ. Calif. Publ. Geog.* 18, 1-164.
- Westermann, J. H. (1953) *Publ. Found. Sci. Res. Surinam & Neth. Antilles* 9, 1-107.
- Rothschild, W. & Jordan, K. (1906) *Novit. Zool.* 13, 411-752.
- Danforth, S. T. (1934) *Auk* 51, 350-364.
- Roughgarden, J. (1983) in *Coevolution*, eds. Futuyma, D. J. & Slatkin, M. (Sinauer, Sunderland, MA).
- Terborgh, J., Faaborg, J. & Brockmann, H. J. (1978) *Auk* 95, 59-72.
- Terborgh, J. & Faaborg, J. (1980) *Am. Nat.* 116, 178-195.