Journal of Mammalogy, 87(1):148–152, 2006

FOSSIL BATS FROM QUATERNARY DEPOSITS ON BERMUDA (CHIROPTERA: VESPERTILIONIDAE)

Frederick V. Grady and Storrs L. Olson*

Department of Paleobiology and Department of Vertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560, USA

Fossil remains of bats have been recovered from caves and fissures in Bermuda dating from middle Pleistocene to late Holocene. Three bones from 2 different localities are identified as eastern pipistrelle (*Pipistrellus subflavus*), which was not recorded from Bermuda until 2004. Remains of an individual eastern red bat (*Lasiurus borealis*), from a 400,000-year-old beach deposit, imply that the migratory pattern in this species, a regular transient in Bermuda today, may have been established by the middle Pleistocene. Fairly common remains of *Lasiurus*, either *L. borealis* or *L. seminolus*, were found in 5 cave deposits. In 1 finely stratified sequence, this bat does not appear until the onset of the last glacial period, suggesting that a resident population may have become established at that time. A strong taphonomic bias, indicated by the preponderance of large wing bones, probably of females, may be the result of hawk predation.

Key words: bat, Bermuda, Chiroptera, fossil, Holocene, *Lasiurus*, paleontology, *Pipistrellus*, Pleistocene, Quaternary

Isolated 1,000 km east-southeast of the North American mainland, the island of Bermuda was never naturally colonized by nonvolant land mammals. Until very recently, only 4 species of vespertilionid bats had been recorded historically on the island (Van Gelder and Wingate 1961), including the silver-haired bat (*Lasionycteris noctivagans*), hoary bat (*Lasiurus cinereus*), eastern red bat (*Lasiurus borealis*), and Seminole bat (*Lasiurus seminolus*). These are all forest bats that roost in trees or leaf litter. Cave-dwelling bats have hitherto been unknown in Bermuda, although the limestone composing most of the island is in places riddled with caverns. Many of these caves, and a few other sites, have yielded an abundant fossil biota. Known fossil vertebrate localities in Bermuda are reviewed in Olson et al. (2005). Here we document the relatively sparse but interesting fossil record of bats in Bermuda.

Materials and Methods

Fossils at some sites were collected by surface picking or were encountered during stratigraphic excavations. At others, particularly the immense talus cone in Admirals Cave (Hearty et al. 2004) and the beach deposits at Calonectris Quarry (Olson and Hearty 2003), bulk samples were wet screened through fine-mesh bags resulting in the recovery of virtually all identifiable vertebrate fossils. Except as specified, all specimen numbers refer to catalogs in the Department of Paleobiology (fossils) and Division of Mammals (modern comparative skeletons), National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM). Letters after fossil numbers indicate whether the element is from the left (s) or right (d) side and are not part of the catalog number.

Comparative material examined: eastern pipistrelle (*Pipistrellus subflavus*) 49352, 564018; little brown myotis (*Myotis lucifugus*) 24664, 574276 (plus 3 unnumbered skeletons in the Paleobiology collection); eastern small-footed myotis (*Myotis leibii*) 552570; *L. noctivagans* 5275, 568097, 574263; *L. borealis* 187716, 240940, 391143, 395118, 448464, 462625, 506216, 512437, 512478, 512489, 512490, 540696, 540697, 540698, 553763, 564028, 567587, 567588, 567590, 568880, 568966, 574275; *L. seminolus* 564632, 564033; southern yellow bat (*Lasiurus ega*) 323612, 508916, 523451; northern yellow bat (*Lasiurus intermedius*) 53026; and *L. cinereus* 187811, 370971, 370972, 370973, 398432. In addition, measurements of humeri were obtained from the following skeletons of *L. seminolus* in the collections of the Florida Museum of Natural History, Gainesville: 2607, 5815, 11710, 11724, 11749, 19033, 19036, 19038–40, 20800, 22778, 24553, 30157, 31117.

Geographic and Stratigraphic Context of the Fossil Deposits

All the fossil deposits in which bats have been found in Bermuda are located in the narrow neck of Walsingham limestone between Castle Harbour and Harrington Sound (Fig. 1). The surface rocks of Bermuda consist almost entirely of calcareous sand that accumulated during interglacial marine highstands. The ages of these rocks have been determined through correlation with dated highstands elsewhere in the world, through radiometric dates on corals and speleothems, and through a refined and thoroughly calibrated chronology based on amino acid (D-alloisoleucine/L-isoleucine) epimerization of whole rock and the shells of terrestrial and marine mollusks (Hearty 2002a; Hearty and Vacher 1994; Hearty et al. 1992).

* *Correspondent: olsons@si.edu*

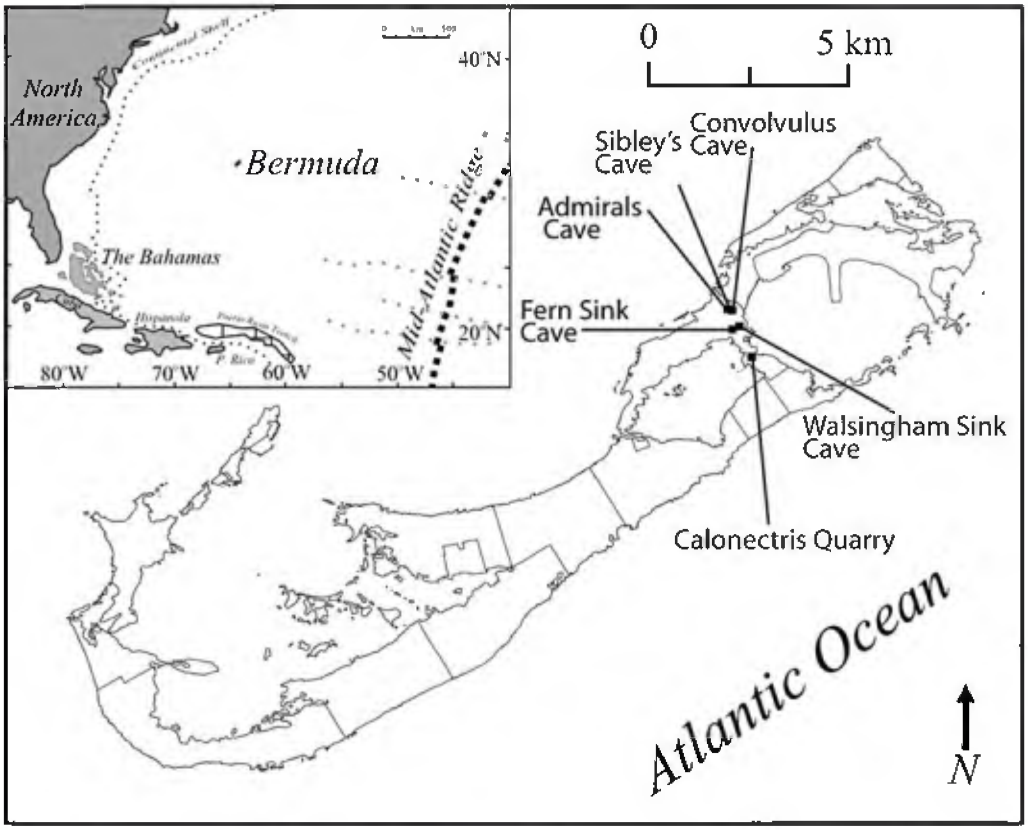

FIG. 1.—Outline map of Bermuda, with parish boundaries, showing localities where fossil bats were obtained. Inset: position of Bermuda relative to eastern North America and the West Indies.

The only bat remains from interglacial carbonates came from a small pocket of beach deposit (Calonectris Quarry) in Government Quarry that formed at 21.3 m above present sea level. Alloisoleucine/isoleucine ratios of marine (*Glycymeris*) and terrestrial (*Poecilozonites*) mollusks from this lens, and those from marine sands in adjacent caves at the same level, are concordant with averages obtained for the Lower Town Hill Formation (Olson and Hearty 2003), which formed during the marine isotope stage (MIS) 11 interglacial interval. Three samples of flowstone directly overlying the beach deposits that formed at more than 20 m above present sea level produced thermal ionization mass spectrometric ages of 420 ± 30, 409 ± 15, and $405 \pm 28 \times 10^3$ years (Olson and Hearty 2003), which is also concordant with MIS 11. Evidence for sea level having exceeded 20 m during MIS 11 has also been found at 2 sites in the Bahamas (Hearty et al. 1999) and on Oahu, Hawaii (Hearty 2002b). At that time, the land area of Bermuda would have been at its all-time minimum, perhaps no more than 20–30% of its present 56 km^2 (Olson and Hearty 2003), and the island was unlikely to have harbored a resident population of bats at that time.

All other bat fossils from Bermuda come from late Pleistocene and Holocene cave and fissure deposits (Olson et al. 2005). The most important accumulation comes from an immense talus cone of sediment that formed under a skylight in a large chamber of Admirals Cave (Hearty et al. 2004). This deposit is marked by highly distinct strata (the units were designated by lowercase letters, with "z" being the top layer and "p" the bottom) containing vertebrate bones, abundant shells of land snails, crab and other invertebrate remains, and charcoal. Calibrated ^{14}C ages on shell and charcoal were obtained for the upper levels and a continuous record of relative ages was obtained from amino acid ratios on shells of the pulmonate land snail *Poecilozonites.* Corroborating thermal ionization mass spectrometric ages from bracketing and intercalated flowstones constrain the entire sequence, which is nearly continuous through the past 120,000 years, from the beginning of the last interglacial (MIS 5e), through the last glacial period (Wisconsinan, MIS 4-2), and past the Pleistocene–Holocene transition about 12,000 years ago (Hearty et al. 2004). The Admirals Cave sequence is the longest continuous, and most accurately dated, terrestrial fossil accumulation ever obtained on an oceanic island.

Deposits in Fern Sink Cave (Grand Canyon Cave of Hearty et al. [2004]) occur in 2 levels separated by a gap in time (Olson et al. 2005). All bat remains are from the superficial deposits, which are late Holocene in age ($1,630 \pm 60$ years ago in conventional radiocarbon years) or younger (Hearty et al. 2004:1160, table 6).

Other deposits from which bat fossils were recovered on Bermuda have not been directly dated. However, with recent refinements of chronostratigraphy of Bermudan cave deposits (Hearty et al. 2004), it is now usually possible to use snails (subgenus *Poecilozonites*) and certain birds to determine to which glacial–interglacial period a given cave deposit may belong. From the exclusive presence of the snail *P. b. bermudensis*, the deposits in Convolvulus Cave are of Holocene age. In Sibley's Cave, deposits appear to derive from the

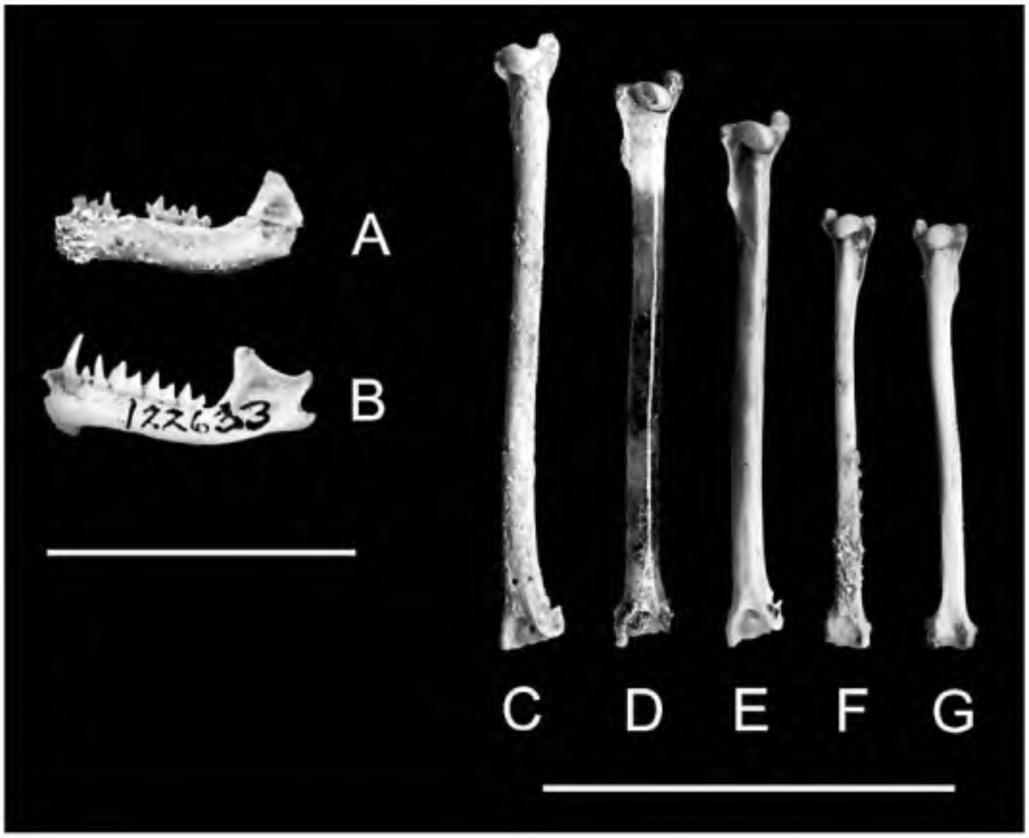

Fig. 2.—Bat fossils from Bermuda (A, C, F) compared with modern specimens. A) *Lasiurus borealis*, fossil mandible (Calonectris Quarry USNM 526355); B) *L. borealis*, modern mandible (USNM 122633); C) *Lasiurus* sp., fossil humerus (Admirals Cave USNM 527804); D) *L. borealis*, female, modern humerus (USNM 553763); E) *L. borealis*, not sexed, probably male, modern humerus (USNM 187716); F) *Pipistrellus subflavus*, fossil humerus (Fern Sink Cave USNM 526359); and G) *P. subflavus*, modern humerus (USNM 49352). Left scale = 1 cm; right = 2 cm.

last glacial period (MIS 4-2) from the presence of *P.* "*nelsoni*," whereas both Holocene and last glacial age deposits occur in Walsingham Sink Cave. We have not seen snails from the fissure in the southeastern face of Government Quarry.

Systematic Paleontology

Eastern Pipistrelle
Pipistrellus subflavus
(Fig. 2)

Fern Sink Cave, surface deposits: humerus 526359-s, radius 526360-s.

Convolvulus Cave, southeastern talus: proximal part of radius 526365-d.

Total minimum number of individuals = 2.

These 3 specimens agree with modern specimens of *P. subflavus* in every detail. The humerus is smaller and less robust than that of *M. lucifugus*, and the deltoid crest is straighter and the styloid process is stouter than in any of the specimens of *Myotis* examined. The nearly complete radius from Fern Sink Cave is more robust than in a modern specimen of *M. leibii* but smaller than in *M. lucifugus*. The somewhat porous nature of the radius indicates that it may have been from a juvenile, whereas the partial specimen from Convolvulus Cave appears to be from an adult, with the remains of the proximal end of the ulna firmly fused to the radius.

Although it is present throughout most of eastern North America (Fujita and Kunz 1984), *P. subflavus* was not recorded from Bermuda until 5 November 2004, when a single individual was discovered under the mudguard of a motorbike (Wingate 2005a, 2005b). It was uncertain whether this specimen may have arrived with human assistance, similar to an individual of big brown bat (*Eptesicus fuscus*) that was taken on Bermuda from the hold of a container ship (Wingate 2005a, 2005b). However, the fossil occurrences prove that the eastern pipistrelle is capable of reaching Bermuda unassisted. The species hibernates in caves in winter and does not appear to be particularly migratory, with the greatest distance recorded between summering ground and a winter hibernaculum being less than 53 km (Fujita and Kunz 1984). Summer roosts are mostly in trees and occasionally in caves.

Eastern Red Bat
Lasiurus borealis
(Fig. 2)

Calonectris Quarry (Government Quarry): upper canines 526354-d, 526356-s; mandible 526355-d; petrosal 526353-d; clavicle 526352-d; proximal end of humerus 526357-s. Minimum number of individuals = 1.

The late Karl Koopman identified the mandible, a canine, and the proximal end of humerus as *Lasiurus borealis*. Although *L. seminolus* cannot be ruled out based on morphology, we have let the identification stand, because this individual was clearly a vagrant and *L. borealis* is decidedly the more migratory of the 2. A petrosal, canine, and clavicle recovered later are probably from one and the same individual, because there is no duplication of elements. The size of the elements indicates a relatively small individual, suggesting it was probably a male (see below). This individual died either at sea or on the beach and was washed by wave action into the site of deposition. The significance of this is discussed below.

Red Bat
Lasiurus sp.
(Fig. 2)

Admirals Cave (stratigraphic units per Hearty et al. [2004]): clavicle 526375-s (unit x); humeri 526368-d (unit u), 526370-s (tailings), 526372-d (unit u/v), 537804-d (unit v), 527810-s (upper unit u/v); proximal parts of humeri 527805-d (unit v), 527812-d (upper unit u/v); distal parts of humeri 526373-d (lower unit u/v), 527806-s (unit v), 527811-s (upper unit u/v); radii 526369-d (unit u), 527807-d (unit v); proximal part of radius 527808-d (unit v); distal parts of radii 526371-s (unit v), 527813-s (upper unit u/v); partial femora 526374-d (lower unit u/v), 527809-d (unit v). Minimum number of individuals = 8 (with each unit considered separately).

Fern Sink Cave (surface deposits): humeri 526358-d, 526362-s. Minimum number of individuals = 1.

Walsingham Sink Cave: proximal part of humerus 526363-s. Minimum number of individuals = 1.

Southeastern face of Government Quarry: proximal part of radius 264986-d. Minimum number of individuals = 1.

Convolvulus cave: humerus 526361-s (northwestern pocket); distal part of humerus 526364-s (southeastern talus); distal part of femur 526366-s (southeastern talus). Minimum number of individuals = 2.

Sibleys Cave: proximal part of radius 526367-s. Minimum number of individuals = 1.

Total minimum number of individuals from all sites = 14.

These specimens belong to a small species of *Lasiurus*, smaller than either *L. cinereus* or *L. intermedius*. In *Lasionycteris*, which also has been recorded in Bermuda, the shafts of the humeri are more slender and the radii are significantly longer than in any of the Bermuda fossils. The largest sample comes from Admirals Cave and includes 5 humeri that are complete except for the styloid process and that can be matched very well by modern specimens of *L. borealis* or *L. seminolus*, as do the humeri from Fern Sink and Convolvulus caves. The fossil humeri are also rather similar to specimens of *L. ega*, but the fossil radii are distinctly shorter and the femora larger than in *L. ega*, a species that has not been recorded from Bermuda.

Lasiurus seminolus has variously been considered either a valid species or a subspecies or color morph of *L. borealis*, although genetic studies have confirmed the distinctiveness of the 2 (see review in Laerm et al. [1999]). Morgan (1985) considered that it was not possible to distinguish between bones of *L. borealis* and *L. seminolus*. The only supposed osteological distinction is in the lacrimal shelf, and even that is not consistent (Laerm et al. 1999). This structure is not preserved in any of the Bermuda fossils in any case.

It is probably significant that in the highly stratified deposits in Admirals Cave, no bat fossils were found in the lower units (q, r, s, t, and most of u), which correspond to the last interglacial period (MIS 5). Bat fossils then become rather numerous at the u/v

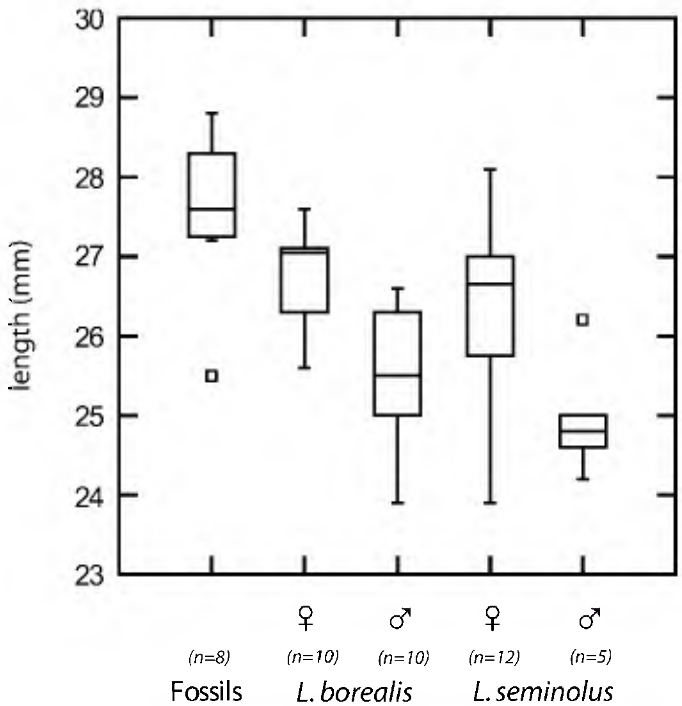

Fig. 3.—Box plots of humerus length (without styloid process), in millimeters on the ordinate, showing large size of most fossils of *Lasiurus* sp. from Bermuda, especially as compared with males of *L. borealis* and *L. seminolus*. Squares represent extreme outliers.

transition marking the onset of the last glacial period (Hearty et al. 2004). The comparative scarcity in unit v is an artifact of that unit's being partially indurated and not amenable to the extraction of small fossils. This rather striking disparity in deposition of red bat fossils in Admirals Cave may reflect the establishment of a resident population during the last glacial period (see "Discussion"), when land area was much greater than at present.

In both *L. borealis* and *L. seminolus*, females are larger than males (Shump and Shump 1982; Wilkins 1987; Figs. 2 and 3). Virtually all of the fossil humeri from the cave deposits are in the large end of the size range, possibly indicating females (Fig. 3). Visual comparison of 18 humeri and radii not included in the measurements classified all but 3 as large, the size of females. This suggests a bias that may have been introduced by a predator that perhaps found heavier females, particularly those gravid or carrying young, easier to capture than males.

Discussion

Van Gelder and Wingate (1961) note that the pristine forested environment of prehuman Bermuda, combined with the abundance of caves, would seemingly have provided ideal habitat for bats, particularly cave-inhabiting species. Our study of the fossil record confirms their conclusion that there never was a population of cave-dwelling bats indigenous to Bermuda. Two fossil and 1 modern record of *P. subflavus* prove that at least 1 species of cave-inhabiting bat is capable of reaching Bermuda, but none ever established a resident population during the latter half of the Pleistocene or its fossil remains should have been abundant.

Apart from the material from Calonectris Quarry, which probably represents the remains of a single beach-washed individual, almost all bat fossils from Bermuda consist of wing bones. No cranial material was encountered except at Calonectris Quarry. We suggest that this biased representation may be the result of predation. We have collected bones of an endemic hawk (Accipitridae) on Bermuda. There was a resident owl as well, but it was too small to prey on bats. Avian predators of bats routinely remove the wings before consuming the bodies. Grady has observed accumulations of bat wings at the entrances of 2 West Virginia caves. Similar behavior in the Bermuda hawk could have resulted in wing elements being washed or otherwise transported into caves. Thus, even the remains of the pipistrelles that were recovered may not have been from individuals roosting in caves. As noted above, there appears to be another taphonomic bias toward females in the fossil sample, as though individuals that were gravid or carrying young may have been easier to catch, and thus implying a resident population.

Lasiurus borealis is a highly migratory species (Shump and Shump 1982), following pathways similar to those of some migratory birds. Notable influxes occur in Bermuda in the autumn that are correlated with waves of birds, after which the bats apparently depart after a recovery period of about 2 weeks, although some attempt to overwinter on the island (Van Gelder and Wingate 1961). The 400,000-year-old specimen from Calonectris Quarry doubtless represents such a migrant individual and suggests that the migratory behavior of this species had been established at least by the middle Pleistocene, an inference that probably could not be derived from any fossil deposit on the mainland.

Whether red bats ever established a resident population on Bermuda is a bit more problematic. During glacial periods, when land area increased dramatically, the great extent of forest habitat may well have been capable of sustaining a resident population of bats. As noted above, in Admirals Cave, remains of red bats 1st appear about the beginning of the last glacial episode. If these cave remains accumulated as the result of predation, the predator was evidently not taking vagrant individuals, given the absence of silver-haired and hoary bats in the fossil record, because these now occur about as commonly as the 2 red bats (D. Wingate, pers. comm.).

Which of the 2 possible species of *Lasiurus* may have been the more likely to have established residency in Bermuda is difficult to evaluate. The more highly migratory *L. borealis* would probably reach Bermuda more frequently, but among birds it is often the more sedentary species that establish resident populations after reaching an island, which would favor *L. seminolus*. In its present range, *L. seminolus* appears to require Spanish moss (*Tillandsia usneoides*) in which to roost (Wilkins 1987). It is not known how the absence of this plant in Bermuda may have affected the ability of that species to establish residence.

Reduced land area during the present interglacial, combined with the windy winter climate, including gales that might remove aerial insects on which bats feed, could prevent overwintering (Van Gelder and Wingate 1961), which may have eliminated any resident population that became established during the last glacial episode.

Acknowledgments

D. B. Wingate has been instrumental in our work on Bermuda, supplied information, and made many useful comments on the manuscript, which was also read by P. J. Hearty. L. Gordon and J. Jacobs, Division of Mammals, National Museum of Natural History, Smithsonian Institution, provided access to modern comparative specimens. We are grateful to the late K. Koopman for identifying material of *L. borealis* from Calonectris Quarry and to D. W. Steadman for supplying measurements of *L. seminolus*. The figures were prepared by B. Schmidt, Division of Birds, Smithsonian Institution, with the assistance of D. Siegel on Fig. 1. We thank L. Green and W. Sterrer of the Bermuda Aquarium, Natural History Museum and Zoo for assistance in many aspects of our research in Bermuda. This is contribution 89, Bermuda Biodiversity Project, of the Bermuda Aquarium, Natural History Museum and Zoo.

Literature Cited

Fujita, M. S., and T. H. Kunz. 1984. *Pipistrellus subflavus*. Mammalian Species 228:1–6.

Hearty, P. J. 2002a. A revision of the late Pleistocene stratigraphy of Bermuda. Sedimentary Geology 153:1–21.

Hearty, P. J. 2002b. The Ka'ena highstand of O'ahu, Hawai'i: further evidence of Antarctic ice collapse during the Middle Pleistocene. Pacific Science 56:65–81.

Hearty, P. J., P. Kindler, H. Cheng, and R. L. Edwards. 1999. Evidence for a +20m middle Pleistocene sea-level highstand (Bermuda and Bahamas) and partial collapse of Antarctic ice. Geology 27:375–378.

Hearty, P. J., S. L. Olson, D. S. Kaufman, R. L. Edwards, and H. Cheng. 2004. Stratigraphy and geochronology of pitfall accumulations in caves and fissures, Bermuda. Quaternary Science Reviews 23:1151–1171.

Hearty, P. J., and H. L. Vacher. 1994. Quaternary stratigraphy of Bermuda: a high-resolution pre-Sangamonian rock record. Quaternary Science Reviews 31:685–697.

Hearty, P. J., H. L. Vacher, and R. M. Mitterer. 1992. Aminostratigraphy and ages of Pleistocene limestones of Bermuda. Geological Society of America Bulletin 104:471–480.

Laerm, J., M. Menzel, D. M. Krishon, and J. L. Boone. 1999. Morphological discrimination between the eastern red bat, *Lasiurus borealis*, and Seminole bat, *Lasiurus seminolus* (Chiroptera, Vespertilionidae), in the southeastern United States. Journal of the Elisha Mitchell Scientific Society 115:131–139.

Morgan, G. S. 1985. Fossil bats (Mammalia: Chiroptera) from the late Pleistocene and Holocene Vero Fauna, Indian River County, Florida. Brimleyana 11:97–117.

Olson, S. L., and P. J. Hearty. 2003. Extirpation of a breeding colony of short-tailed albatross (*Phoebastria albatrus*) on Bermuda by Pleistocene sea-level rise. Proceedings of the National Academy of Sciences 100:12825–12829.

Olson, S. L., D. B. Wingate, P. J. Hearty, and F. V. Grady. 2005. Prodromus of vertebrate paleontology and geochronology of Bermuda. Pp. 219–232 in Insular vertebrate evolution: the palaeontological approach (J. A. Alcover and P. Bover, eds.). Monografies de la Societat d'Història Natural de les Balears 12.

Shump, K. A., Jr., and A. U. Shump. 1982. *Lasiurus borealis*. Mammalian Species 183:1–6.

Van Gelder, R., and D. Wingate. 1961. The taxonomy and status of bats in Bermuda. American Museum Novitates 2029:1–9.

Wilkins, K. T. 1987. *Lasiurus seminolus*. Mammalian Species 280: 1–5.

Wingate, D. B. 2005a. A new bat species for Bermuda. P. 42 in Bermuda Audubon Society. 50th anniversary 1954–2004 (A. Dobson, ed.). Bermuda Press, Hamilton, Bermuda.

Wingate, D. B. 2005b. First record of the eastern pipistrelle bat, *Pipistrellus subflavus*, from Bermuda. Critter Talk [Bermuda Zoological Society] 28(1):6–7.

Submitted 29 May 2005. Accepted 8 June 2005.

Associate Editor was Eric A. Rickart.