Pacific Science, vol. 53, no. 2: 129–143

First Highly Stratified Prehistoric Vertebrate Sequence from the Galápagos Islands, Ecuador[1]

DAVID W. STEADMAN[2] AND VALERIE BURKE DELEON[3]

ABSTRACT: We report an assemblage of ca. 6900 vertebrate fossils from a preliminary excavation at Barn Owl Cave, Isla Floreana, Galápagos Islands, Ecuador. Age of this stratified deposit ranges from historic times (less than 200 yr old) to the early Holocene (at least 8290 $\pm$ 70 radiocarbon years B.P., which equals 7485–7055 B.C.). Five of the 11 indigenous species identified thus far from the bone assemblage no longer occur on Floreana. Their extirpation is due to human influence over the past two centuries. The sedimentary and faunal compositions of the Barn Owl Cave bone deposit may reflect paleoclimatic changes, with relatively wet intervals indicated by darker, more clayey sediments and a relative scarcity of bones of the Floreana lava lizard (*Microlophis grayii*). Further excavation at Barn Owl Cave is likely to yield insights into the timing and extent of late Quaternary climatic and faunal changes in the Galápagos Islands.

MANY INDIGENOUS SPECIES of vertebrates are unable to survive the environmental changes that accompany human activities on oceanic islands. For example, in the Galápagos Islands (Figure 1), the terrestrial reptile, bird, and mammal communities have undergone many changes in species composition since the first arrival of people several centuries ago. These changes consist primarily of the extinction of indigenous species or populations and the establishment of populations of nonnative species (Hoeck 1984, Anonymous 1998). Even though vertebrate populations in the Galápagos are subjected to climatically induced fluctuations in size (Boersma 1998), rich assemblages of vertebrate fossils suggest that extinctions were rare events before humans colonized the Galápagos. In fact, the rate of vertebrate extinction after the arrival of people in the archipelago has been estimated to be at least 100 times greater than before human arrival (Steadman et al. 1991). This is consistent with the long-term vegetation record of the Galápagos, where Colinvaux and Schofield (1976a) found no recurrent pattern of nonanthropogenic extinction and colonization in the archipelago during the Holocene (the past 10,000 yr).

Prehistoric data on plants and vertebrates from tropical islands are valuable for conservation biology because they show the composition and rate of change of communities in the absence of human impact (James 1987, Franklin and Steadman 1991, Pregill et al. 1994, Steadman 1995). The prehistoric remains also link modern species to their evolutionary and biogeographic past, incorporating much longer time scales (10^{2-5} yr) than are possible in studies based solely upon living organisms.

Within many of the younger pāhoehoe basalt flows in the Galápagos are lava tubes that formed during volcanic eruptions (Montoriol-Pous and Escolá 1975). By preserving bones that range in age up to tens of

[1] Manuscript accepted 22 April 1998. Field and laboratory research was sponsored by The Discovery Channel (as part of a documentary film directed by David Clark and Al Giddings), the Smithsonian Institution, the National Science Foundation (grants BSR-8607535, EAR-9714819), and the National Geographic Society.

[2] Florida Museum of Natural History, University of Florida, P.O. Box 117800, Gainesville, Florida 32611 (telephone, 352-392-6571; fax, 352-846-0287; E-mail, steadman@flmnh.ufl.edu).

[3] Department of Anthropology, University of Florida, Gainesville, Florida 32611.

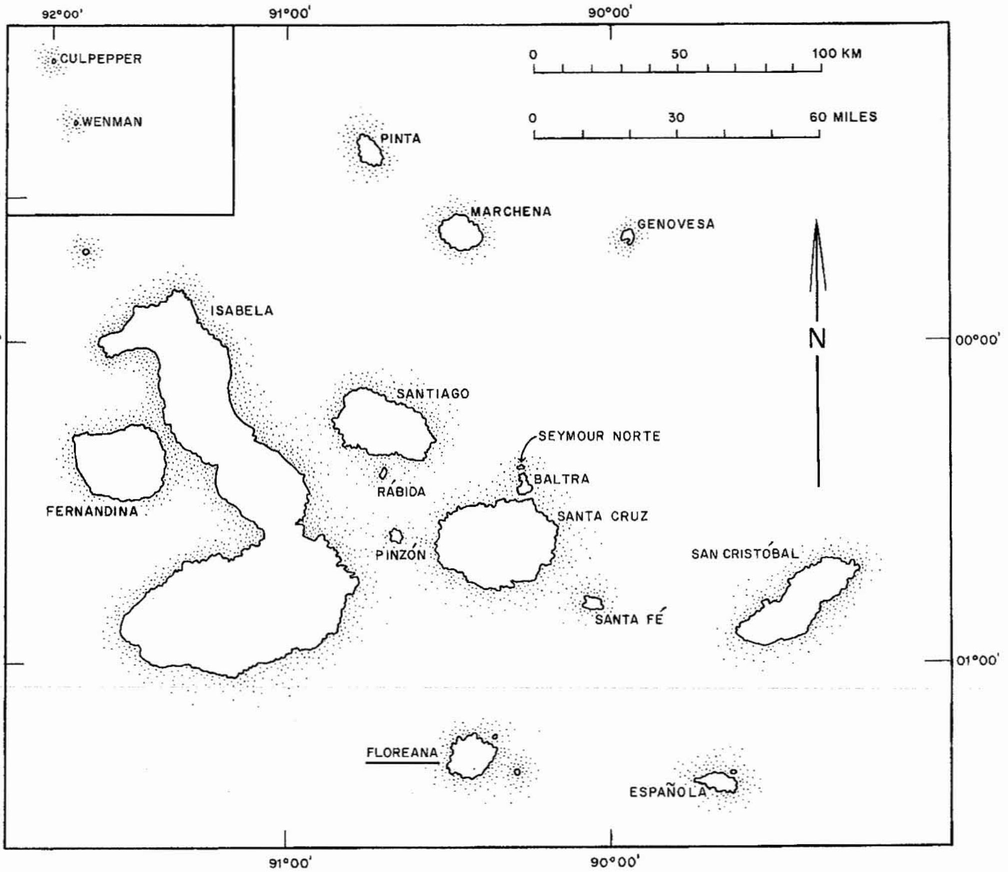

FIGURE 1. The Galápagos Islands. Floreana is underlined.

millennia, these lava tubes offer abundant evidence of prehistoric terrestrial vertebrates (Steadman and Ray 1982, Steadman 1986, Steadman and Zousmer 1988) as well as land snails (Chambers and Steadman 1986).

In this paper we describe a newly obtained prehistoric faunal sample on Isla Floreana, the sixth largest island in the archipelago and one with much potential for studying long-term changes in vertebrate communities (Steadman 1986).

THE FOSSIL FAUNA OF BARN OWL CAVE

Geologic Background

Floreana is a roughly circular, low shield composed of basalts of predominantly reversed magnetic polarity (> ca. 700,000 yr old; known as the "Main Series") as well as normal-polarity basalts (the younger "Flank Series") that are related to numerous parasitic cones and pyroclastic deposits (Bow and Geist 1992, White et al. 1993). The lava flows immediately southeast of Post Office Bay consist of xenolith-bearing alkali-olivine basalts that probably belong to the Flank Series. Within these basalt flows are numerous lava tubes that act as sediment traps for the accumulation of bones. Barn Owl Cave is one such lava tube that lies at 33 m (110 ft) elevation, ca. 300 m inland from Post Office Bay (Figures 2, 3).

K-Ar dates of 0.72 ± 0.40 and 0.6 ± 0.3 million yr (Ma) have been determined on Main Series basalts within 2 km to the east

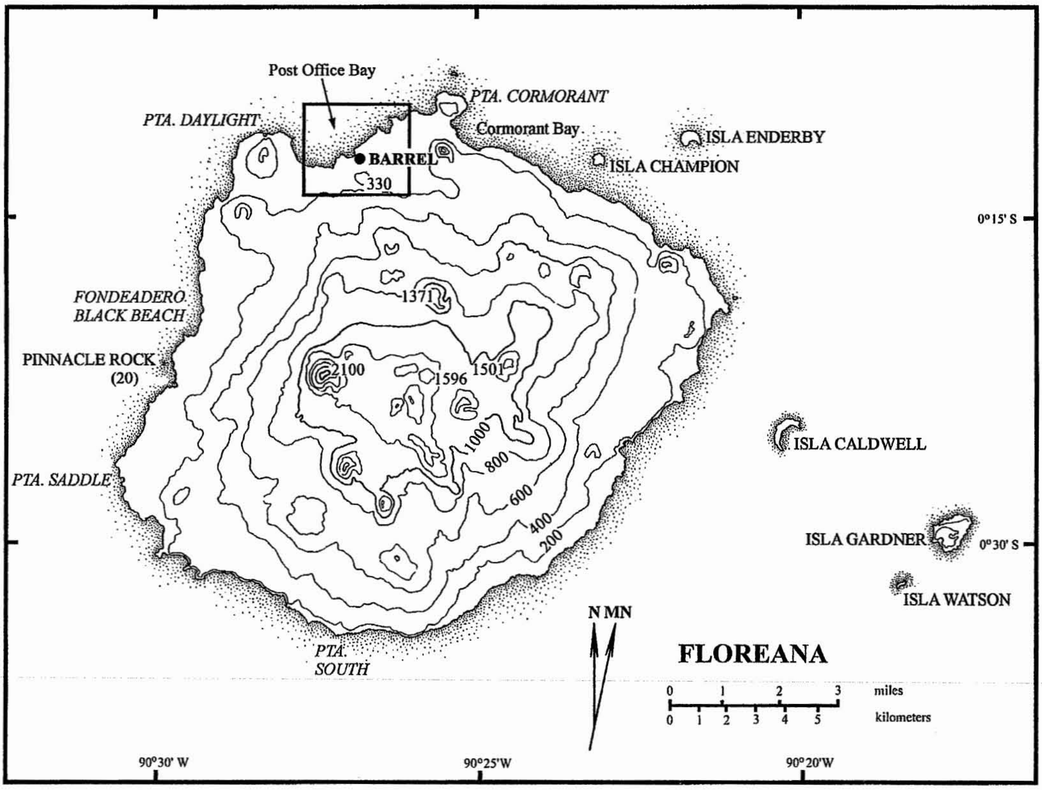

FIGURE 2. Isla Floreana, showing the location of Post Office Bay. Contour intervals in feet. From Steadman (1986).

and west of Post Office Bay (Cox and Dalrymple 1966, Bow and Geist 1992). The precise age of the basalt flow containing Barn Owl Cave is undetermined. Other K-Ar dates from Floreana are 1.52 ± 0.08 Ma from the Main Series and 0.08 ± 0.13 Ma and 0.35 ± 0.11 Ma from the Flank Series (White et al. 1993). The exact locations of these last three samples are unreported.

Field and Museum Methods

Barn Owl Cave was sampled initially (Excavation 1) on 30–31 October 1980 and visited subsequently, without excavation, on 23 May 1983 (Steadman 1986). Excavation 1 (hereafter Ex1) reached the bedrock floor of the cave at a depth of 43 cm. The cave was visited again on 5 November 1995. Over the next three days D.W.S. excavated a 1 by 1 m test pit (Excavation 2 in Figure 4) in arbitrary 7- to 14-cm levels that also followed, when discernible, the natural changes in stratigraphy. Because of an inflexible boat schedule, Excavation 2 (hereafter Ex2) was halted at a depth of 70/73 cm without reaching the bedrock floor of the cave. The deepest extent of the sediment in this section of Barn Owl Cave, therefore, is undetermined. All excavated sediment was sieved by D.W.S. and Sr. Winter Vera through screens of 12.5-, 6.4-, 3.35-, and 1.6-mm mesh and subsampled with 0.80-mm mesh. All bones and land snails were saved. No other organic materials were found. This study is based upon the bones recovered from screens with mesh as fine as 3.35 mm. The abundant but

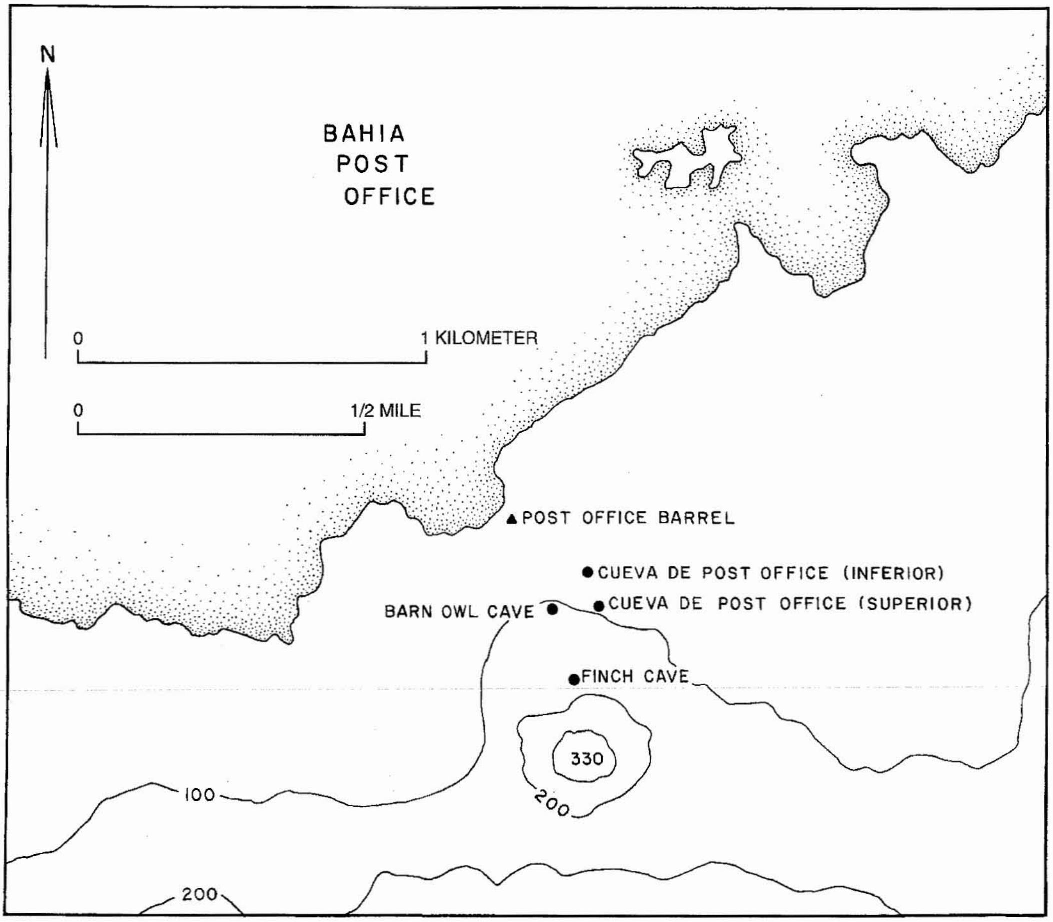

FIGURE 3. The Post Office Bay region of Isla Floreana, showing the location of paleontological sites. Contour intervals in feet. From Steadman (1986).

very small (and often fragmentary) bones from the 1.6- and 0.80-mm mesh screens are still being sorted but have not been identified or counted.

The bones from Ex2 of Barn Owl Cave will be divided among the Florida Museum of Natural History (University of Florida, Gainesville), the Charles Darwin Research Station Museum, and the Galápagos National Park (to forward to appropriate Ecuadorian institutions). This will maximize the long-term utility of the collections for education and research by both Ecuadorian and non-Ecuadorian students and scientists.

Stratigraphy

The stratigraphy of Ex2 is portrayed in Tables 1 and 2 and Figure 5. We interpret Layer I to represent sediment deposition that occurred during the 1982–1983 El Niño. Layer I consists of dark allochthonous soils that washed into the cave and then mixed with sediments that had been deposited in the cave before the mid-nineteenth century. The age assignment of the older, reworked sediment fraction of Layer I is based upon the presence of numerous bones of the tortoise *Geochelone elephantopus;* Floreana Mock-

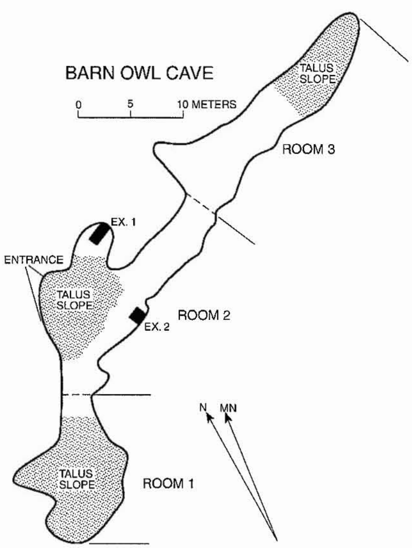

FIGURE 4. Plan view of Barn Owl Cave (Cueva de la Lechuza), showing the location of Excavation 1 (conducted in 1980) and Excavation 2 (conducted in 1995). Modified from Steadman (1986).

ingbird, *Mimus trifasciatus;* and Floreana Large Ground Finch, *Geospiza magnirostris magnirostris*, three species that have been extirpated on Floreana for more than a century (Steadman 1984, 1986). The allochthonous soils are the source of the minor clay fraction in Layer I. On 23 May 1983, G. Davis, G. Merlen, and D.W.S. witnessed deposition of this sediment in Barn Owl Cave during the height of the torrential rains that fell on Floreana from November 1982 through July 1983. The entire surface of Room 2 was covered in wet, sticky sediment that was washing into the entrance and down the talus slope.

The very porous soil and fractured lavas on Floreana (and elsewhere in the Galápagos) promote infiltration of rainwater rather than run-off (Steadman 1986). In a site with a small catchment, such as Barn Owl Cave, sedimentation occurs only during times of extremely high precipitation. The floor of this cave had been dry during 1980 when it was littered with the bones of *Geochelone elephantopus*, *Mimus trifasciatus*, and *Geospiza m. magnirostris.* That the sediment deposited in Barn Owl Cave during the 1982–1983 El Niño buried nearly all of these bones of extinct species that were lying on the surface in 1980 suggests that the 1982–1983 El Niño had provided the first substantial sedimentation in Barn Owl Cave for more than a century. The 1982–1983 El Niño event (described for the Galápagos by E. Cruz [1985], F. Cruz and J. Cruz [1985], Kogelschatz et al. [1985], and Merlin [1985]) has been regarded independently as "probably the strongest warming of the equatorial Pacific Ocean to occur during this century and perhaps for several centuries before that" (Glynn 1990 : vii). (The 1997–1998 El Niño event is another very strong one [Webster and Palmer 1997]. Precisely how it compares

TABLE 1

STRATIGRAPHIC DESCRIPTION OF EXCAVATION 2, BARN OWL CAVE, ISLA FLOREANA, GALÁPAGOS

LAYER[a]	LEVEL[b]	CMBD[c]	SEDIMENT TYPE
I	1	1/3–9/10	Compacted, poorly stratified, pebbly, slightly sandy, clayey silt
I/II	2	9/10–20/22	As I, 1 but more pebbly, less clayey
II	3	20/22–28/32	Loose, stratified, pebbly, slightly sandy silt
II	4	28/32–36/39	Very loose, stratified, slightly pebbly, slightly sandy silt
III	5	36/39–47/50	Very loose to indurated, stratified, slightly bouldery, slightly to very pebbly, sandy silt
III	6	47/50–59/64	As III, 5 but more pebbly, pebbles more angular
III	7	59/64–70/73	As III, 6 but cobbles more angular

[a] Natural sedimentary unit.
[b] Arbitrary vertical interval, averaging 10 cm (range 7–14 cm).
[c] Cm below datum.

TABLE 2

SEDIMENT SAMPLES A–D FROM EXCAVATION 2, BARN OWL CAVE, ISLA FLOREANA

SAMPLE	LAYER	LEVEL	CMBD[a]	VOL. (cm^3)	SEDIMENT TYPE	COLOR (DRY)	COLOR (WET)	CLASTS	NO. BONES/ LAND SNAILS
A	I	1	7–10	190	Pebbly, slightly sandy, clayey silt	Dark reddish brown 5YR 3/3	Reddish brown 5YR 4/4	Basalt with rare olivine, plagioclase, augite, hornblend; angular to subrounded; max. diam. 16 mm	5/0
B	II	3	24–27	150	Very pebbly, slightly sandy silt	Yellowish red 5YR 4/6	Reddish brown 5YR 4/4	As in A but max. diam. 23 mm	4/1
C	III	5	41–44	170	As in B	Light brown 7.5YR 6/4	Dark reddish brown 5YR 3/3	As in A but max. diam. 14 mm and very angular to subangular	6/6
D	III	6	57–60	180	As in B	Pink 7.5YR 7/4	Dark brown 7.5YR 4/4	As in C but max. diam. 23 mm	2/5

NOTE: Sample locations shown in Figure 5. Sample A is from a dark band. Samples B–D are from light bands.
[a] Cm below datum.

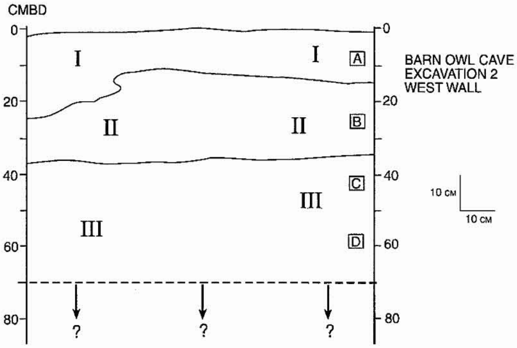

FIGURE 5. Stratigraphic section, Excavation 2, Barn Owl Cave, Isla Floreana.

with the 1982–1983 event is yet to be determined.)

Layer II is a well-stratified Late Holocene unit with six to eight sets of alternating bands of light and dark sediment. About 70% of the total vertical extent of Layer II is dark, but never as dark or clayey as in Layer I. The Middle to Early Holocene Layer III is also well stratified and features 10–12 sets of alternating bands of light and somewhat darker sediment. On average, the sediment in Layer III is lighter in color and has larger, more angular clasts (pebbles, cobbles) than that in Layer II. The lighter bands of sediment have a higher component of autochthonous, angular, secondary minerals precipitated within the cave, namely gypsum ($CaSO_4 \cdot 2H_2O$), fluorite (CaF_2), apatite [$Ca_5(PO_4)_3(F, Cl, OH)$], and calcite ($CaCO_3$). The lightly colored sediments are interpreted to have been deposited during relatively dry times, whereas the darker sediments have a much larger fraction of the allochthonous sediment derived from soils washed into the cave during strong and sustained precipitation, most likely during El Niño events. Some reworking of sediments undoubtedly has occurred during each pulse of deposition of darker sediments. This reworking dampens to some extent the faunal and/or climatic signals contained within each sediment type. All other things being equal, one would expect a lower overall rate of sediment accumulation in Barn Owl Cave during periods of relatively dry climate.

Chronology

Two radiocarbon (^{14}C) dates had been determined previously from wood found on the sediment-covered floor of Barn Owl Cave (Steadman 1986). Both of these dates (640 ± 50 and 2420 ± 25 yr B.P.) are conventional (beta-decay) age measurements (Table 3). Such prehistoric ages for surface materials provide additional evidence that rates of sediment deposition are low in Barn Owl Cave except during times of extremely high precipitation. Both ^{14}C-dated pieces of wood were collected in October 1980, ca. 2.5 yr before the major influx of sediment described above. After the 1982–1983 El Niño, no old pieces of wood remained exposed on the surface of Barn Owl Cave; just as with the bones

TABLE 3

RADIOCARBON DATES FROM BARN OWL CAVE, ISLA FLOREANA, GALÁPAGOS

LAB NO.[a]	MATERIAL	LOCALITY	^{14}C AGE[b]	CALENDAR DATES[c]
A-3280	cf. *Cordia* sp. (wood; ~5 g)	Excavation 1: Surface	640 ± 50	cal AD 1280–1415
A-2512	*Acacia* sp. (wood; ~17 g)	Room 3: Surface	2,420 ± 25	cal BC 745–700 and cal BC 530–400
CAMS-31064	*Geochelone elephantopus* (humerus)	Excavation 2: Layer III: Level 7	8,290 ± 70	cal BC 7485–7055

NOTE: All ages are corrected for $\Delta^{13}C$ as reported.
[a] A, University of Arizona Radiocarbon Laboratory; CAMS, Lawrence Livermore National Laboratory's Center for Accelerator Mass Spectrometry.
[b] Reported in radiocarbon years before "present" (= A.D. 1950).
[c] Cal AD/BC, calibrated calendar dates at 2σ (95% confidence).

of extirpated species, such wood had been buried by the new sediment that was washed into the cave during heavy rains.

As a first step in compiling a chronology for sequential changes in the subsurface species assemblages, a new ^{14}C date was determined on a single bone of *Geochelone elephantopus* from Ex2 with the same accelerator-mass spectrometer (AMS) techniques used previously for ^{14}C dates on bones of the extinct Galápagos giant rat, *Megaoryzomys curioi* (Steadman et al. 1991). The methodology for pretreatment and AMS ^{14}C-dating of the *Geochelone* bone follows Stafford et al. (1987, 1988, 1991). The new age determination of 8290 ± 70 yr B.P. (CAMS-31064; Layer III, Level 7) is the oldest ^{14}C date for vertebrate fossils from Floreana. Elsewhere in the archipelago it is exceeded in ^{14}C age only by the much older dates of $21{,}570 \pm 280$ and $21{,}820 \pm 300$ yr B.P. from Grieta de Gordillo on San Cristóbal (Steadman et al. 1991).

CAMS-31064 suggests an average sediment accumulation rate of 8 cm/1000 yr in this part of Barn Owl Cave. This rate undoubtedly varies through time and with location in the cave. Thus the two ^{14}C dates on surface wood, being from Ex1 and Room 3 rather than from Ex2, are not incompatible with the sedimentation rate (8 cm/1000 yr) calculated for Ex2. The currently unexcavated sediments (below Level 7) in Ex2 are likely to exceed 10,000 yr B.P. in age and therefore sample vertebrates of the Late Pleistocene as well as Holocene.

The Prehistoric Bones

Bones were deposited in Barn Owl Cave as the prey remains of the Galápagos Barn Owl (*Tyto punctatissima*) and as the remains of animals that fell into the natural trap formed by the roof collapse (entrance) in the lava tube. (Bones of *T. punctatissima* were recovered in both Ex1 and Ex2 and are the only evidence that barn owls once inhabited Floreana.) Barn owls accumulate bones of small vertebrates by regurgitating bone-filled pellets that accumulate beneath ledges where the owls roost. Barn owls probably were responsible for depositing nearly all prehistoric bones in the caves on Floreana except those of the tortoise *Geochelone elephantopus*, which make up most or all of the bones attributable to natural trap activity.

Ex2 of Barn Owl Cave was highly fossiliferous, with about two-thirds of the bones representing four species of reptiles (Table 4). Birds make up nearly all of the remaining fauna, with a minor component of mammals. Except for the Galápagos Dove (*Zenaida galapagoensis*) and most other nonpasserines, most of the bones of birds (Aves) from Ex2 have not yet been identified to species because the difficult species-level identification of Darwin's finches (*Geospiza* spp.) by D.W.S. (as part of a much larger, multi-island effort to reconstruct prehistoric finch assemblages) awaits availability of additional comparative skeletons. Nevertheless, the fossil avifauna is dominated by *Zenaida galapagoensis*, the Floreana Mockingbird (*Mimus trifasciatus*), and various Darwin's finches, especially the extinct Large Ground Finch (*G. magnirostris magnirostris*). Less common species in the fossil avifauna from Ex2 include a storm-petrel (Oceanitidae sp.), Galápagos Hawk (*Buteo galapagoensis*), Black Rail (*Laterallus jamaicensis*), *Tyto punctatissima*, Galápagos Vermilion Flycatcher (*Pyrocephalus nanus*), and Large-billed Flycatcher (*Myiarchus magnirostris*).

The relative abundance of bones of the lava lizard *Microlophis grayii* is greatest in Levels 4–6 and peaks in Level 5 (Figure 6). The high values for *Microlophis* bones in Levels 4–6 depress the relative abundances of all other taxa. For example, the relative abundances of bones of the snake *Alsophis biserialis*, dove *Zenaida galapagoensis*, and all other birds (non-*Zenaida* Aves) appear as troughs (rather than peaks) centered on Level 5. Many of the largest changes in relative abundance within taxa do not correspond to the major stratigraphic boundaries (those between Layers) but occur within Layers II and III. This suggests that finer vertical resolution is needed to discern more biologically informative signals in the bone data. This greater resolution, difficult to obtain in an initial test

TABLE 4

FAUNAL SUMMARY, EXCAVATION 2, BARN OWL CAVE, ISLA FLOREANA, GALÁPAGOS

BONES[a]	I:1	I/II:2	II:3	II:4	III:5	III:6	III:7	TOTAL
Geochelone elephantopus (E) tortoise	117	214	139	326	210	338	615	1,959
Phyllodactylus baurii gecko	3	5	5	12	31	38	7	101
Microlophis grayii lava lizard	34	86	78	756	1,276	300	78	2,608
Alsophis biserialis (E) snake	94	158	76	178	34	33	54	627
Zenaida galapagoensis Galápagos Dove	20	45	9	19	21	13	12	139
Aves spp. Non-*Zenaida* birds	131	223	89	332	425	151	113	1,464
Lasiurus borealis red bat	0	0	2	1	2	5	4	14
Mus musculus (I) house mouse	4	1	0	0	0	0	0	5
Total	403	732	398	1,624	1,999	878	883	6,917
Total without *Geochelone* or *Mus*	282	517	259	1,298	1,789	540	268	4,953

NOTE: Layers (natural strata) are indicated by Roman numerals I–III. Levels (arbitrary sediment intervals 7–14 cm thick) are indicated by Arabic numerals 1–7. Because of excessive bone breakage, the data for *Geochelone* reflect only the tortoise bones retained in sieves of 5.6 mm or greater mesh. For all other taxa, these data represent all bones retained in sieves of 3.35 mm or greater mesh.

[a] E, extirpated on Floreana; I, introduced species.

excavation, could be achieved in an expanded excavation in which the individual light and dark bands are mapped in the excavation wall and then carefully removed with improved horizontal and vertical integrity (see *Future Research*).

The apparent decreases in bones of *Zenaida* and non-*Zenaida* birds in Levels 4–6 are not supported by the bone influx data (Table 5), which demonstrate that overall bird bones per liter of excavated sediment actually increased in both Levels 4 and 5. The bone influx data for *Microlophis* and *Alsophis*, on the other hand, roughly parallel the percentage data in Figure 6. Bone influx for *Microlophis* increased substantially in both Levels 4 and 5, whereas for *Alsophis* it dropped dramatically in Level 5 and remained low in Level 6. Most of the increase in total bone influx in Levels 4 and 5 is attributable to increases in the number of bones of *Microlophis* and birds, thus suggesting an increase in barn owl activity within the cave (see "Total without *Geochelone* or *Mus*" in Table 5) relative to the rate of sedimentation.

The relative scarcity of bones of introduced rodents (*Mus musculus* and *Rattus rattus*) suggests that *Tyto punctatissima* was extirpated from Floreana shortly after the introduction of these species. Studies elsewhere in the Galápagos have indicated that *T. punctatissima* preys heavily on nonnative rodents when they are available (Niethammer 1964, Abs et al. 1965, Groot 1983; D.W.S., pers. obs.).

DISCUSSION AND CONCLUSIONS

Comparison of Excavations 1 and 2

The test pit done at Barn Owl Cave in 1980 (Ex1), as well as the sediment surface of all three rooms, yielded 11,113 bones or bone fragments representing 16 extant species and six extirpated species of indigenous reptiles, birds, and mammals (Steadman 1986 : Table 6). The bones from Ex1 are summarized (Tables 6, 7) in formats that allow direct comparison with the same seven taxa ana-

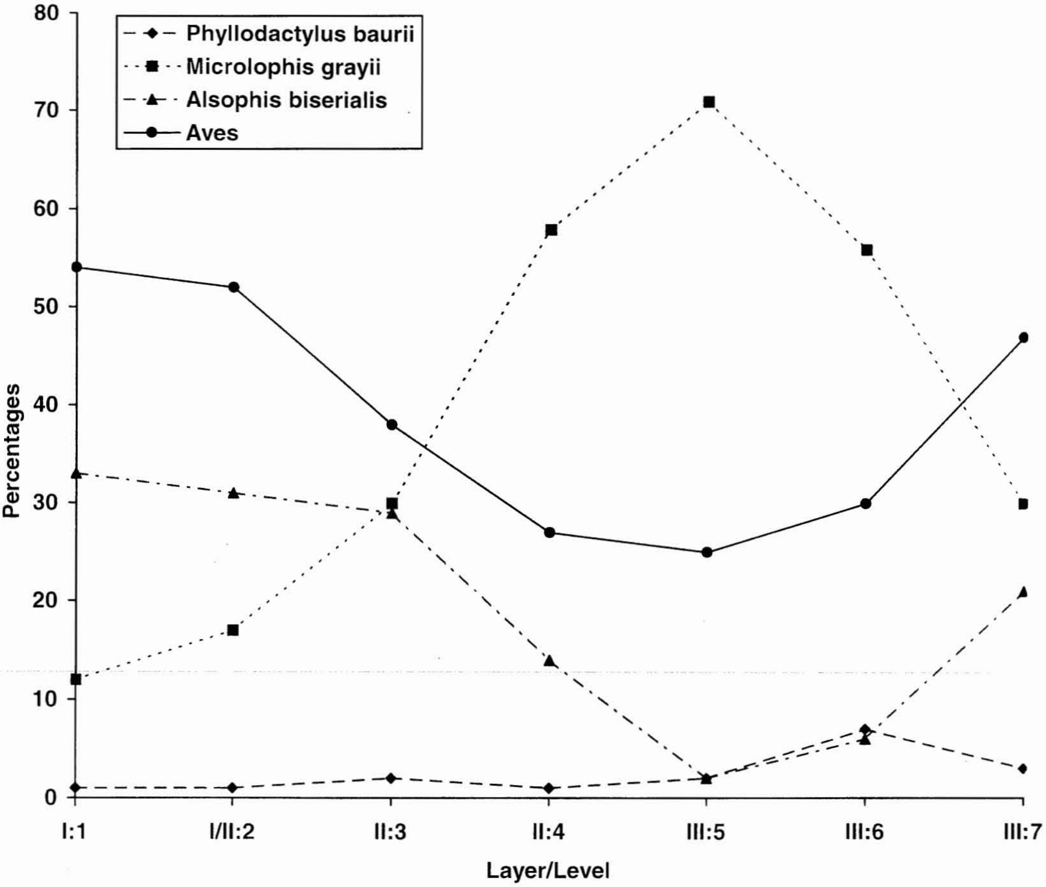

FIGURE 6. Relative abundance of bones, Excavation 2, Barn Owl Cave, Isla Floreana, expressed as percentage of "Total without *Geochelone* or *Mus*" in Table 4. *Geochelone* is removed from the calculations because of its different taphonomic history (natural traps) from the microvertebrates. *Mus* is nonnative.

TABLE 5

INFLUX OF BONES, EXCAVATION 2, BARN OWL CAVE, EXPRESSED AS BONES PER LITER (L) OF SEDIMENT

BONES	I:1 (80 L)	I/II:2 (145 L)	II:3 (115 L)	II:4 (125 L)	III:5 (120 L)	III:6 (155 L)	III:7 (130 L)	TOTAL (870 L)
Geochelone elephantopus	1.46	1.48	1.21	2.61	1.75	2.18	4.73	2.25
Phyllodactylus baurii	0.04	0.03	0.04	0.10	0.26	0.25	0.05	0.12
Microlophis grayii	0.42	0.59	0.68	6.05	10.63	1.94	0.60	3.00
Alsophis biserialis	1.18	1.09	0.66	1.42	0.28	0.21	0.42	0.72
Zenaida galapagoensis	0.25	0.31	0.08	0.15	0.18	0.08	0.09	0.16
Non-*Zenaida* Aves	1.64	1.54	0.78	2.66	3.54	0.98	0.87	1.68
Lasiurus borealis	0	0	0.02	0.01	0.02	0.03	0.03	0.02
Mus musculus	0.05	0.01	0	0	0	0	0	<0.01
Total	5.04	5.05	3.46	13.00	16.66	5.67	6.79	7.95
Total without *Geochelone* or *Mus*	3.53	3.56	2.25	10.39	14.89	3.49	2.03	5.70

NOTE: For each Layer/Level, the quantity of excavated sediment is given. Layers and Levels as in Table 4.

TABLE 6

ABBREVIATED FAUNAL SUMMARY, EXCAVATION 1, BARN OWL CAVE, ISLA FLOREANA, GALÁPAGOS

BONES[a]	A 0–10	B 10–16	C_1 16–38	C_2[b] 38–43	TOTAL
Geochelone elephantopus (E)	175	40	49	1	265
Phyllodactylus baurii	242	79	73	0	394
Microlophis grayii	778	1,372	1,428	5	3,583
Alsophis biserialis (E)	446	90	109	13	658
Zenaida galapagoensis	60	12	34	7	113
Non-*Zenaida* Aves	431	354	606	73	1,464
Lasiurus borealis	2	1	2	2	7
Rattus rattus (I)	cf. 1	0	0	0	1
Total	2,135	1,948	2,301	101	6,485
Total without *Geochelone* or *Rattus*	1,959	1,908	2,252	100	6,219

NOTE: These data represent all bones retained in sieves of 1.6 mm or greater mesh. Layers are represented by A–C_2, with their depths in cm below surface.

[a] E, extirpated species; I, introduced species.

[b] Excludes the extremely fragmentary 560 bones listed in Steadman (1986: Table 6) as "Non-passerine Aves," because those bones are likely to represent a single individual.

TABLE 7

INFLUX OF BONES, EXCAVATION 1, BARN OWL CAVE, EXPRESSED AS BONES PER LITER (L) OF SEDIMENT

BONES	A (100 L)	B (60 L)	C_1 (220 L)	C_2[a] (30 L)	TOTAL (410 L)
Geochelone elephantopus	1.75	0.67	0.22	0.03	0.65
Phyllodactylus baurii	2.42	1.32	0.33	0	0.96
Microlophis grayii	7.78	22.87	6.49	0.17	8.74
Alsophis biserialis	4.46	1.50	0.50	0.43	1.60
Zenaida galapagoensis	0.60	0.20	0.15	0.23	0.28
Non-*Zenaida* Aves	4.31	5.90	2.76	2.44	3.57
Lasiurus borealis	0.02	0.07	0.01	0.67	0.02
Total	21.34	32.53	10.46	3.97	15.82
Total without *Geochelone*	19.59	31.86	10.24	3.94	15.17

NOTE: Sediment volumes are approximate (±10%). Layers as in Table 6.

[a] Excludes the extremely fragmentary 560 bones listed in Steadman (1986: Table 6) as "Non-passerine Aves," because those bones are likely to represent a single individual.

lyzed from Ex2 (Tables 4, 5), although the data from Ex1 represent all bones retained in sieves as small as 1.6-mm mesh, whereas those from Ex2 include only bones retained in sieves of 3.35-mm or larger mesh.

Layer I of Ex2 was deposited wholly or primarily during the 1982–1983 El Niño, precluding stratigraphic correlation between it and any layer in Ex1, which was excavated in 1980. Layer I of Ex2 differs further from Layer A of Ex1 in having bones of *Microlophis* less common than those of non-*Zenaida* birds. Together these observations support the notion that Layer A of Ex1 is stratigraphically equivalent to Layer II, Level 3 (and perhaps part of Level 2) of Ex2.

Layer B of Ex1 shows an increase in the relative abundance of *Microlophis grayii* specimens and corresponding decrease in the relative abundance of bones of *Alsophis biserialis* (Figure 7) that are similar to those in Layer II, Level 4 and Layer III, Level 5 of Ex2 (Figure 6). The relative abundance of *Zenaida* and non-*Zenaida* bird bones in Ex1 also reaches its lowest point in Layer B,

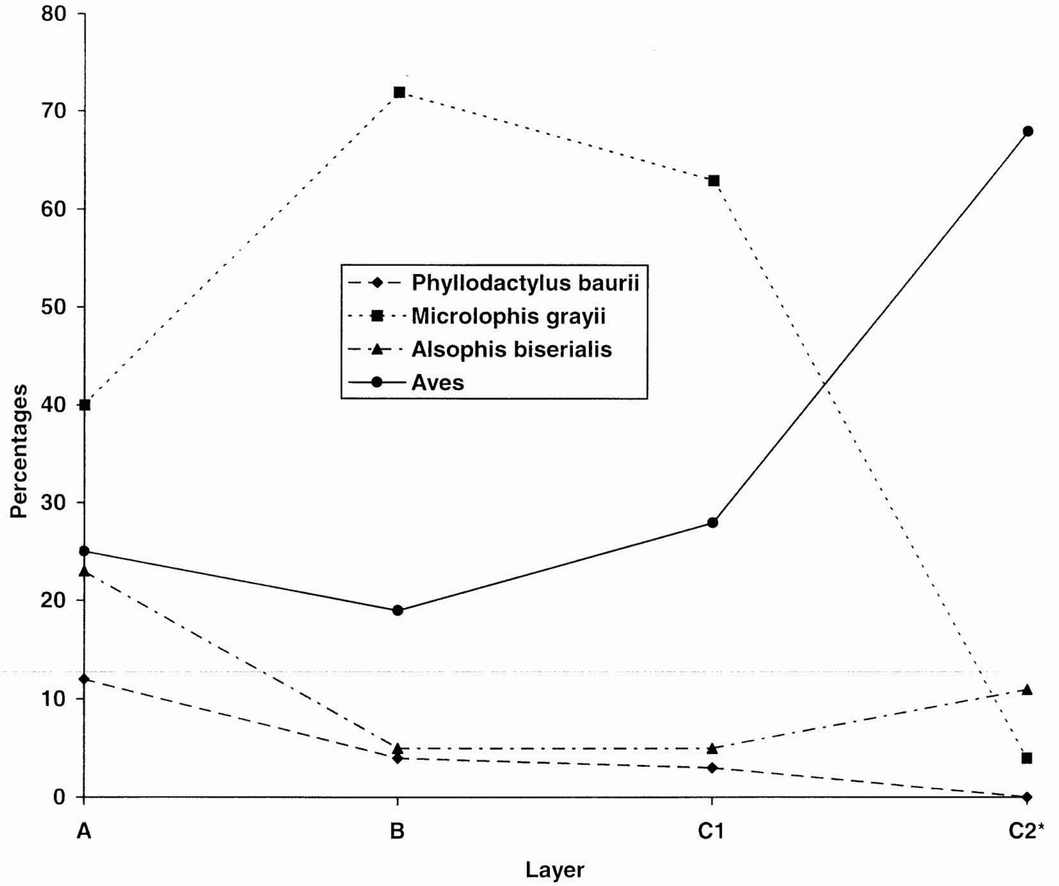

FIGURE 7. Relative abundance of bones, Excavation 1, Barn Owl Cave, Isla Floreana, expressed as percentage of "Total without *Geochelone* or *Rattus*" in Table 6. *Geochelone* is removed from the calculations because of its different taphonomic history (natural traps) from the microvertebrates. *Rattus* is nonnative.

which has the greatest value for bone influx. Again as in Ex2, the bone influx of *Alsophis* and birds remains the same or increases in the same strata where the number of *Microlophis* specimens increases sharply. The overall bone influx values are higher for Ex1 compared with Ex2 at least in part because the bone counts for Ex1 are based on bones retained in screens with smaller mesh (see above).

Continuing with faunal evidence (Figures 6, 7), Layers C_1 and C_2 of Ex1 seem equivalent to Layer III, Level 6 and Layer III, Level 7, respectively, of Ex2. Lying at a lower point in the cave, the sediments of Ex2 probably have accumulated over a longer period (and perhaps at a faster rate, based on maximum depth of sediment) than those of Ex1. Thus the deepest, unexcavated part of Ex2 probably does not correlate with any strata in Ex1.

The sedimentological data from Ex1 (Steadman 1986:24) and Ex2 (Tables 1, 2 herein) support the stratigraphic correlations suggested by the faunal data, although the potential resolution is finer in Ex2 than in Ex1. For example, the two thickest dark bands in Layer II are expressed in Layer B as a single band. Also, the overall lighter color of Layers C_1 and C_2 corresponds to the color change between Layers II and III.

Paleoclimatic Implications

Increases in total influx of bones (bones per liter of sediment) indicate an increased use of the cave by barn owls relative to the rate of sedimentation. Regardless of overall bone influx (Tables 5, 7), however, the proportion of bones belonging to the taxa analyzed in Figures 6 and 7 should reflect changes in taxa consumed by the barn owls, which eat small vertebrates opportunistically. Although barn owls obviously do not sample small vertebrates without biases, changes through time in relative abundance of prey species should be manifested roughly proportionately in the bones being deposited by the owls. Thus the high relative abundance of *Microlophis grayii* specimens in Layers B and C_1 of Ex1 and Levels 4 and 5 of Ex2 may reflect time intervals when the population size of this lizard increased relative to that of other potential prey items for the barn owl.

The various species of *Microlophis* in the Galápagos prefer arid habitats and are rare or absent in the humid highlands of large islands (Slevin 1935, Stebbins et al. 1967, Burger 1993). Assuming that populations of *Microlophis* thrive under conditions of long-term aridity, then increases in relative abundance of *Microlophis* bones would be expected where the sediments suggest an arid climate. This can be tested with rigor only by conducting more refined excavations. Alternatively, major changes in influx and relative abundance of *Microlophis* bones might be related to frequency of snakes (*Alsophis biserialis*). If *Alsophis* preys heavily on *Microlophis* (as reported by Slevin [1935]), depressed numbers of snakes may lead to high numbers of lizards, as suggested by the changes between Levels 4 and 5 (Table 5).

Regardless of its fossil content, the sediment in Ex2 of Barn Owl Cave may exhibit climatically important signals within the Holocene (see *Stratigraphy*), perhaps comparable with those documented in alluvium from coastal Perú by Wells (1987). Based on changes in sediment type, pollen, and spores in sediment cores from El Junco Lake on San Cristóbal, the Late Pleistocene probably was much drier than the Holocene, a time of relatively minor climate change in the Galápagos (Colinvaux 1972, Colinvaux and Schofield 1976a,b). The sediment/pollen/spore record at El Junco also provided evidence of a somewhat drier climate from ca. 8000 to 3000 yr B.P. than during earlier or later periods of the Holocene. The scale of this climate change was, however, much smaller than that at the Pleistocene/Holocene transition. Layer III of Ex2 may represent this relatively dry interval of the Holocene.

Future Research

To extract more biologically or climatologically informative data from the bone assemblages will require finer stratigraphic resolution than the ca. 10-cm levels used thus far. On average, each light or dark band is only 1–3 cm thick, meaning that each 10-cm level subsumes about five bands and averages the faunas of each while adding the time represented by them all.

Future research at Barn Owl Cave calls for these tasks: (1) expand Ex2, in 3- to 5-cm vertical levels to the cave's bedrock floor; (2) from a freshly exposed and mapped wall of Ex2, expand the aerial extent of the excavation laterally up to 2 by 2 m, removing each light or dark band individually; (3) in Room 3, conduct a methodologically similar 2 by 2 m excavation (Ex3); (4) identify all bones from both excavations to the species level; and (5) determine additional AMS ^{14}C dates from identified bones of extirpated species across the stratigraphic range of Ex2 and Ex3. The resulting 8 m^2 of excavations would represent ca. 2% of the total sediment surface in Barn Owl Cave. The new faunal samples would represent about a 10-fold increase in bones. Such a huge bone assemblage should yield prehistoric evidence of most species of terrestrial vertebrates that have occurred on Floreana in recent millennia.

Additional excavations of the finely stratified bone deposit at Barn Owl Cave will shed light on residency times, turnover rates, and possibly on relative abundance of species under natural conditions. Another avenue of future research will be to examine evolutionary rates over long time intervals, such as done by Chiba (1996) for an endemic land snail in the Bonin Islands. Being relatively well studied from osteological and evolutionary standpoints (Steadman 1982, Grant 1986, Grant and Grant 1989), various species of Darwin's finches would be excellent candidates for these long-term analyses, once further excavations yield larger samples of individual species. We may even be able to compare molecular versus morphological rates of evolution, because of the excellent organic preservation of the prehistoric bones in Barn Owl Cave.

ACKNOWLEDGMENTS

We thank the staffs of the Galápagos National Park Service, Charles Darwin Research Station, and Charles Darwin Foundation for research permits and other guidance. For able assistance or advice in the field or laboratory, we thank L. Cayot, D. Clark, G. Davis, R. Day, R. Hanna, L. J. Justice, C. Macfarland, B. McCullough, G. Merlen, and especially W. Vera. Comments that improved the manuscript were kindly provided by S. C. Antón, K. R. Reis, and M. I. Williams.

LITERATURE CITED

ABS, M., E. CURIO, P. KRAMER, and J. NIETHAMMER. 1965. Zur Ernaehrungsweise der Eulen auf Galapagos: Ergebnisse der deutschen Galapagos-Expedition 1962/63, IX. J. Ornithol. 106: 49–57.

ANONYMOUS. 1998. Extinction on San Cristóbal, Galápagos. Cotinga 8: 7.

BOERSMA, P. D. 1998. Population trends of the Galápagos Penguin: Impacts of El Niño and La Niña. Condor 100: 245–253.

BOW, C. S., and D. J. GEIST. 1992. Geology and petrology of Floreana Island, Galápagos Archipelago, Ecuador. J. Volcan. Geotherm. Res. 52: 83–105.

BURGER, J. 1993. Colony and nest site selection in lava lizards *Tropidurus* spp. in the Galápagos Islands. Copeia 1993: 748–754.

CHAMBERS, S. M., and D. W. STEADMAN. 1986. Holocene terrestrial gastropod faunas from Isla Santa Cruz and Isla Floreana, Galápagos: Evidence for late Holocene declines. Trans. San Diego Soc. Nat. Hist. 21: 89–110.

CHIBA, S. 1996. A 40,000-year record of discontinuous evolution of island snails. Paleobiology 22: 177–188.

COLINVAUX, P. A. 1972. Climate and the Galápagos Islands. Nature (Lond.) 240: 17–20.

COLINVAUX, P. A., and E. K. SCHOFIELD. 1976a. Historical ecology in the Galápagos Islands I. A Holocene pollen record from El Junco Lake, Isla San Cristóbal. J. Ecol. 64: 989–1012.

———. 1976b. Historical ecology in the Galápagos Islands II. A Holocene spore record from El Junco Lake, Isla San Cristóbal. J. Ecol. 64: 1013–1026.

COX, A., and G. B. DALRYMPLE. 1966. Palaeomagnetism and potassium-argon ages of some volcanic rocks from the Galápagos Islands. Nature (Lond.) 209: 776–777.

CRUZ, E. 1985. Efectos de "El Niño" en la Isla Floreana. Pages 497–503 *in* G. Robinson and E. M. del Pino, eds. El Niño en las Islas Galápagos: El Evento de 1982–1983. Fundación Charles Darwin, Quito, Ecuador.

CRUZ, F., and J. CRUZ. 1985. The effect of El Niño on the breeding of the Dark-rumped Petrel on Cerro Pajas, Floreana. Pages 259–272 *in* G. Robinson and E. M. del Pino, eds. El Niño en las Islas Galápagos: El Evento de 1982–1983. Fundación Charles Darwin, Quito, Ecuador.

FRANKLIN, J., and D. W. STEADMAN. 1991. The potential for conservation of Polynesian birds through habitat mapping and species translocation. Conserv. Biol. 5: 506–521.

GLYNN, P. W. 1990. Preface and acknowledgements. Pages vii–ix *in* P. W. Glynn, ed. Global ecological consequences of the 1982–83 El Niño–Southern Oscillation. Elsevier, Amsterdam, the Netherlands.

GRANT, B. R., and P. R. GRANT. 1989. Evolutionary dynamics of a natural population: The large cactus finch of the Galápagos. University of Chicago Press, Chicago, Illinois.

GRANT, P. R. 1986. Ecology and evolution of Darwin's finches. Princeton University Press, Princeton, New Jersey.

GROOT, R. S. de. 1983. Origin, status and ecology of the owls in Galápagos. Ardea 71: 167–182.

HOECK, H. N. 1984. Introduced fauna. Pages 233–245 *in* R. Perry, ed. Galápagos. Pergamon Press, Oxford, U.K.

JAMES, H. F. 1987. A late Pleistocene avifauna from the island Oahu, Hawaiian Islands. Doc. Lab. Geol. Fac. Sci. Lyon 99: 221–230.

KOGELSCHATZ, J., L. SOLORZANO, R. BARBER, and P. MENDOZA. 1985. Oceanographic conditions in the Galápagos Islands during the 1982/1983 El Niño. Pages 91–123 *in* G. Robinson and E. M. del Pino, eds. El Niño en las Islas Galápagos: El Evento de 1982–1983. Fundación Charles Darwin, Quito, Ecuador.

MERLIN, G. 1985. The nature of El Niño: A perspective. Pages 133–150 *in* G. Robinson and E. M. del Pino, eds. El Niño en las Islas Galápagos: El Evento de 1982–1983. Fundación Charles Darwin, Quito, Ecuador.

MONTORIOL-POUS, J., and O. ESCOLÁ. 1975. Contribución al conocimiento vulcano-espeleológico de la isla Floreana (Galápagos, Ecuador). Speleon (V Symposium de Espeleología) 1: 57–67.

NIETHAMMER, J. 1964. Resultats de l'expedition allemande aux Galápagos 1962/63, VII: Contribucion al connaissance des mammiferes terrestres de l'ile Indefatigable (= Santa Cruz), Galápagos. Mammalia 28: 593–606.

PREGILL, G. K., D. W. STEADMAN, and D. R. WATTERS. 1994. Late Quaternary vertebrate faunas of the Lesser Antilles: Historical components of Caribbean biogeography. Bull. Carnegie Mus. Nat. Hist. 30: 1–51.

SLEVIN, J. R. 1935. An account of the reptiles inhabiting the Galápagos Islands. N.Y. Zool. Soc. Bull. 38: 3–24.

STAFFORD, T. W., JR., A. J. T. JULL, K. BRENDEL, R. C. DUHAMEL, and D. J. DONAHUE. 1987. Study of bone radiocarbon dating accuracy at the University of Arizona NSF accelerator facility for radioisotope analysis. Radiocarbon 29: 24–44.

STAFFORD, T. W., JR., K. BRENDEL, and R. C. DUHAMEL. 1988. Radiocarbon, ^{13}C and ^{15}N analysis of fossil bone: Removal of humates with XAD-2 resin. Geochim. Cosmochim. Acta 52: 2257–2267.

STAFFORD, T. W., JR., P. E. HARE, L. CURRIE, A. J. T. JULL, and D. J. DONAHUE. 1991. Accelerator radiocarbon dating at the molecular level. J. Archaeol. Sci. 18: 35–72.

STEADMAN, D. W. 1982. The origin of Darwin's finches (Fringillidae, Passeriformes). Trans. San Diego Soc. Nat. Hist. 19: 279–296.

———. 1984. The status of *Geospiza magnirostris* on Isla Floreana, Galápagos. Bull. Br. Ornithol. Club 104: 99–102.

———. 1986. Holocene vertebrate fossils from Isla Floreana, Galápagos. Smithson. Contrib. Zool. 413: 1–103.

———. 1995. Prehistoric extinctions of Pacific island birds: Biodiversity meets zooarchaeology. Science (Washington, D.C.) 267: 1123–1131.

STEADMAN, D. W., and C. E. RAY. 1982. The relationships of *Megaoryzomys curioi*, an extinct cricetine rodent (Muroidea, Muridae) from the Galápagos Islands, Ecuador. Smithson. Contrib. Paleobiol. 51: 1–23.

STEADMAN, D. W., and S. ZOUSMER. 1988. Galápagos: Discovery on Darwin's islands. Smithsonian Institution Press, Washington, D.C.

STEADMAN, D. W., T. W. STAFFORD, JR., D. J. DONAHUE, and A. J. T. JULL. 1991. Chronology of Holocene vertebrate extinction in the Galápagos Islands. Quat. Res. (New York) 35: 126–133.

STEBBINS, R. C., J. M. LOWENSTEIN, and N. W. COHEN. 1967. A field study of the lava lizard (*Tropidurus albemarlensis*) in the Galápagos Islands. Ecology 48: 839–851.

WEBSTER, P. J., and T. N. PALMER. 1997. The past and future of El Niño. Nature (Lond.) 390: 562–564.

WELLS, L. E. 1987. An alluvial record of El Niño events from northern coastal Peru. J. Geophys. Res. 92: 14,463–14,470.

WHITE, W. M., A. R. MCBIRNEY, and R. A. DUNCAN. 1993. Petrology and geochemistry of the Galápagos Islands: Portrait of a pathological mantle plume. J. Geophys. Res. 98: 19,533–19,563.