Holocene Vertebrate Fossils from Isla Floreana, Galápagos

DAVID W. STEADMAN

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ABSTRACT

Steadman, David W. Holocene Vertebrate Fossils from Isla Floreana, Galápagos. *Smithsonian Contributions to Zoology*, number 413, 103 pages, 25 figures, 4 plates, 12 tables, 1986.—This study surveys the late Holocene vertebrate fossil record from Isla Floreana, Galápagos. Over 20,000 fossils from four lava tubes in the arid lowlands near Post Office Bay are associated with six radiocarbon dates of 2400 years B.P. or younger. The fossils, most of which originated as regurgitated pellets of barn owls, represent more than 1100 individual animals of 24 indigenous species. They include six species now extinct on Floreana: *Geochelone elephantopus* (tortoise), *Alsophis biserialis* (snake), *Tyto punctatissima* (Galápagos Barn Owl), *Mimus trifasciatus* (Floreana Mockingbird), *Geospiza nebulosa* (Sharp-beaked Ground Finch), and *Geospiza magnirostris* (Large Ground Finch). These species are, respectively, 1st, 7th, 16th, 6th, 15th, and 2nd in abundance among all species recorded as fossils, making up 57% of the individuals in the fossil fauna. In addition, the 3rd and 4th most common fossil taxa, *Tropidurus grayii* (lava lizard) and *Zenaida galapagoensis* (Galápagos Dove), are extremely rare today on Floreana. Thus, extinction probably has changed the composition of Floreana's fauna even more than is suggested by the number of extinct species alone.

While the evidence is circumstantial, I believe that all extinction on Floreana is related to human impact, directly through predation and habitat alteration, and indirectly through the effects of alien animals (rats, mice, cats, dogs, pigs, goats, cattle, and donkeys). People and feral mammals have lived on Floreana since 1832, and most or all vertebrate extinction occurred within the succeeding 40–50 years. Direct predation by man and introduced mammals was probably the main cause of extinction only for *Geochelone elephantopus*, although such predation may have been involved to some extent in each of the other extinctions. Loss of preferred prey species and human predation probably caused the extinction of *Tyto punctatissima*. Extinction of *Mimus trifasciatus* and *Geospiza magnirostris* may have resulted from destruction of *Opuntia* cactus by feral herbivores. Extinction of *Geospiza nebulosa* may be related to habitat changes in the highlands. *Buteo galapagoensis* (Galápagos Hawk), though not recorded as a fossil, is also apparently extinct on Floreana, with direct human predation likely to be the main cause. All extinction on Floreana occurred in historic times; whether this is true elsewhere in the Galápagos awaits more research.

Lasiurus borealis (Red Bat) is the only indigenous mammal recorded as a fossil. The absence of fossils of cricetine rodents or *Conolophus* spp. (Land Iguana) is evidence that these forms never occurred on Floreana. The lack of fossils of *Coccyzus melacoryphus* (Dark-billed Cuckoo) and *Dendroica petechia* (Yellow Warbler), which occur commonly on Floreana today, is evidence that these two species colonized the Galápagos very recently.

Fossil records depend upon suitable environments of deposition. The Galápagos Islands, being of recent volcanic origin, lack many potentially fossiliferous geological features such as fine-grained alluvial sediments, indurated sand dunes, or limestone caves and sinkholes. Fortunately, lava tubes, which are very well suited for accumulation and preservation of vertebrate fossils, are common on certain islands in the Galápagos.

Fossils enable us to reconstruct undisturbed (pre-human) insular faunas more completely than previously possible. Modern biogeographical studies usually do not consider how natural the faunas are; they would benefit by considering changes wrought by human impact. The field of island biogeography would profit from a renewed emphasis on the collection of original field data rather than the current trend of theoretical studies that often are based upon inadequate or poorly understood data.

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Holocene Vertebrate Fossils
from Isla Floreana, Galápagos.

David W. Steadman

Introduction

Biologists have long held the Galápagos Islands in high esteem. Even non-biologists are impressed by the living things they see there, especially by the tameness of the native animals. Situated in the equatorial Pacific Ocean, the Galápagos Islands possess a terrestrial flora and fauna that is derived almost entirely from the South American mainland, nearly 1000 km to the east. More than any other locality in the world, these inhospitable volcanic islands have been regarded as a Mecca to which many natural historians sooner or later pay homage. Evolutionary biologists, biogeographers, and ecologists have found the Galápagos particularly enticing as an unparalleled "natural laboratory." In attempting to reconstruct the evolution of the vertebrates that inhabit the Galápagos, biologists have lacked any paleontological evidence. During five trips to the Galápagos since 1978, I have collected fossils of reptiles, birds, and mammals from lava tubes on five of the larger islands in the group—Santa Cruz, San Cristóbal, Floreana, Rábida and Isabela. These specimens represent the first serious paleontological effort to document the evolution, past distribution, and extinction of vertebrates in the Galápagos.

This paper will report comprehensively on the fossils of Floreana, an island with a colorful human history and a tragic biological history. My studies of the fossils from the other four islands are still incomplete. The fossils described herein, none of which predates with certainty even the Holocene, provide critical new evidence for understanding the extinction and biogeography of the vertebrates of Floreana and the entire Galápagos Archipelago.

ABBREVIATIONS.—Terminology used throughout this work includes the following:

B.P.	before present (= before A.D. 1950)
CDRS	Charles Darwin Research Station, Santa Cruz, Galápagos
ITCZ	Intertropical convergence zone
MNI	minimum number of individuals

The following persons, listed in Table 1, assisted in field work on Floreana:

MJC	María José Campos
GD	Gayle Davis
DG	David Graham
HH	Harvey Helman
JRH	James R. Hill, III
GM	Godfrey Merlen
MP	Miguel Pozo
DWS	David W. Steadman
ENS	Edward N. Steadman

For species accounts in the "Systemic Paleontology" section, the following acronyms are used for the four fossil caves. Many fossils were catalogued as lots, so a single catalogue number may represent many fossils.

CPOI	Cueva de Post Office (Inferior)
CPOS	Cueva de Post Office (Superior)
FC	Finch Cave
BOC	Barn Owl Cave

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I examined modern specimens of reptiles, birds, and mammals from the collections that follow. These specimens, listed below, are skeletons (or, for some mammals, skin and skulls) unless stated otherwise.

BM(NH)   British Museum (Natural History)
CAS   California Academy of Sciences
NMNH   National Museum of Natural History, Smithsonian Institution
RIB   Robert I. Bowman Collection, San Francisco State University
UCMVZ   Museum of Vertebrate Zoology, University of California, Berkeley
USNM   former United States National Museum, collections in the National Museum of Natural History, Smithsonian Institution

dination of the insect identifications was done with assistance and information from L. Burham, T.L. Erwin, R.C. Froeschner, L. Masner, A.F. Newton, L.M. Roth, R.R. Snelling, D.R. Whitehead, and N.E. Woodley.

This paper represents a revision of my doctoral dissertation in the Department of Geosciences, University of Arizona. Debbie Gaines and Jim I. Mead kindly provided much assistance in dealing with the academic bureaucracy. I thank the members of my graduate committee, Paul S. Martin, Owen Davis, C. Vance Haynes, Storrs L. Olson, and Stephen M. Russell, for their helpful criticisms of my dissertation. Charles R. Crumly and Peter R. Grant commented on an earlier draft of this manuscript. The final draft was read by W. Ronald Heyer, Paul S. Martin, Storrs L. Olson, and Gregory K. Pregill. This is contribution number 370 of the Charles Darwin Foundation for the Galápagos.

Finally, I would like to thank Marsha S. Cox, Paul S. Martin, Storrs L. Olson, and S. Dillon Ripley for their undying interest in, and support for, my paleontological research in the Galápagos.

Materials and Methods

Throughout this paper, I will refer to the bones collected in the caves as "fossils." I prefer not to use the term "subfossil," which is often associated with non-mineralized Holocene bones, because many of the specimens from Floreana are well mineralized and were collected from within sediments. The fossils from Floreana vary in preservation, however, from that of nearly fresh bone to complete mineralization. It is simpler to refer to all of them as fossils than to attempt to distinguish unmineralized from mineralized bones by using the awkward term "subfossil."

FIELD WORK.—I visited Floreana 5 times (25 June–9 July 1978, 22 October–1 November 1980, 26 December 1980, 10 April 1982, 24, 25 May 1983). All fossil collections were made during the first two trips (Table 1). I also visited the

satellite islands of Champion (4 July 1978, 26 October 1980, 24 May 1983) and Caldwell (26 December 1980) to observe living plants and animals. On Floreana, I spent at least 2–3 hours per day outside of the caves, observing plants and wildlife, especially the birds.

We (names listed in Table 1) visited the Bahia de las Cuevas region from 22–26 October 1980. The caves of this area, described in Montoriol-Pous and Escolá (1975), are not lava tubes but are weathering features in the sides of scoria cones. The sediments in these shallow caves were essentially unfossiliferous, and seemed to be of very little antiquity. Fossils of boney fish, tortoises (*Geochelone elephantopus*), and Dark-rumped Petrels (*Pterodroma phaeopygia*) were collected in small numbers from these caves, but the only organic material commonly found here was the trampled dung of feral goats. The limited faunal remains from these caves will not be discussed further.

With the maps of Montoriol-Pous and Escolá (1975), we searched for the caves they reported, Cueva de Post Office (Inferior and Superior), on 25–27 June 1978. Upon finding these lava tubes, we collected fossils for the next 10 days. On 7–9 July 1978, we searched for new caves and completed the screening, sorting, and packaging of fossils and sediment. We discovered Finch Cave at this time, but collected no fossils there. We visited the Post Office Bay region again from 26 October to 1 November 1980, collecting fossils in Cueva de Post Office (Inferior and Superior), Finch Cave, and the newly discovered Barn Owl Cave. In each instance, the basic procedure was as follows:

1. Search for and locate lava tubes.
2. If fossiliferous, make maps of the location of the lava tube and the plan of the floor.
3. Collect bones and other organic material on the surface.
4. Look for areas of sediment accumulation and excavate a test pit, saving sediment samples from all designated levels.
5. Describe the stratigraphy of a wall of the test pit.

TABLE 1.—Fossil localities on Floreana (abbreviations of collectors' names explained in "Introduction").

Locality	Collectors	Date of collection
Cueva de Post Office (Inferior)		
Edge of inundated zone	DWS, DG	2 Jul 1978
Room 1	DWS, DG, HH, MP	27 Jun 1978
	DWS, MJC, JRH, ENS	27 Oct 1980
Room 2	DWS, MP	27 Jun 1978
	DWS, MJC, JRH, ENS	26 Oct 1980
Room 3	DWS, HH, MP	30 Jun 1978
	DWS, MJC, JRH, ENS	27 Oct 1980
Room 4	DWS, HH	30 Jun 1978
Excavations 1, 2	DWS, MP	4 Jul 1978
Excavation 3	DWS, MP	6 Jul 1978
Cueva de Post Office (Superior)		
Area 1	DWS, MP	28 Jun 1978
	DWS, MJC, JRH, ENS	28 Oct 1980
Area 2	DWS, MP	28, 30 Jun 1978
	DWS, MJC, JRH, ENS	28 Oct 1980
Area 3	DWS, MP	31 Jun 1978
Excavations 1, 2	DWS, DG, HH, MP	1 Jul 1978
Excavations 3, 4	DWS, MJC, JRH, ENS	28 Oct 1980
Finch Cave		
All areas	DWS, MJC, JRH, ENS	29 Oct 1980
Barn Owl Cave		
Rooms 1–3	DWS, MJC, JRH, ENS	30, 31 Oct 1980
Excavation 1	DWS, MJC, JRH, ENS	31 Oct 1980

6. Screen the sediment from the test pit at a convenient location outside of the lava tube.

7. If the sediment is highly fossiliferous, then enlarge the excavation laterally, following any discernible stratigraphic units.

8. Double-check the original description of the stratigraphic section, taking additional sediment samples if necessary.

9. Line the excavation with a plastic sheet and fill it in with rubble.

10. Screen all remaining excavated sediment at a point outside the cave.

11. Package fossils and sediment samples.

12. Transport by boat all collected materials to CDRS for further sorting and packaging, in preparation for shipment to NMNH.

We used two sizes of screens, ¼ inch mesh and 1/16 inch mesh (window screen). All maps were made by doing a traverse with a Brunton pocket transit and a 20 m line. The vegetation made a longer line impractical outside of the caves. Within the caves, the width of the floor was measured by holding a 25 m steel tape at right angles to 1 m intervals on the directionally oriented 20 m line. These measurements were rounded to the nearest 0.1 m or 0.5 m, depending on limitations of time.

MUSEUM RESEARCH.—At NMNH I unpacked and cleaned the fossils, which then I sorted into broad taxonomic categories. Precise identifica-

tions were made by comparisons with modern skeletons, often aided by a binocular dissecting microscope. Measurements were made with dial calipers of 0.05 mm increments, rounded to the nearest 0.1 mm. The approximately 20,000 fossil specimens are catalogued in the collection of the Department of Paleobiology, NMNH. Representative samples of the fossils have been presented to the museum of CDRS.

MODERN SPECIMENS EXAMINED.—Reptiles: *Phyllodactylus galapagensis:* USNM 223988, 223989. *Tropidurus bivittatus:* USNM 223987. *Alsophis barringtonensis:* USNM 223986.

Birds: *Pterodroma phaeopygia:* USNM 502214, 547924. *Puffinus lherminieri:* USNM 488422, 498002. *Oceanites gracilis:* USNM 491398. *Pelagodroma marina:* USNM 496759. *Fregetta tropica:* USNM 553239. *Nesofregetta albigularis:* USNM 498012. *Halocyptena microsoma:* USNM 498395. *Oceanodroma tethys:* USNM 321612. *Oceanodroma castro:* USNM 490825, 491205. *O. leucorhoa:* USNM 498389, 498391. *O. tristrami:* USNM 289202. *O. monorhis:* USNM 500261. *O. markhami:* USNM 497962. *O. hornbyi:* USNM 491400. *O. homochroa:* USNM 500220. *O. furcata:* USNM 556268. *O. melania:* USNM 498407. *Nyctanassa violacea:* USNM 18028, 18501, 318840–318842. *Zenaida galapagoensis:* USNM 320829. *Tyto punctatissima:* UCMVZ 140963. *T. alba:* USNM 500619. *Pyrocephalus nanus:* UCMVZ 130127. *Myiarchus magnirostris:* UCMVZ 151395. *Mimus trifasciatus:* BM(NH) 1837.2.21.401 (skin), 1899.9.1.3 (skin), 1899.9.1.4 (skin); RIB 436SLB, 437SLB. *M. macdonaldi:* BM(NH) 1899.9.1.6 (skin), 1899.9.1.9 (skin); RIB 1424RIB, 1431RIB; UCMVZ 140968, 140971, 140972. *M. parvulus:* BM(NH) 1899.9.1.64 (skin), 1899.9.1.68 (skin); RIB 1507RIB, 1509RIB; UCMVZ 140974–140978; USNM 19802, 321068, 321069. *M. melanotis:* BM(NH) 1899.9.1.17 (skin). *Dendroica petechia:* UCMVZ 130131. *Geospiza nebulosa:* UCMVZ 93213–93219; USNM 116117. *G. fuliginosa:* UCMVZ 93181, 93182, 130277, 130278, 130285, 130286, 130296, 130298, 130299, 141019–141021; USNM 321070,

345594, 345595. *G. fortis:* UCMVZ 93140, 93141, 93143, 93169–93174, 130137, 130149, 130175, 130178, 130181, 130190, 130191, 130195, 130198, 130204, 130206, 130247–130249, 141004, 141006; USNM 344819, 345593. *G. magnirostris:* BM(NH) 1885.12.14.280 (skin), 1899.9.1.171 (skin); UCMVZ 93084, 130150, 130160, 130164, 130170, 140985 (skin), 140993, 140996; USNM 291411. *G. scandens:* UCMVZ 93116–93119, 93121–93124; USNM 20734, 345597. *G. conirostris:* UCMVZ 93105. *G. crassirostris:* UCMVZ 93205, 93207, 93208, 130335. *G. parvula:* UCMVZ 93210, 93211, 130429, 130431, 130438, 130454, 130459, 130483, 130490, 130508, 141056; USNM 20533. *G. pauper:* UCMVZ 141054. *G. psittacula:* UCMVZ 130354, 130365, 130367, 130378, 130381, 130383, 130386, 130387, 130393, 130397, 130402, 130413–130415. *G. pallida:* UCMVZ 93203, 130534, 130544, 130550, 150551, 130553, 130554. *G. olivacea:* UCMVZ 93220, 93221, 130563, 130569, 130585; USNM 345598.

Mammals: *Lasiurus borealis:* UCMVZ 65510, 101913, 108974, 119904, 126482, 130987, 136563, 145006, 145016, 152154. *L. ega:* UCMVZ 85284, 136048, 140885, 144959, 144960. *L. cinereus:* CAS 13272; UCMVZ 145371. *L. semotus:* UCMVZ 114344, 114345. *L. seminolus:* UCMVZ 6844. *L. floridanus:* UCMVZ 70507, 126103. *L. intermedius:* UCMVZ 84219, 104131. *Mus musculus:* USNM 271417, 361409. *Rattus rattus:* USNM 664, 503767. *Felis catus:* USNM 253239, 278658. *Sus scrofa:* USNM 651.

PLACE NAMES.—Place names in the Galápagos either have both Spanish and English versions, or are a combination of the two languages. Thus the reader must forbear such hybrid combinations as "Cueva de Post Office." In this paper, I will attempt to use the name that is used most often today by residents and scientists in the islands, showing no partiality to Spanish or English. For the past 20 years, there has been a trend among English-speaking peoples to use an increased amount of Spanish for place names in

the Galápagos. I will abide by this trend as much as possible.

Throughout this paper, I will use the name Floreana. Like most major islands in the Galápagos, Floreana is blessed with several names, reviewed here in an attempt to minimize confusion. "Santa Maria," the official Ecuadorean name for the island, is used only occasionally. "Charles," in honor of King Charles II of England, a Stuart king of the late 17th century, was the name used by most English-speaking persons, including buccaneers, explorers, whalers, and scientists, until a decade or two ago. The name Charles is derived from the name "King Charles's Island" that was used on the map prepared by William Ambrose Cowley in 1684, and reproduced in Beebe (1924, fig. 78) and Slevin (1955, map 1; 1959:19). The island named "Santa Maria de l'Aguada" on Cowley's map (this name presumably added after 1684) apparently is also Floreana (Markham, 1880; personal observation). The island designated on Cowley's map as "King Charles's Island" is less accurate, in both location and shape, than the one named "Santa Maria de l'Aguada." The name "Isle de Saute" was used for Floreana by Ensign Le Sieur de Villefort of the French frigate *Philippeaux* in 1700. The name "Mercedes" was used by General Jose Villamil during his stay on Floreana in the 1830s and 1840s, according to the account of Captain Henri Louns, Compte de Gueydon, of the French brig-of-war *Le Genie* (Slevin, 1959:89), although later in the same account Captain Gueydon used the name "Mercedes" for Isla San Cristóbal. Floreana is the name used invariably today by residents and most scientists, regardless of their native tongue. Occasionally Floreana is spelled "Floriana," especially in works of the 19th century. The name Floreana is attributed to General Villamil, in honor of General Flores, the first president of Ecuador (Wittmer, 1961:33). In 1832, Villamil established on Floreana the first human colony in the Galápagos. As we shall see, this settlement proved disastrous for many of the native plants and animals of the island.

Background Studies

I will introduce the geology, past and present climate, and vegetation of Floreana, to provide an understanding of the environment in which the vertebrates of Floreana once thrived. As much as seems necessary, I will preface the situation on Floreana with more generalized information on the whole archipelago. The vertebrates themselves have been reviewed in many scientific and semi-popular publications. They need no introduction here, but certain aspects of their biology will be mentioned when appropriate.

GEOLOGY.—Perhaps 100 biologists have visited the Galápagos for every geologist who has made the same journey. Detailed geological descriptions are lacking for most individual islands, and Floreana is no exception. McBirney and Williams (1969:21–28) provide the only meaningful description of the geomorphology of Floreana, but their study is based upon only five days of field work. General accounts of the geology of the Galápagos are found in Darwin (1869, and earlier editions), Chubb (1933), and Williams (1966). Many important advances have been made in the regional geology of the Galápagos during the past twenty years, thanks to plate tectonic theory in combination with techniques of age determination. Modern geological accounts that consider plate tectonics, potassium-argon dating, and magnetic polarity determination appear in McBirney and Williams (1969), Hey et al. (1977), Cox (1983), and Simkin (1984). Much of the following is taken from these four references.

The Galápagos Islands are situated on the Nazca Plate. They are approximately 30 to 300 km south of the Galápagos Spreading Center (Galápagos Island Fracture Zone), which separates the southward accreting Nazca Plate from the northward accreting Cocos Plate (Hey et al., 1977, fig. 1; Cox, 1983, figs. 1, 2). The islands emerge atop the submarine Galápagos Platform, which is the youngest, highest, and westernmost portion of the Carnegie Ridge. This ridge trends

S82°E from the Galápagos nearly to mainland South America, but is obliterated, along with the rest of the eastern margin of the Nazca Plate, in the subduction zone (Chile-Peru Trench) just west of the South American coast. The Cocos Ridge trends N43°E from the Galápagos Platform toward Costa Rica. There is no evidence, however, that either the Cocos Ridge or the Carnegie Ridge ever served as a land bridge or chain of islands to connect the Galápagos to Cocos Island or to the mainland. The Galápagos Islands, as well as the Carnegie Ridge, may have formed from the Nazca Plate passing over an area of magma outpouring from the earth's mantle (a "hotspot"). There is no geological evidence for subsidence of the Galápagos in general, as has been suggested by some biologists to explain the distributions of organisms. Faulting has caused localized dropping of the land, such as on Baltra, but the regional picture for this young, volcanically active archipelago is not one of sinking.

The youngest islands in the group are probably the large western islands of Isabela and Fernandina, while the oldest islands are the eastern ones (San Cristóbal, Española, Santa Fé, Plaza, Baltra, and northeastern Santa Cruz). Potassium-argon dating, magnetic polarity determination, geomorphology, and current volcanic activity all support the east to west trend of decreasing ages of the islands. The oldest islands probably have been emergent above the ocean for 3 to 5 million years, while the youngest islands are probably less than 1 million years old. Thus the Galápagos are a very youthful group of islands, a fact of utmost importance to those pondering the evolution of their flora and fauna. Based on the present rate of eastward movement of the Nazca Plate, the Galápagos probably were approximately 200 km west of their present location when they first began to appear above the sea. They are still moving toward South America, at an estimated rate of 55 mm per year, and thus should be subducted beneath South America in approximately 20 million years.

Floreana is located in the south-central portion of the archipelago (Figure 1). It is the 6th largest island in the group, having an area of 171 square kilometers (66 square miles) (Wiggins and Porter, 1971). The highest point on Floreana is Cerro Paja or Cerro de Pajas (Straw Mountain), which reaches an elevation of 640 meters (2100 feet; McBirney and Williams, 1969, pl. 2; Figure 2 herein). Although Floreana is roughly circular in shape and attains its highest elevations near the center of the island, it is not dominated by a single large shield volcano with a caldera. McBirney and Williams (1969:21) noted that a caldera may have existed at one time on Floreana, but was obliterated by the many younger cones and flows, thus placing Floreana in the "Mauna Kea stage" of volcanic development. Floreana has many parasitic cones, scattered nearly randomly, that vary much in size (McBirney and Williams, 1969, fig. 8). Nearly all of the cones are scoria or lava-scoria cones. In between these cones are pahoehoe lava flows and many types of basaltic ejecta, ranging from ash and cinders up to large boulders. The small satellite islands to the north and east of Floreana are formed from tuff or scoria cones that have undergone differing degrees of erosion.

Most of the surface lavas of Floreana are of the Bruhnes Normal Polarity Epoch (0.0–0.79 million years old, following Johnson, 1982), although lavas of the Matuyama Reversed Polarity Epoch (0.79–2.47 million years old) are exposed along the northwestern, northeastern, eastern, and southern coasts (Cox and Dalrymple, 1966; McBirney and Williams, 1969:22, 106; Craig S. Bow, pers. comm.; Cox, 1983). Within the Galápagos, Floreana is an island of intermediate age, i.e., one that emerged during the Matuyama Reversed Polarity Epoch (Cox, 1983). Floreana thus is roughly equivalent in age to Pinzon, Rábida, and Wenman. It is younger than the old eastern islands, such as San Cristóbal, Española, Sante Fé, and Santa Cruz, but older than the western and northern islands of Santiago, Isabela, Fernandina, Genovesa, Marchena, Pinta, and Culpepper. McBirney and Williams (1969:22) said that "almost surely some [of the
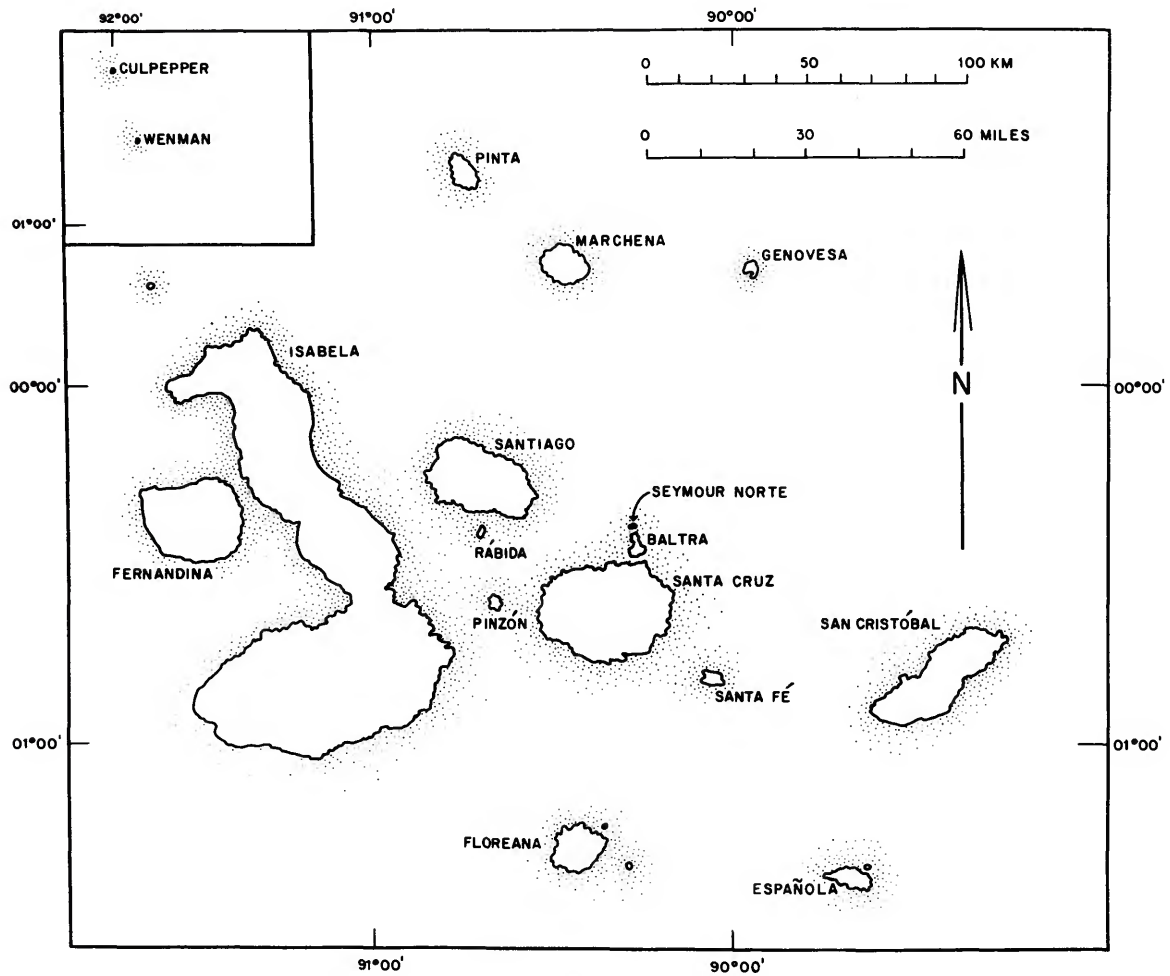
FIGURE 1.—The Galápagos Islands.

lavas on Floreana] were discharged within the last thousand years, if not within the last few centuries." I disagree with this statement, for I have never seen fresh lavas on Floreana. Although some of Floreana's lavas are still rather devoid of vegetation, they are, nevertheless, much more weathered than are any of the known historic lavas in the Galápagos. McBirney and Williams (1969:22) also mentioned the report from Captain David Porter, of the U.S. frigate *Essex*, of seeing a volcanic eruption on Floreana in July 1813. Neither McBirney and Williams nor any other geologists, however, have found

any lava or other ejecta suggestive of this activity. Simkin et al. (1982:98) listed this eruption as "uncertain (more likely Sierra Negra eruption)." Volcano Sierra Negra, on southern Isabela, is thought to have erupted in 1813 (Simkin et al., 1982:98), and Porter's account of the eruption (in Porter, 1822) did not state specifically that it occurred on Floreana (T. Simkin, pers. comm.). Until contrary evidence is brought forth, the volcanoes of Floreana should be regarded as extinct. Probably there has been no volcanic activity on Floreana for at least several thousand years.
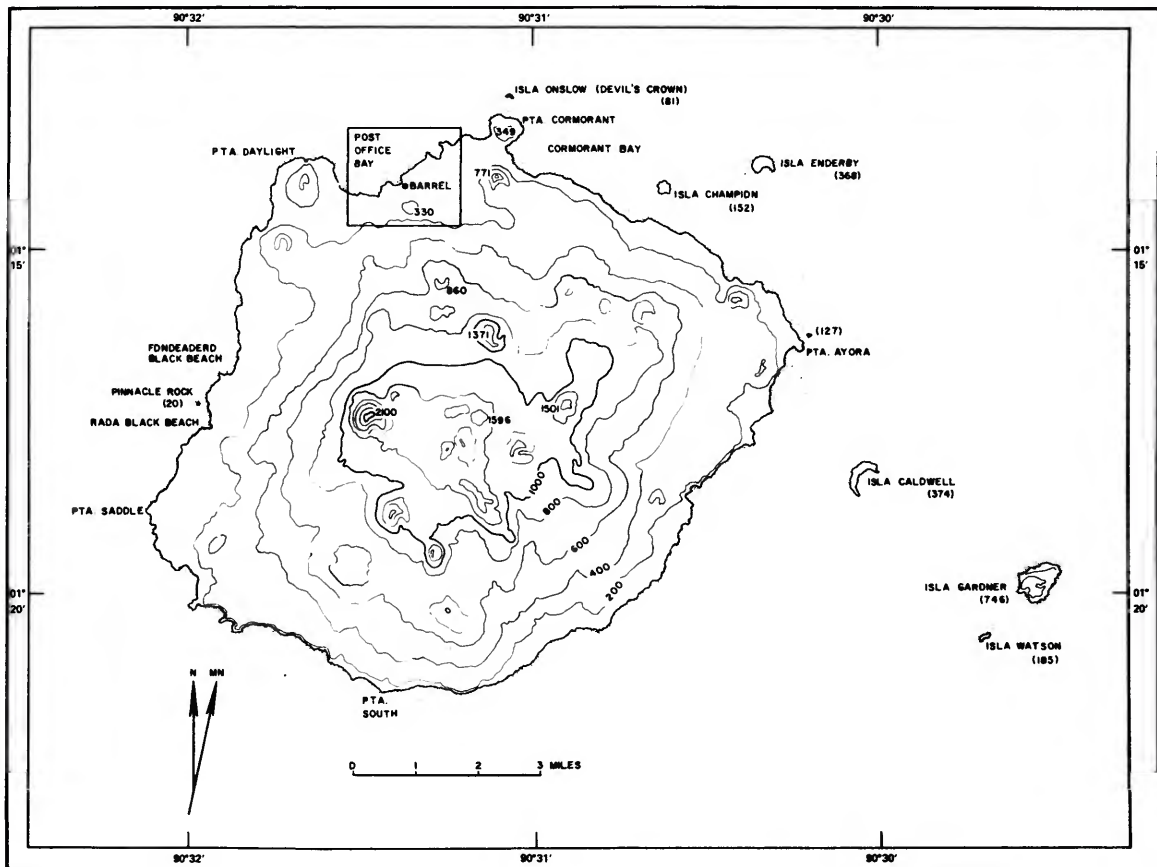
FIGURE 2.—Floreana and its satellite islands (area enclosed by box shown in greater detail in Figure 4; contour intervals in feet; modified from map prepared by CDRS).

Floreana is composed mainly of alkaline olivine basalts. Richardson (1933:61) listed the following rock types from Floreana: "basalt with olivine only phenocrysts, amygdaloidal basalt, basalt scoriae, olivine bronzite lapilli." McBirney and Aoki (1966) and McBirney and Williams (1969:26) reported that plagioclase phenocrysts are rare on Floreana, whereas porphyritic olivine is very common. I have found, however, that phenocrysts of plagioclase, pyroxene, and olivine are all common in the basalts of the Post Office Bay region. Further, Chesterman (1963) reported phenocrysts of plagioclase in a rock from Floreana (see below), and Chubb (1933:18) found "felspar" (sic) in large broken crystals near

Post Office Bay. Chemical analyses or detailed descriptions have been published for rock specimens from Floreana as follows: Richardson (1933), 4 specimens (porphyritic olivine basalts); Chesterman (1963), 2 specimens (a crystal-vitric-lithic tuff from Cormorant Bay, and a basalt with phenocrysts of plagioclase and pyroxene from near Black Beach); McBirney and Aoki (1966) and McBirney and Williams (1969:26–28, 123, 131, 132, 158), 4 specimens (a typical alkaline olivine basalt, a dunite inclusion and a peridotite inclusion from the same basalt, and a chrome-diopside from the same peridotite).

As one would expect in a young volcanic archipelago, sedimentary deposits and rocks are

uncommon in the Galápagos. Non-marine sedimentary deposits are especially rare. Alluvium occurs as small, unindurated, high-energy deposits that are, as one would expect, unfossiliferous. The very porous volcanic soil of the Galápagos promotes infiltration of rain water rather than run-off. The only thorough description of soils in the Galápagos is in Laruelle (1966), based upon an altitudinal sequence on Santa Cruz. Fine-grained lacustrine sediments are found in crater lakes on San Cristóbal, Genovesa, Santiago, Isabela, and Fernandina. These sediments are described by Colinvaux (1968, 1969), How-miller and Dahnke (1969), and Colinvaux and Schofield (1976a,b), the last authors also reporting on the fossil pollen and spores from El Junco Lake, on San Cristóbal. Bogs are found in the highlands of Santa Cruz, Isabela, Floreana, and perhaps Santiago (Colinvaux, 1968; Hamann, 1975, fig. 2).

Localized marine sedimentary rocks occur on over half of the major islands in the Galápagos. Hickman and Lipps (1985) have divided the marine deposits into 6 categories (tuff cones with marine fossils; limestone and sandstone interbedded with basalt flows; terrace deposits above sea level; beach rock; supratidal talus debris; recently uplifted tidal and subtidal rocks and sand) that correspond to those mentioned by Pitt and James (1983). At Punta Cormorant, Floreana, I have collected beach rock riddled with marine gastropods. Previous workers (Hertlein, 1972, and references therein) have regarded certain of the marine deposits in the Galápagos to be as old as Miocene or Pliocene, but Hickman and Lipps (1985) report that the ages of these deposits range from only several hundred years up to approximately 2 million years, and thus all are probably either Holocene or Pleistocene. These deposits typically are dominated by mollusks, with coelenterates and echinoids also present. Among the mollusks, gastropods usually outnumber pelecypods.

The volcanic rocks that make up most of the Galápagos have been regarded as an extremely poor environment for preservation of terrestrial

fossils. As mentioned above, there is very little alluvial sedimentation, and no exposures of fine-grained, stratified terrestrial sediment such as often contains fossil material on continents. Until recently, therefore, vertebrate paleontology in the Galápagos lagged well behind other branches of geology and biology. Research on fossil vertebrates began in the Galápagos only in the past two decades with the realization that caves (lava tubes) can be rich sources of fossils. Niethammer (1964) reported on mammalian bones from owl pellets on Santa Cruz; only the large extinct rodent "*Megalomys*" (= *Megaoryzomys*) *curioi* occurred in what might be termed a paleontological context. Ray and Whitmore (1973) expressed the great need for paleontological research in the Galápagos, and through the interest and encouragement of them and others at the Smithsonian Institution, various field biologists collected bones (mainly of *M. curioi*) from caves on Santa Cruz and Isabela in the 1960's. These fossils, and others of *M. curioi* more recently collected, have now been described by Steadman and Ray (1982).

Birds and reptiles, for which the Galápagos are so well known, remained unknown as Holocene fossils until very recently. Based on field work in 1978 and 1980, I reported fossil reptiles, birds, and mammals from Santa Cruz, Floreana, and Isabela (Steadman, 1981). I briefly discussed fossils of Darwin's finches from Santa Cruz in re-evaluating the evolution and systematics of that famous group (Steadman, 1982).

CLIMATE.—The climate of the Galápagos has been reviewed by Alpert (1963), Palmer and Pyle (1966), and Hamann (1979), but we still lack a comprehensive treatment of this subject. The Galápagos lie in the "dry zone" of the equatorial Pacific. They are not subject to the violent storms that can readily occur only several hundred miles to the north. The oceanic currents of the eastern equatorial Pacific (reviewed by Wyrtki, 1966, 1967) strongly affect climate in the Galápagos. Relatively high islands such as San Cristóbal, Floreana, Santa Cruz, and Santiago, have a climatic gradient characterized by increasing pre-

cipitation and decreasing temperature as the altitude increases. (The large, very high islands of Isabela and Fernandina do not quite fit this generalized pattern.) For Floreana, Hamann (1979) reported mean annual precipitations of 214.1 mm at the "En la Playa" station (= Black Beach; elevation 4 m; on the western coast) and 806.0 mm at the "Asilo la Paz" station (= Wittmer Farm; elevation 300 m; on the south-central part of the island). The number of years upon which these means were based was not given, nor were any temperatures. Cruz and Beach (1983) reported two years of data on rainfall and wind direction from five weather stations on Floreana. Their results are discussed below in connection with El Niño.

There are two principal seasons in the Galápagos—the rainy season lasting approximately from January through April, and the dry season that makes up the rest of the year. The distinction between these seasons is pronounced, in both the arid lowlands and moist highlands. The rainy season is a period of contrast, as the most precipitation as well as the hottest, sunniest days occur at this time. The dry season is characterized by a fog or mist known as "garua." The frequency and intensity of the garua varies from year to year. Typically, the garua is more persistent in the highlands than in the lowlands. The weather patterns of the Galápagos may be summarized as follows (based mainly on Alpert 1963, and Hamann 1979).

Rainy, Hot Season: January–April; ITCZ (Intertropical Convergence Zone) moves southward to just north of the Galápagos (usually 1°–2°N); air pressure is relatively low; relatively warm temperatures (at sea level, CDRS weather station, Santa Cruz, mean = 25.9°C, max. = 27.9°C, min. = 24.1°C; at 194 m elevation, Bella Vista weather station, Santa Cruz, mean = 24.0°C, max. = 24.8°C, min. = 22.6°C); temperature inversion weakens or dissipates; rain showers at midday, especially in higher parts of the islands; high levels of sunlight; good visibility, especially in the morning; relatively low wind velocities; dominant wind direction east or east-northeast;

low cumulus and altocumulus clouds typically present; cumulus clouds moving from easterly direction.

Dry, Cool Season: May–December; ITCZ is well north of the Galápagos (approximately 10°N); air pressure relatively high; relatively cool temperatures (at sea level, CDRS weather station, Santa Cruz, mean = 22.7°C, max. = 27.6°C, min. = 18.8°C; at 194 m elevation, Bella Vista weather station, Santa Cruz, mean = 20.6°C, max. = 24.5°C, min. = 17.8°C); low-level temperature inversion operative; often overcast with poor visibility, especially in the morning; usually good visibility in the afternoon, at least in the lowlands; fog, mist, or drizzle (garua) forms in the morning and usually dissipates before noon, but often persists in the highlands; very little measurable precipitation at lower elevations, but garua may produce measurable precipitation in the highlands; dominant wind direction southeast or east-southeast; stratocumulus and altocumulus clouds typically present; stratocumulus clouds moving from southerly or southeasterly direction.

Changes in temperature, whether seasonal or daily, are not extreme in the Galápagos. For example, on low and barren Baltra, the mean daily maximum and minimum for March (the warmest month) are 31.1°C and 23.9°C, while the same for September (the coolest month) is 26.7°C and 18.9°C (Alpert 1963). (I have converted all of the figures in Alpert (1963) and Cruz and Beach (1983) from Fahrenheit to Celsius, and from inches to millimeters.) The relative consistency in temperature is contrasted, however, by a great variability in precipitation. At Wreck Bay on coastal southwestern San Cristóbal, Alpert (1963) reported that the annual rainfall for 1950–1958 varied from 37.1 to 1424 mm (mean = 503 mm), while mean monthly rainfall varied from 4.3 mm (June) to 151.4 mm (February). Rainfall also varies greatly from year to year for any given month in the rainy season. Alpert (1963) reported 1.5 mm for February 1950, compared to 487 mm for February 1953, and 0.0 mm in April 1952 and 1954, compared

to 458 mm in April 1953. Indeed the "rainy" season in the Galápagos can be extremely arid in some years. For the weather station at Wreck Bay, mean precipitation during 1950–1958 was 417 mm in the rainy season (January through April) and only 86 mm in the dry season (the remaining 8 months).

"El Niño" refers to the sudden appearance of anomalously warm surface water in low latitude regions of the central and eastern Pacific, especially along coastal regions of Peru and southern Ecuador, westward through the Galápagos. The waters of this region are normally much cooler because of upwelling of cool sub-surface waters, as well as the influence of the cool surface waters of the northward flowing Peru current. El Niño can last from several months to nearly two years. It is not an annual event, but occurs at irregular intervals of 1–12 years (Quinn and Burt 1970). The years 1828, 1845, 1864, 1871, 1877–1878, 1891, 1904, 1918, 1925–1926, 1929, 1932, 1939–1941, 1943, 1953, 1957–1958, 1965–1966, 1972–1973, and 1982–1983 are generally regarded as years of well-developed El Niño activity (Alpert, 1963; Quinn and Burt, 1970; Ramage, 1975). The actual cause of El Niño is controversial and beyond the purposes of this paper.

El Niño normally sets in during January to March, although it can begin as early as October or as late as May (Wyrtki, 1975; Wooster and Guillen, 1974). Sea surface temperatures in the Galápagos are highest from January through March regardless of the presence or absence of El Niño, because of increased solar radiation associated with the austral summer, as well as a southward shift in December to February of the warm tropical surface water that otherwise occurs north of the Equator (Wyrtki, 1966). During times of El Niño, however, sea temperatures are extremely high. This warm water is less saline than the displaced, cooler water. Many climatological and oceanographic phenomena of the 1972–1973 El Niño, the best documented severe El Niño until that of 1982–1983, are described by Wooster and Guillen (1974) and Ramage

(1975). The extremely severe El Niño of 1982–1983 is described in detail by Cane (1983), Rasmusson and Wallace (1983), and Barber and Chavez (1983), and many other papers are appearing on this topic.

Heavy rainfall in the Galápagos and coastal Peru and Ecuador is associated with El Niño. Cruz and Beach (1983) have documented the drastic increase in precipitation on Floreana during the 1982–1983 El Niño. At Black Beach they recorded only 4 mm per month from June through November 1982, but an astonishing 316 mm per month from December 1982 through March 1983. Extremely heavy rainfall occurred on mainland Ecuador and throughout the Galápagos during the 1982–1983 El Niño, enough to form streams and pools in areas of the Galápagos that never before experienced surface water (personal observation). Marchant (1958, 1959) noted that the great majority of nesting in terrestrial birds of Ecuador's arid Santa Elena Peninsula occurred directly after periods of significant rainfall. Rates of successful avian reproduction were much lower in 1955–1956 than in the El Niño interval of 1957–1958. The same heavy rainfall that means highly successful reproduction for terrestrial birds spells disaster, however, for the marine birds of the Galápagos and coastal Peru and Ecuador. The most famous biological consequence of El Niño is a massive mortality in fish (especially anchovies), whose planktonic food resources have been altered by the lack of adequate upwelling of cool, phosphate-rich waters. This results in large-scale mortality among marine birds that feed on the fish (Murphy, 1936:101–108; Wyrtki, 1966; Boersma, 1978). During the 1982–1983 El Niño, the nesting success of land birds in the Galápagos was truly phenomenal, as was the lack of reproduction in the seabirds. Many of these events were well monitored by biologists, whose reports should be forthcoming in the next year or two.

PALEOCLIMATE.—On the basis of sediments from El Junco Lake on San Cristóbal, Colinvaux (1972) postulated that the Quaternary of the Galápagos was characterized by dry glacial inter-

vals and relatively wet interglacials. This was substantiated further by the pollen and spores from these sediments (Colinvaux and Schofield, 1976a,b). The organic sediments of the past 10,000 years in El Junco were underlain by undatable inorganic sediments that contained a lens of organic sediment dated at >48,000 years B.P. The physical and chemical nature of the inorganic sediment suggested alluvial deposition in a dessicated lake bed, rather than typical lacustrine deposition. To account for the apparently dry conditions indicated by the inorganic sediments, Colinvaux (1972) theorized that the ITCZ was north of the equator during the entire year in glacial times, and therefore was unable to produce the rains from January to March or April that characterize its annual southward movement today. The unstable, mixing air of the ITCZ is responsible for any "normal," heavy rainfall today in the Galápagos, as well as in adjacent areas to the north where the ITCZ is present for more than several months. El Niño may be only a very intense southward movement of the ITCZ, which would involve a southward displacement of the Equatorial Countercurrent and the South Equatorial Current. If this is so, then El Niño probably did not affect the Galápagos during Pleistocene glacial intervals, and Colinvaux's theory is corroborated. If El Niño has a less obligatory relationship to the ITCZ, such as in the causal theory of Wyrtki (1975), then El Niño still could have influenced the climate of the Galápagos during glacial advances.

The suggestion by Colinvaux (1972) of a more northern ITCZ in glacial times touched off several responses by researchers who did not question that the Galápagos were probably more arid during glacial intervals, but who instead proposed different mechanisms to account for this aridity. Newell (1973) was the first to challenge Colinvaux's theory, suggesting that Pleistocene aridity could be attained through the ITCZ remaining south of the equator instead of north. Newell's statement is based upon the relationship between modern seasonal, latitudinal temperature gradients, and the modern seasonal positions of the ITCZ, with the southward displacement of ITCZ increasing with increasing temperature gradients, especially those of the Northern Hemisphere. Newell (1973) used $^{18}O/^{16}O$ data from ice cores to state that latitudinal temperature gradients at 20,000 years B.P. were much higher that those of any season today, thus the southward displacement of ITCZ at 20,000 years B.P. was greater than even the largest southward seasonal displacement today. A major flaw that I see in Newell's hypothesis is that a southern movement of the ITCZ would result in wetter, not drier, conditions in the Galápagos. (For example, see the rainfall map in Palmer and Pyle, 1966.) Houvenaghel (1974) stated that the higher temperature gradient of glacial times resulted in stronger southeasterly trade winds that increased both the rate and duration of upwelling of cool water in the Galápagos. This would result in drier weather than at present, without involving a southward shift in the ITCZ. Simpson (1975) proposed a model for glacial climates in the eastern tropical Pacific, and in doing so, she discounted the models of Colinvaux, Newell, and Houvenaghel as being largely unsubstantiated and ignorant of relevant data. However, Simpson's "all-encompassing" model called upon the upwelling of cool water in the Galápagos and coastal South America, just as the model of Houvenaghel (1974). Although Simpson's methodology was somewhat different from Houvenaghel's, the two models do not seem incompatible, and each deserves testing from other workers.

VEGETATION.—The major botanical surveys of the Galápagos are those of Hooker (1847), B.L. Robinson (1902), Stewart (1911), Svenson (1935), Wiggins and Porter (1971), and Hamann (1981). My description of Floreana's diverse vegetation is based upon the last two references, supplemented by my own observations. The nature of the vegetation in the Galápagos is controlled largely by precipitation, which in turn is controlled mainly by elevation, directional exposure, and size of the island (Alpert, 1963). On the higher islands, such as San Cristóbal, Santa Cruz, Floreana, Santiago, Isabela, Fernandina,

FIGURE 3.—Arid zone vegetation on Floreana during dry season, October 1980 looking northeast toward Punta Cormorant from entrance to Cueva de Post Office (Inferior) (leafless trees are *Bursera graveolens*).

Pinzón, and Pinta, clear-cut altitudinal changes in vegetation are evident. Wiggins and Porter (1971) divide the vegetation of the Galápagos into 6 zones: littoral, arid, transition, *Scalesia, Miconia,* and fern-sedge. Excellent photographs of these vegetational zones are found in Wiggins and Porter (1971) and Hamann (1979, 1981). Floreana may have each of the 6 zones, although the status of the *Miconia* and fern-sedge zones is uncertain because of the severe alteration of the highland vegetation. Hamann (1981:20) divides the Galápagos plant communities into 9 broad categories, most of which have two or more subdivisions. They are: forest; closed scrub with scattered trees; scrub; steppe forest (woodland); steppe scrub (scrub woodland); shrub steppe sa-

vanna; desert scrub; broad leaved herb vegetation; and closed bryoid vegetation.

All of the fossil sites are in the arid lowlands, so only that type of vegetation will be described. I will stress woody plants because of their importance in the physiognomy of the vegetation. Species marked with an asterisk (*) are particularly dominant or conspicuous, at least locally. The arid zone (Figure 3) covers more area on Floreana than any other vegetational zone. It occurs from near the coast (just in from the littoral zone) upslope to elevations from approximately 80–120 m on the south-facing side of the island to 200–300 m on the north-facing side. The highest diversity of shrubs and small trees is found in the arid zone. Most of these species are deciduous,

resulting in a drastic change in the appearance of the arid zone in the rainy versus the dry season. Many of the trees and shrubs are spiny and have relatively small leaves. The trees are spaced rather evenly and far apart, giving this region an open appearance. Soil occurs only in isolated, shallow pockets; most of the surface is barren basaltic rock. Two large arborescent cacti (*Opuntia megasperma and *Jasminocereus thouarsii) occur in this zone and may be the tallest plants present. These cacti have been reduced in numbers by feral mammals. As a result, the tree *Bursera graveolens is by far the most conspicuous plant today in the arid zone of Floreana. The following other species of trees and shrubs occur in the arid zone: Acacia macracantha, A. rorudiana, Alternanthera echinocephala, Borreria dispersa, B. linearifolia, Castela galapageia, Chamaesyce nummularia, C. punctulata, C. viminea, Clerodendrum molle, Cordia leucophlyctis, *C. lutea, C. revoluta, *Croton scouleri, *Cryptocarpus pyriformis, Desmanthus virgatus, Geoffroea spinosa, Gossypium barbadense, Lantana peduncularis, Maytenus octogona, *Parkinsonia aculeata, *Prosopis juliflora, *Scalesia affinis, *S. villosa, *Scutia pauciflora, Vallesia glabra, and *Waltheria ovata.

The Fossil Sites

THE CAVES.—The four fossiliferous caves (lava tubes) are all very close to one another and can be reached on foot from the Post Office Barrel in under 20 minutes (Figures 4, 5). A tourist trail, constructed in 1980, now leads to Cueva de Post Office (Inferior). The elevations of the caves, at their entrances, range approximately from 20 to 50 m. Blockage from roof collapses made it impossible to reach the true origin or termination of the lava tubes. The flow that contains the four caves is of relatively youthful pahoehoe lava thought to be derived from a large scoria cone approximately 2 miles (3.2 km) SSE of Post Office Bay (McBirney and Williams, 1969:22, 25). This lava is of the Brunhes Normal Polarity Epoch, and thus is no older than 0.79 million years (see "Geology"). I am not aware of any potassium-argon age determinations from the Post Office Bay region to complement the paleomagnetic information. Many pressure ridges and mounds also occur in the Post Office Bay region.

Cueva de Post Office was named, mapped, and described by Montoriol-Pous and Escolá (1975). Although it is actually a single lava tube, the two entrances to this cave lead to separate passageways ("Inferior" and "Superior") that are blocked from each other by a massive roof collapse, with the southern end of "Inferior" being separated from the northern end of "Superior" by a talus cone of boulders (Montoriol-Pous and Escolá, 1975, fig. 2A). The entrances are formed by smaller roof collapses and are such that escape would be impossible for any large, non-volant animal that fell into them. Cueva de Post Office (Inferior) (Figures 6–8) runs downslope to the sea, its lower portion being inundated by salt water. Large boulders of roof spall are very common in the southern portion of Cueva de Post Office (Inferior), especially in Room 2 and in the low-roofed area separating Room 3 from Room 4. North of Room 2, most of the floor of the cave is barren basalt, free of any sediment. In Room 2 and south thereof, much of the floor is often covered by poorly sorted sediment ranging in size from clay to boulders. In Cueva de Post Office (Superior) (Figures 9, 10), thick deposits of poorly sorted clays to boulders cover the entire floor.

Finch Cave and Barn Owl Cave have not been named, mapped, or described previously. Miguel Pozo and I discovered Finch Cave (Figures 11, 12) in 1978. The entrance to Finch Cave is the highest roof collapse that I have found in the Galápagos, being a drop of 18 m to the floor of the cave. A large, bouldery talus cone of roof spall dominates the area below the entrance. The southeastern edge of the talus cone is met by a talus slope originating from roof spall concentrated in the southeastern portion of the cave (only partially mapped). As with most thick talus accumulations in caves on Floreana, these slopes have a dip of 30°–35°. The original basaltic floor
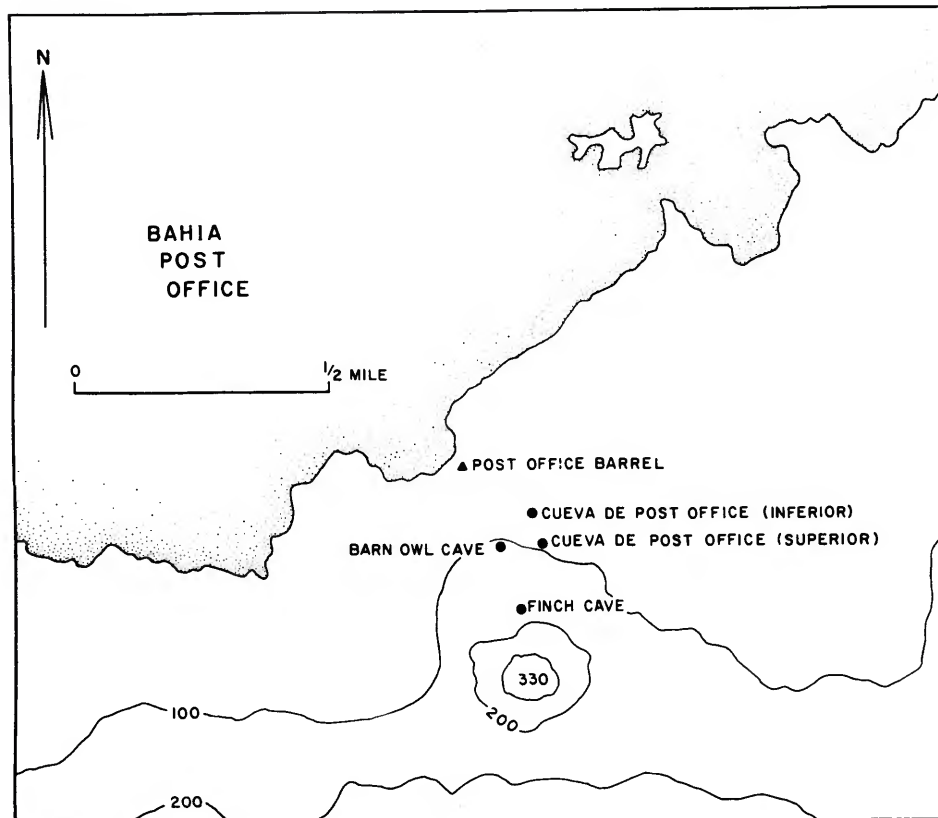
FIGURE 4.—Post Office Bay region, showing location of four fossiliferous caves (contour intervals in feet).

FIGURE 5.—Post Office Bay, looking southeast toward Floreana (all fossil caves located between beach and prominent scoria cone just behind beach).
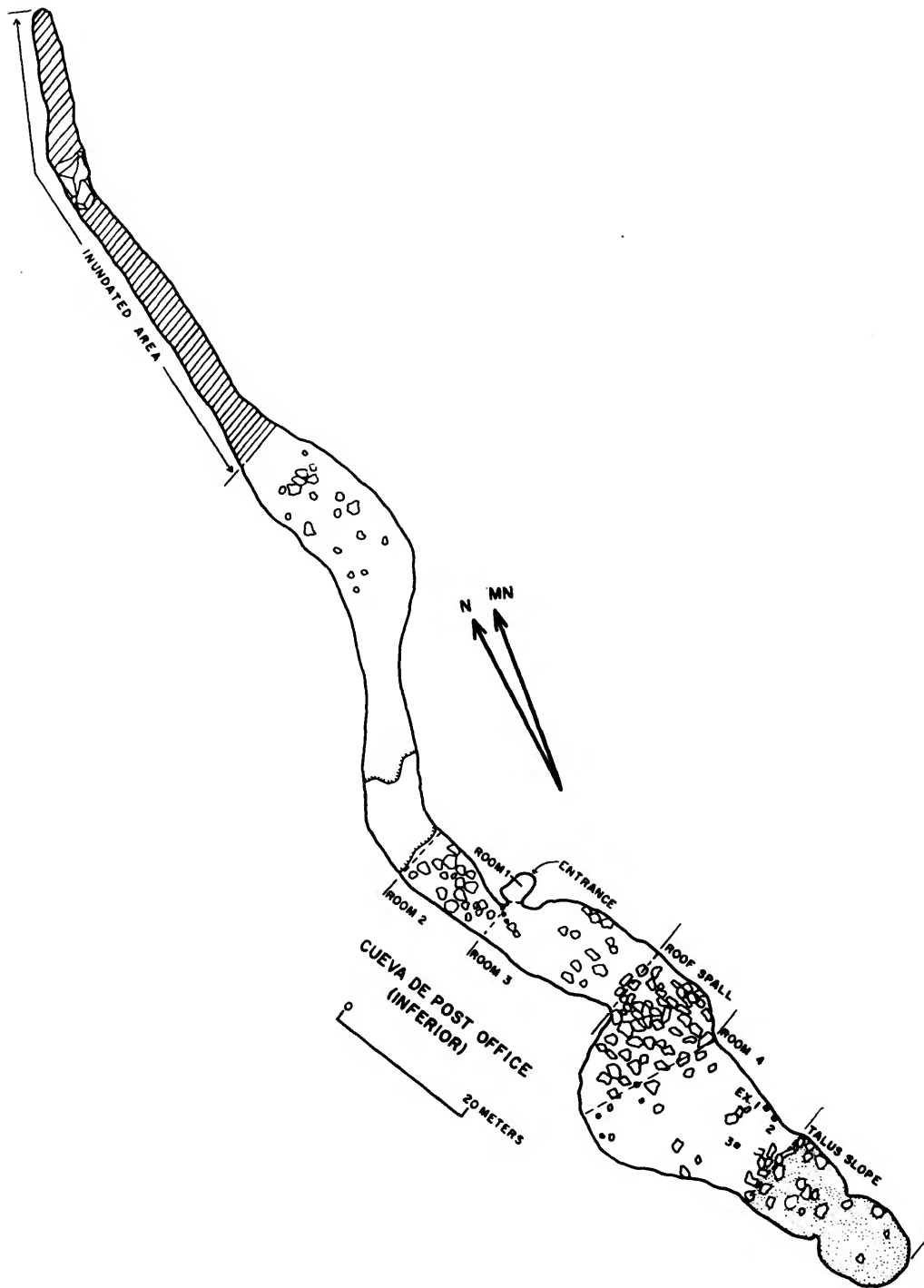
FIGURE 6.—Plan view of floor of Cueva de Post Office (Inferior) (note entrance (Figures 7, 8) and location of Excavations 1–3 in Room 4 (Figures 15–17); modified from Montoriol-Pous and Escolá, 1975).

is exposed in much of the northern two-thirds of Finch Cave. Essentially unfossiliferous, fine-grained sediments (mainly clays and silts) occur in the low-lying sections of the North Room of Finch Cave. These sediments appear to be derived from soil that periodically washed into the cave via the roof collapse, for they are darker and better sorted than the fossil-bearing sediments excavated from the other three caves.

Barn Owl Cave (Figures 13, 14) was discovered by James R. Hill on 30 October 1980. This cave is more diverse faunally than any of the other caves, but because we already had scheduled a boat to take us from Floreana on 1 November 1980, our paleontological endeavors in Barn Owl Cave were limited to two hurried days. Much of Room 1 is exposed to the surface by a huge roof collapse that did not, however, allow as easy access to the cave as the entrance in Room 2. Essentially the entire floor of Barn Owl Cave is covered by some sort of sediment, ranging from

FIGURE 7.—Looking northeast out of entrance of Cueva de Post Office (Inferior), October 1980, from Room 1 toward María José Campos above ground.

FIGURE 8.—Entrance of Cueva de Post Office (Inferior), October 1980, looking south (María José Campos and Edward N. Steadman wait to enter).
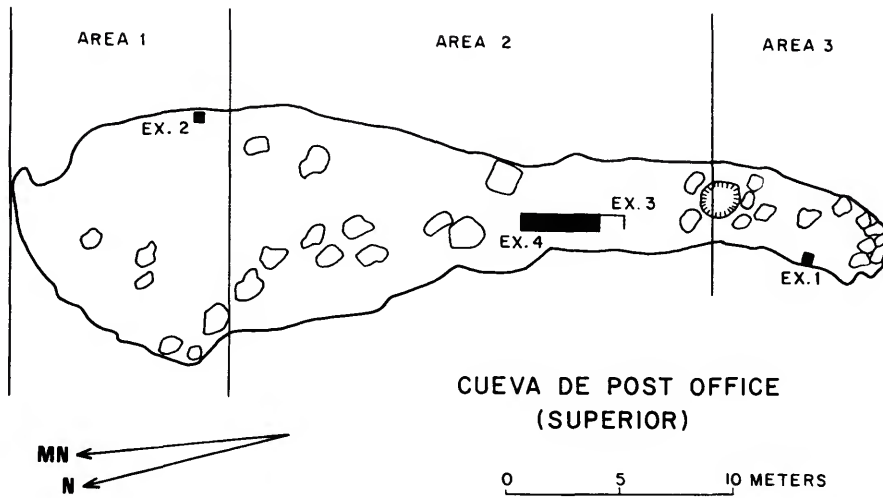
FIGURE 9.—Plan view of Cueva de Post Office (Superior) floor (note Excavations 1–4 (1 and 2 detailed in Figures 18, 19); entrance (Figure 10) straddles boundary between areas 2 and 3; modified from Montoriol-Pous and Escola, 1975).

FIGURE 10. —Entrance of Cueva de Post Office (Superior) María José Campos, October 1980; because of diagonal orientation and smaller size, entrance was ineffective as a natural trap for large tortoises.

FINCH CAVE

0 _____ 20 M.

N

NORTH
ROOM

MAIN TALUS
CONE

INNER
OPENING
OF ROOF
COLLAPSE

SOUTH TALUS SLOPE

UNMAPPED PORTION OF LAVA TUBE →
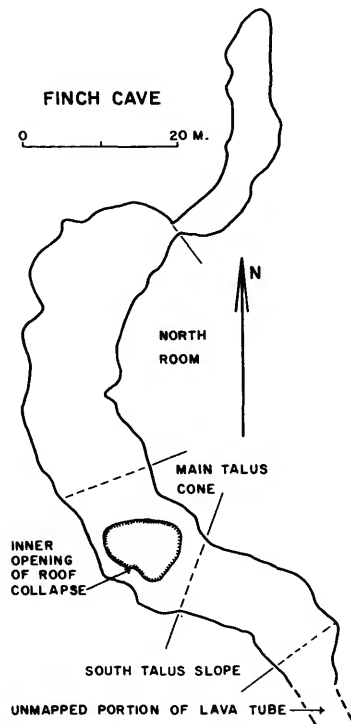
mainly boulders on the talus slopes to various fine-grained sediments in low-lying areas. For example, the talus slopes in Rooms 1–3 are composed mainly of angular basaltic pebbles and boulders up to 1.2 m in diameter, whereas much of the floor of Room 3 is covered by loose, fine sediments (clays through sands). Sediments of many particle sizes (clay through pebbles) occur near the edges of the talus slopes, such as at Excavation 1.

STRATIGRAPHY.—Near the entrance, the floor of each cave was littered with hundreds of bones, as well as pieces of wood. I dug five small test pits in the sediments of Cueva de Post Office, stratigraphic profiles of which are shown in Figures 15–19. Careful sorting of the fine fraction of the matrix yielded a fair number of small, often fragmentary, fossils. With minor excep-

FIGURE 11.—Plan view of Finch Cave floor.
FIGURE 12.—Looking into Finch Cave, October 1980 (James R. Hill stands at bottom (arrow), near edge of main talus cone).
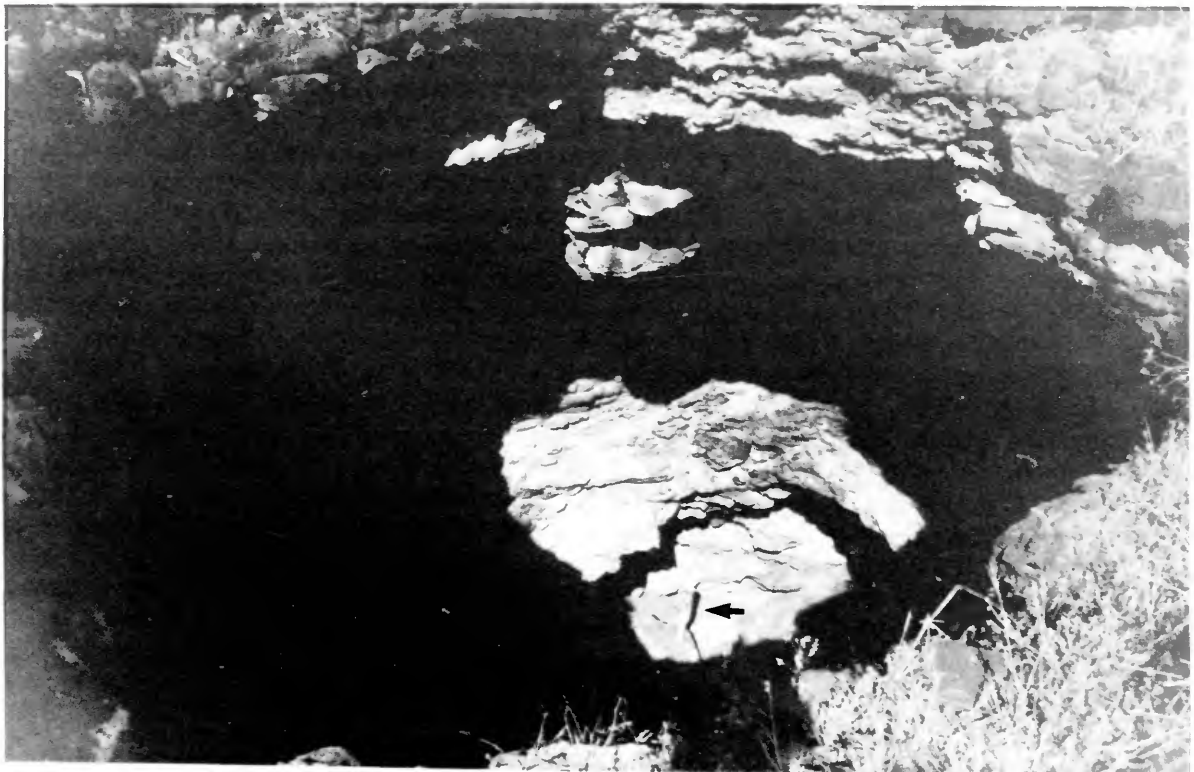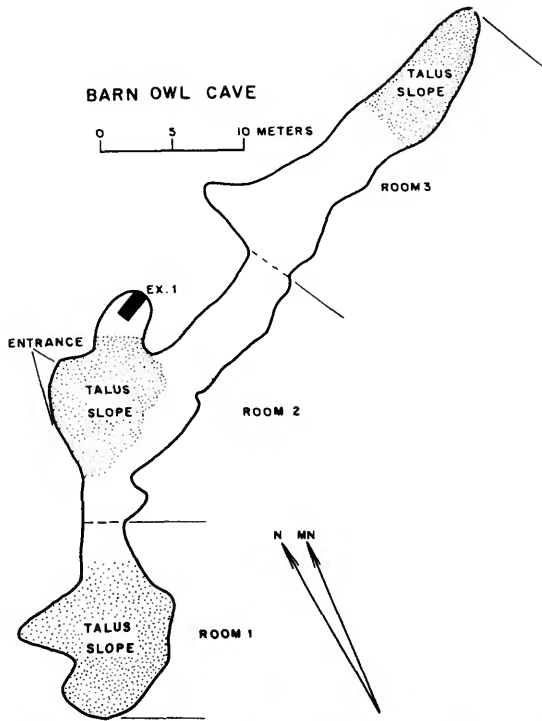
tions, the fossils within the sediments are of the same species as occur on the surface of the floor.

The sediments from the different test pits are broadly similar to each other. They are very inorganic, being derived from basalts, with some secondary minerals (gypsum, flourite, apatite, minor calcite). De Paepe (1967) and Montoriol-Pous and Escolá (1975) reported gypsum, flourite, and apatite as secondary minerals from Cueva de Post Office (Inferior). Gypsum has been reported elsewhere in the Galápagos from the salt deposits of Tagus Crater Lake, Isabela (Howmiller and Dahnke, 1969).

The occasional indistinct stratigraphic units in these poorly sorted clays to pebbles are suggestive of very brief water transport, although the lack of well-developed laminations, in combination with the angular nature of the clasts and the

FIGURE 13.—Plan view of Barn Owl Cave floor (note Excavation 1, shown in Figures 20, 21).

FIGURE 14.—Entrance of Barn Owl Cave, May 1983 (Gayle Davis and Godfrey Merlen prepare to enter).
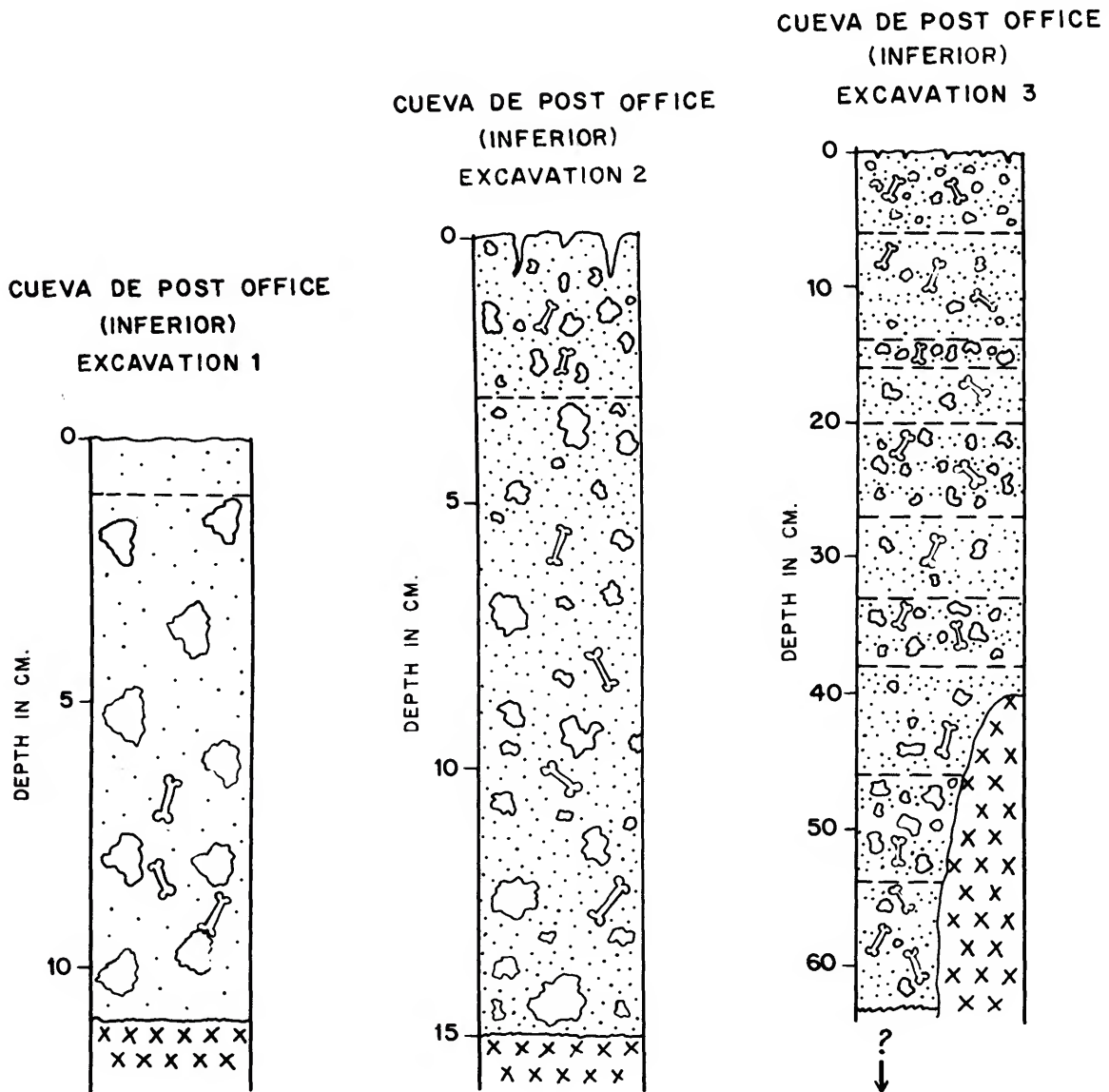
FIGURE 15.—Stratigraphic profile of Excavation 1, Cueva de Post Office (Inferior), Isla Floreana, Galápagos (description of sediment: light yellowish brown (10 YR 8/4 dry), light brown (7.5 YR 7/6 wet), unlaminated, poorly sorted; slightly silty, slightly sandy gravel; contact poorly defined (dashed line); clasts of basalt and flourite, very angular to sub-angular, averaging smaller in the top 1 cm; slight reaction with 10% HCl; no fossils in upper 6 cm; maximum observed thickness = 11 cm; lower contact basaltic bedrock).

FIGURE 16.—Stratigraphic profile of Excavation 2, Cueva de Post Office (Inferior), Isla Floreana, Galápagos (description of sediment: light yellowish brown (10 YR 6/4 dry), dark reddish brown (5 YR 3/3 wet), unlaminated, poorly sorted; pebbly, sandy, silty clay; contact poorly defined

(dashed line); clasts of basalt and gypsum, very angular to sub-angular, averaging smaller in the upper 3 cm; reaction with 10% HCl; maximum observed thickness = 15 cm; lower contact basaltic bedrock).

FIGURE 17.—Stratigraphic profile of Excavation 3, Cueva de Post Office (Inferior), Isla Floreana, Galápagos (description of sediment: yellowish brown (10 YR 5/6 to 10 YR 5/4 dry), reddish brown (5 YR 4/4 wet), poorly laminated, poorly sorted; pebbly, slightly sandy, slightly silty clay, alternating with slightly pebbly, slightly sandy, slightly silty clay; poorly defined contacts (dashed lines); basaltic clasts, angular to sub-angular; reaction with 10% HCl; maximum observed thickness = 63 cm; partial lower contact basaltic bedrock).

CUEVA DE POST OFFICE
(SUPERIOR)
EXCAVATION 1

CUEVA DE POST OFFICE
(SUPERIOR)
EXCAVATION 2
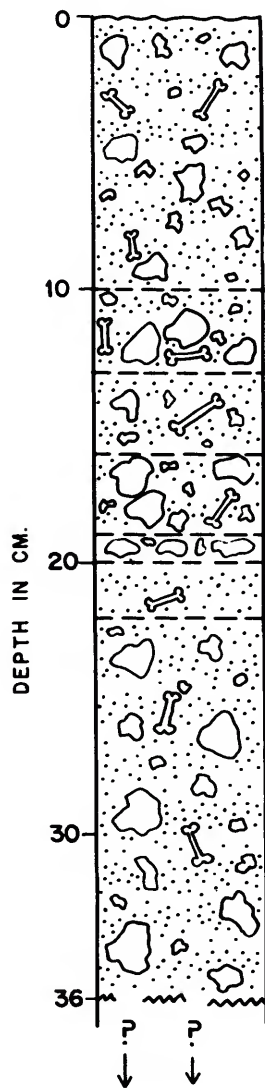
FIGURE 18.—Stratigraphic profile of Excavation 1, Cueva de Post Office (Superior), Isla Floreana, Galápagos (description of sediment: light yellowish brown (10 YR 6/4 dry) dark reddish brown (5 YR 3/4 wet), poorly laminated, poorly sorted; pebbly, sandy, silty clay alternating with sandy, silty clay; contacts poorly defined (dashed lines); clasts basaltic, very angular to sub-rounded; no reaction with 10% HCl; maximum observed thickness = 36 cm; basaltic bedrock not reached).
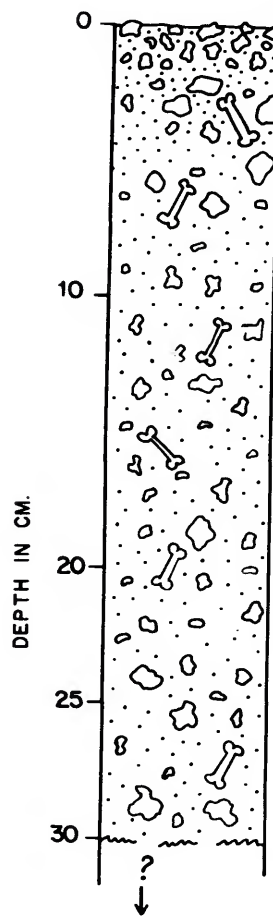
FIGURE 19.—Stratigraphic profile of Excavation 2, Cueva de Post Office (Superior), Isla Floreana, Galápagos (description of sediment: dark yellowish brown (10 YR 6/4 dry), reddish brown (5 YR 4/4 wet), unlaminated, very poorly sorted, pebbly, sandy, silty clay; no discernible stratigraphic contacts; clasts basaltic, angular to sub-rounded, more common in upper 2 cm; very slight reaction with 10% HCl; maximum observed thickness = 30 cm; basaltic bedrock not reached).

BARN OWL CAVE
EXCAVATION 1

FIGURE 20.—Stratigraphic profile of Excavation 1, Barn Owl Cave, Isla Floreana, Galápagos (description of sediment: *Unit A*: brown (7.5 YR 4/4 dry), reddish brown (5 YR 4/4 wet), moderately well laminated, poorly sorted, clayey, sandy, pebbly silt, alternating with well-laminated, poorly sorted, clayey, silty, sandy gravel; basaltic clasts very angular to sub-rounded; no reaction with 10% HCl; maximum observed thickness = 10 cm; indistinct lower contact (dashed line). *Unit B*: brown (7.5 YR 4/4 dry), reddish brown (5 YR 4/4 wet), unlaminated, moderately well sorted; silty, sandy, pebbly clay; basaltic clasts sub-angular; overall prismatic texture; strong reaction with 10% HCl; maximum observed thickness = 6 cm; sharp lower contact (solid line). *Unit C_1*: Yellowish brown (10 YR 5/6 dry), dark brown (7.5 YR 4/6 wet), unlaminated, moderately well sorted, silty, sandy clay to clayey, sandy, gravely silt; basaltic clasts, rarely up to 20 cm in diameter, sub-angular to sub-rounded; strong reaction with 10% HCl; maximum observed thickness = 22 cm; indistinct lower contact (dashed line). *Unit C_2*: light yellowish brown (10 YR 6/6 dry), dark brown (7.5 YR 4/6 wet), unlaminated, very poorly sorted, clayey, sandy, gravely silt; basaltic clasts rarely up to 20 cm in diameter, smaller clasts of flourite and calcite, very angular to sub-rounded; strong reaction with 10% HCl; maximum observed thickness = 6 cm; lower contact basaltic bedrock).)

poor sorting, suggests that these sediments were not transported very far. Probably both water and gravity sliding were involved, but only for short distances. When one considers that nearly all of the sediment in the caves is derived either from weathering products of roof spall or from loose soils washed into the cave from the surface, it appears that this sediment has seldom been transported for more than 20 m. There is no ground water in the caves, and occasional heavy rains are the only source of water. The only time that I saw sediment entering the caves was during

the torrential rains of May 1983, when at least several cm of new sediment had been washed into Barn Owl Cave, and a lesser amount into Cueva de Post Office (Inferior). The sediments in the caves of Floreana seem to be unaffected by rains of ordinary strength and duration. Instead, the fossils became incorporated into the sediments only during very rare intervals when sheetwash from exceptional rains enters the cave through the roof collapse. At least in Cueva de Post Office (especially Inferior), trampling of the sediment by tortoises and humans was also im-

FIGURE 21.—Excavation 1, Barn Owl Cave, October 1980 (test pit on left; excavation enlarged toward wall, following stratigraphic units).

portant in mixing the bones into the loose sediment.

Excavation 1 of Barn Owl Cave (Figures 20, 21) was by far the richest of any excavation on Floreana. The sediment of Excavation 1 was basically similar to that of the other caves in its poor development of lamination, rounding, and sorting. The major difference was that Excavation 1 was divisible into several distinct stratigraphic units that were highly fossiliferous. The sediments of Excavation 1 must have formed directly below a roost of *Tyto punctatissima*.

CHRONOLOGY.—There is little potential for developing a Quaternary alluvial chronology in the Galápagos because of the scarcity of alluvium. The very porous volcanic soil of the Galápagos is conducive to infiltration of rain water rather than run-off. Another shortcoming is the appar-

ent absence of cultural remains from the period before the discovery of the islands by the Spanish in the 16th century. This means that cultural chronologies based on lithics, ceramics, and associated radiocarbon dates are not possible in the Galápagos, except that the presence of any human artifacts or introduced animals is almost surely indicative of the past 400 years. Several more recent faunal datum points can be used to provide minimum ages for certain deposits. For example, historical records show that tortoises (*Geochelone elephantopus*) became extinct on Floreana around 1850. Therefore, tortoise bones in any deposit on Floreana would indicate that the deposit is at least 130 years old. Snakes (*Alsophis biserialis*), hawks (*Buteo galapagoensis*), barn owls (*Tyto punctatissima*), mockingbirds (*Mimus trifasciatus*), and two species of Darwin's finches (*Geo-*

spiza nebulosa and *G. magnirostris*) also became extinct on Floreana in the mid-1800s, although the timing of these extinctions is less well documented than that of *Geochelone*. Nevertheless, these species are also useful indicators of the minimum age of a fossil site.

Three of the six radiocarbon dates in Table 2 were first reported in Steadman (1981). The only other published radiocarbon dates from the Galápagos are associated with palynological studies of late Quaternary lacustrine sediments in El Junco Lake, San Cristóbal (Colinvaux, 1972; Colinvaux and Schofield, 1976a,b). Unfortunately, no excavations on Floreana have yielded charcoal or plant remains suitable for radiocarbon dating. Each of the dates in Table 2 is from surface material. All ages are corrected for ^{13}C as reported. The delta ^{13}C values for these samples are about as expected; those for the wood samples correspond to values characteristic of those modern woody plants that are generally C$_3$ plants (Stuiver and Polach, 1977; DeNiro and Epstein, 1978). The delta ^{13}C value for the horny scute of *Geochelone* is reasonable for an animal that eats a wide variety of plants, but dominantly cactus (a CAM plant), as well as a fair amount of tropical grasses, many of which may be C$_4$ plants (Stuiver and Polach, 1977; DeNiro and Epstein, 1978).

Potassium-argon age determinations on basalts from the walls of the lava tubes would give a maximum age for the sediments and fossils. Combined with the radiocarbon determinations on surface material, this could bracket the age of the sediments and sub-surface fossils. I have not sampled these basalts to determine their suitability for dating, but recent advances in potassium-argon dating can permit determinations as young as 30,000 years B.P. or less under favorable conditions (Gramlich et al., 1971). Future paleontological endeavors in the Galápagos or any other volcanic areas should keep this technique in mind. Another technique with promise for future studies in the Galápagos is the radiocarbon dating of land snail shells as described by Goodfriend and Hood (1983) and Goodfriend and Stipp (1983). Land snails occur commonly in most vertebrate fossil sites in the Galápagos, where the generally non-carbonate environment of the basaltic substrate should eliminate the problem of contamination of the shells by "dead" carbonate.

The radiocarbon data provide no evidence that any of the fossil sites is older than the Holocene. The presence of numerous fossils of historically extinct species on the surface means that the sub-surface fossils in each of the caves are more than approximately 130 years old. By superposition alone, the fossils in Excavation 1 of Barn Owl Cave are more than 640±50 years old, while those of Excavation 4 of Cueva de Post Office (Superior) must be older than 1030±160 years B.P. (Table 2). That organic material continued to accumulate in caves during historic times is indicated by the modern radiocarbon date on *Prosopis* and the presence of introduced mammals. With the extinction of tortoises and barn owls, however, the present rate of accumulation of vertebrates in the caves of Floreana can be no more than a trickle compared with the rate before human colonization of the island.

The main chronological shortcoming in the Floreana caves is not being able to establish both stratigraphic and chronological control for the fossils within a single deposit. The sub-surface levels consist only of bones and inorganic sediment; they lack plant material suited for radiocarbon dating. The surface of the sediments, on the other hand, contains wood or epidermal scutes of tortoises that are excellent for radiocarbon dating, but lacks the stratigraphic framework needed to relate the dated material unequivocally to the fossils or to other datable material on the surface of the same cave. This uncertainty of chronology is well demonstrated by the discordant ages of the three radiocarbon samples from the surface of Cueva de Post Office (Inferior) and the two samples from Barn Owl Cave. There simply is no way to demonstrate that a dated piece of wood is contemporaneous with the undated bones that lie next to it. Nevertheless, the chronological discrepancies here are measured only in hundreds or at most a few

TABLE 2.—Radiocarbon age determinations from Floreana (all done at the University of Arizona Radiocarbon Laboratory).

Number	Material	Locality	Age
A-2088	*Bursera graveolens* (wood; ~9gm)	Cueva de Post Office (Inferior) Room 3: surface	990± 120 yrs. B. P. delta^{13}C = −23.7% PDB
A-2089	*Prosopis juliflora* (wood; ~10gm)	Cueva de Post Office (Inferior) Room 1: surface	80±110 yrs. B. P. (modern) delta ^{13}C = −25.4% PDB
A-2090	*Geochelone elephantopus* (horny epidermal scute of carapace; ~7gm)	Cueva de Post Office (Inferior) Room 1: surface	310±80 yrs. B. P. delta ^{13}C = −13.9% PDB
A-3283	*Bursera graveolens* (wood; ~5gm)	Cueva de Post Office (Superior) Excavation 4	1030±160 yrs. B. P. delta ^{13}C = −26.01% PDB
A-2512	*Acacia* sp. (wood; ~17gm)	Barn Owl Cave Room 3: surface	2420±25 yrs. B. P. delta ^{13}C = −25.5% PDB
A-3280	cf. *Cordia* sp. (wood; ~5gm)	Barn Owl Cave Excavation 1: surface	640±50 yrs. B. P. delta ^{13}C = −26.9% PDB

thousands of years; most or all of the fossil fauna can safely be assumed to be late Holocene in age.

The Fossil Fauna

All of the fossil sites on Floreana are in lava tubes with roof collapses that permit the entry of animals for potential fossilization. Tables 3–6 list systematically the fossils from each locality within each cave, and Table 7 summarizes the fauna from all of the caves. The fossils originate mainly or entirely in two different ways—from prey items of barn owls (*Tyto punctatissima*), or from the roof collapse acting as a natural trap into which an animal falls but cannot escape.

Natural trap localities are dominated by tortoises (*Geochelone elephantopus*), especially large individuals, that fell into the roof collapses and were unable to escape from the cave. Boney accumulations resulting solely from natural traps are less rich, both in number of species and in number of individuals, than those derived from the regurgitations of barn owls. Fossils tend to be concentrated near the entrance (roof collapse) of the lava tube in either situation, but in natural traps the fossils cluster rather randomly about the entrance, thinning as one goes farther from the entrance. In former barn owl sites, the fossils usually are concentrated below ledges on the walls that served as the owls' roosts.

Townsend (1928:157, 159) made this graphic description of the tortoises that had been trapped in Cueva de Post Office (Inferior).

It would be difficult to imagine a more effective trap for tortoises than the well-like entrance to the cave from which the skeletons were taken. It must have operated automatically as a death trap for centuries. The brushy half-concealed entrance is merely a hole in the ground a dozen feet in diameter and twenty feet deep. With a steep slope at one side, the unlucky tortoise that tumbled in did not necessarily strike bottom with a fatal crash, but rather rolled down an incline it could not ascend.

TABLE 3.—Faunal summary of Cueva de Post Office (Inferior) (E = extinct; I = introduced by man; for each taxon, first number = number of specimens; number in parentheses = minimum number of individuals represented by specimens (MNI); introduced species not considered in calculation of totals and percentages).

Species	Edge of inundated zone: surface	Room 1: surface	Room 2: surface	Room 3: surface	Room 4: surface	Excavation 1
Osteichthyes, sp. indet.						
Geochelone elephantopus (E)		1096(33)	286(21)	512(16)	6(1)	
Phyllodactylus baurii						
Tropidurus grayii			2(1)		1(1)	
Alsophis biserialis (E)	637(2)	8(1)	1(1)			
Puffinus lherminieri			1(1)			141(1)
Nyctanassa violacea		2(1)				
Zenaida galapagoensis		58(7)	11(2)	31(7)	28(5)	
Mimus trifasciatus (E)		7(3)	37(3)	8(3)	6(2)	
Geospiza nebulosa (E)						
G. fuliginosa		1(1)			1(1)	
G. magnirostris (E)	37(1)	35(8)	13(2)	42(5)	5(1)	
G. olivacea						
Geospiza, sp. indet.						
Passeriformes, sp. indet.		2(0)		1(1)		
Aves, sp. indet.			22(0)			
Mus musculus (I)	1(1)					
Rattus rattus (I)	120(2)				cf.1(1)	
Equus asinus (I)		1(1)				
Mammalia, sp. indet. (I)		1(1)				
Total	674(3)	1209(54)	373(31)	594(32)	47(11)	141(1)
Percentage of total	12.4(1.2)	22.2(21.3)	6.8(12.2)	10.9(12.6)	0.9(4.3)	2.6(0.4)

TABLE 4.—Faunal summary of Cueva de Post Office (Superior) (E = extinct; I = introduced by man; for each taxon, first number = number of specimens; number in parentheses = minimum number of individuals represented by specimens (MNI); introduced species not considered in calculation of totals and percentages).

Species	Area 1: surface	Area 2: surface	Area 3: surface	Excavation 1	Excavation 2
Geochelone elephantopus (E)	3(2)	191(21)	8(3)	198(11)	17(6)
Phyllodactylus baurii		1(1)	1(1)	17(5)	2(1)
Tropidurus grayii		13(5)	18(2)	11(4)	1(1)
Alsophis biserialis (E)		2(1)		44(4)	8(4)
Zenaida galapagoensis	3(2)	22(4)	1(1)	1(1)	
Mimus trifasciatus (E)	5(2)	36(5)	30(3)	1(1)	1(1)
Geospiza fuliginosa					
G. fortis					
G. magnirostris (E)	51(4)	414(42)	4(1)	4(3)	
Geospiza, sp. indet.				2(2)	
Passeriformes, sp. indet.		13(3)		1(0)	3(2)
Aves, sp. indet.		33(0)	6(0)		
Mus musculus (I)		2(1)		3(1)	
Rattus rattus (I)		1(1)			
Total	62(10)	725(82)	68(11)	279(31)	32(15)
Percentage of total	2.2(4.1)	26.4(33.7)	2.5(3.0)	10.2(12.8)	1.2(6.2)

Excavation 2	Excavation 3	Total	Percentage of total
	1(1)	1(1)	0.0(0.4)
204(7)	1770(25)	3874(103)	71.1(40.7)
3(2)	44(16)	47(18)	0.9(7.1)
1(1)	143(20)	147(23)	2.7(9.1)
9(2)	109(11)	764(17)	14.0(6.7)
		142(2)	2.6(0.8)
		2(1)	0.0(0.4)
3(2)	31(11)	162(34)	3.0(13.4)
	8(6)	66(17)	1.2(6.7)
	cf.2(2)	2(2)	0.0(0.8)
		2(2)	0.0(0.8)
1(1)	23(8)	156(26)	2.9(10.3)
1(1)	2(2)	3(3)	0.0(1.2)
	1(1)	1(1)	0.0(0.4)
1(0)	23(2)	27(3)	0.5(1.2)
	32(0)	54(0)	1.0(0.0)
	1(1)	2(2)	
		121(3)	
		1(1)	
		1(1)	
223(16)	2189(105)	5450(253)	
4.1(6.3)	40.2(41.5)		

Excavation 3	Excavation 4	Total	Percentage of total
494(15)	345(25)	1256(83)	45.7(34.2)
11(3)		32(11)	1.2(4.5)
15(3)	8(1)	66(16)	2.4(6.6)
26(1)	1(1)	81(11)	2.9(4.5)
5(2)	5(3)	37(13)	1.3(5.3)
7(2)	4(2)	84(16)	3.0(6.6)
	1(1)	1(1)	0.0(0.4)
	1(1)	1(1)	0.0(0.4)
159(8)	372(23)	1004(81)	36.5(33.3)
		2(2)	0.1(0.8)
12(2)	13(1)	42(8)	1.5(3.3)
102(0)		141(0)	5.1(0.0)
		5(2)	
cf.1(1)		2(2)	
831(36)	750(58)	2747(243)	
30.2(14.8)	27.3(23.9)		

The rocky floor of the cave is not wide but leads into a few low passages under the lava, all strewn with dry bones of tortoises that had crept everywhere in search of an outlet. The brittle remains of the earlier victims had been crawled over repeatedly and gradually broken up by those that were entrapped subsequently from time to time.

The bleached and bony remains of those not too antiquated and fragile to be removed, had long lost their dark horny plates which lay curled and twisted beside them. In a dozen of these, both carapace and plastron were practically intact, while skulls and leg bones had usually been disturbed and scattered. A considerable amount of broken tortoise remains had long since become mixed with the soil of the cave floor. The later arrivals lay where they died, their large white carapaces showing conspicuously as our flashlights were turned in their direction.

On 16 January 1929, K.P. Schmidt, S.N. Shurcliff, and an unnamed Ecuadorean also visited Cueva de Post Office (Inferior) during the Crane Pacific Expedition of the Field Museum of Natural History. Shurcliff (1930:104) described their activities as follows.

We let ourselves down a dark narrow shaft with a long rope and came into a large underground cavern. There were no good tortoise shells in this cavern for Schmidty says that Dr. C.H. Townsend had been there ahead of us but we found another adjoining cavern which Dr. Townsend must have overlooked for therein we discovered several dozen shells of the extinct Charles Island tortoise, three in perfect condition. Schmidty is delighted to secure these shells for the museum, for this type of tortoise has been extinct for more than a hundred years.

The "adjoining cavern" described by Shurcliff is probably Room 3 or Room 4 of Cueva de Post Office (Inferior) and not Cueva de Post Office (Superior), as the latter has a completely separate entrance from the former and contained very few surface remains of large tortoises. Townsend probably obtained most or all of his tortoise specimens from Room 2 and the northern part of Room 3 in Cueva de Post Office (Inferior).

I believe that Tyto punctatissima was responsible for the deposition of nearly all non-tortoise fossils in the Floreana caves. This belief is substantiated by its occurrence in the fossil fauna of Barn Owl Cave, these fossils being the first specimens of T. punctatissima ever taken on Floreana. Except for non-hatchling tortoises, the fossil fauna of each

TABLE 5.—Faunal summary of Finch Cave (E = extinct; I = introduced by man; for each taxon, first number = number of specimens; number in parentheses = minimum number of individuals represented by specimens (MNI); introduced species not considered in calculation of totals and percentages).

Species	South talus slope: surface	Main talus cone, south slope: surface	Main talus cone, east slope: surface	Main talus cone, west slope: surface	North Room: surface	Total	Percentage of total
Geochelone elephantopus (E)	11(3)	11(2)	35(5)	9(3)	11(4)	77(17)	9.2(18.7)
Phyllodactylus baurii				2(1)		2(1)	0.2(1.1)
Tropidurus grayii	12(2)	7(3)	4(1)	21(3)	1(1)	45(10)	5.4(11.0)
Alsophis biserialis (E)		1(1)		39(1)		40(2)	4.8(2.2)
Zenaida galapagoensis	1(1)	11(2)	29(6)	26(5)	4(1)	71(15)	8.5(16.5)
Myiarchus magnirostris				1(1)		1(1)	0.1(1.1)
Mimus trifasciatus (E)			4(2)	7(2)		11(4)	1.3(4.4)
Geospiza fuliginosa	1(1)			2(1)		3(2)	0.4(2.2)
G. fortis		23(1)			1(1)	24(2)	2.9(2.2)
G. magnirostris (E)	87(5)	223(9)	66(7)	86(7)	20(3)	482(31)	57.7(34.1)
G. pauper				1(1)		1(1)	0.1(1.1)
Passeriformes, sp. indet.	1(0)		4(1)	5(0)	1(0)	11(1)	1.3(1.1)
Aves, sp. indet.			6(0)	14(0)		20(0)	2.4(0.0)
Lasiurus borealis				24(2)	23(2)	47(4)	5.6(4.4)
Rattus rattus (I)				10(2)		10(2)	
Mammalia, sp. indet. (I)			1(1)			1(1)	
Total	113(12)	276(18)	148(22)	237(27)	61(12)	835(91)	
Percentage of total	13.5(13.2)	33.0(19.8)	17.7(24.2)	28.4(29.7)	7.3(13.2)		

cave consists almost entirely of animals that are potential prey items for barn owls. Although *T. punctatissima* is extinct now on Floreana, it still occurs commonly in lava tubes on several other islands in the Galápagos, where it is responsible for rich deposits of both modern and fossil bones (Niethammer, 1964; Abs et al., 1965; Steadman, 1981; Steadman and Ray, 1982; Groot, 1983). The only other owl in the Galápagos is *Asio flammeus*, the Short-eared Owl, which is not known to roost in lava tubes. Owls, and barn owls in particular, are known elsewhere to have been important accumulators of bones in caves, occasionally resulting in fossil deposits (for example, see Davis, 1959; Trost and Hutchison, 1963; Guilday et al., 1977; Olson, 1978; Pregill, 1981, 1982; Levinson, 1982; Olson and Hilgartner, 1982).

Excavation 1 of Barn Owl Cave clearly demonstrates the importance of rich, ancient, barn owl roosts in determining the past fauna of an island. This site yielded many more fossils than the excavations in any of the other caves (Tables 3, 4, 6, 7), and also provided the first unequivocal evidence that *T. punctatissima* once occurred on Floreana. The barn owls that deposited the bones of Excavation 1 sampled the local fauna very thoroughly; except the seabird *Puffinus lherminieri*, each native taxon that was recovered as a fossil from Floreana occurred in this deposit. In addition to *T. punctatissima*, the following taxa of birds were found in Barn Owl Cave but not in the other nearby caves: *Pterodroma phaeopygia*, *Oceanodroma castro*, *Pyrocephalus nanus*, *Geospiza crassirostris*, *Geospiza scandens*, and *Geospiza parvula*. Of these, only *Pterodroma phaeopygia* may not have been brought into the cave by *T. punctatissima*.

Table 8 depicts the past feeding habits of *T. punctatissima* on Floreana, considering only native animals that are small enough to be prey items. Note the large difference in relative abun-

dance of reptiles and birds in surface versus sub-surface levels. Reptiles make up only 19.4% of the MNI recovered from surface collections, but they represent 57.0% of the MNI from excavations. The same values for birds are 79.0% and 42.0%, respectively. These values are remarkably similar to each other for all four of the surface collections. Those of the excavations from Cueva de Post Office (Inferior) and Barn Owl Cave resemble each other closely, but differ significantly from those of Cueva de Post Office (Superior). This difference is due to the method of collection used in Excavation 4 of Cueva de Post Office (Superior), explained at the end of this section. Bats are a minor component (less than 2%) in either case. Tortoises average much larger in size in the surface collections than from sub-surface levels. Therefore, a lower percentage of tortoises from the surface were potential prey items of *T. punctatissima*. I have allowed for this difference by including only a small percentage of their MNI in calculating Table 8 (see caption). Even if one were to omit tortoises from consideration altogether, the remaining reptiles (= lizards and snakes) are still relatively much more common in the sub-surface levels (Table 7). Much or all of this difference probably is due to a collecting bias, because persons making the surface collections had a better sight image for skulls, rostra, and mandibles of *Geospiza magnirostris* than for any of the bones of lizards and snakes. Further, these elements of *G. magnirostris*, as well as many of the post-cranial elements of *Zenaida galapagoensis*, are larger and more conspicuous than most bones of lizards or snakes. For these reasons I believe that the excavations are more truly representative of the actual relative abundances of nearly all the species in the fossil fauna. This idea is discussed further below. A testimony to the importance of one's sight image is shown by the fact that experienced field scientists such as Charles Haskins Townsend and Karl Patterson Schmidt could collect numerous tortoise bones from Cueva de Post Office (Inferior) while overlooking entirely the abundant bones of many smaller species.

Barn owls prefer to eat rodents when they are available. Rodents and other small mammals usually make up over 90% of the diet in species of *Tyto* on continents, as seen in innumerable studies, such as Wallace (1948) and Trost and Hutchison (1963) in North America, Vernon (1972) in Africa, De Bruijn (1979) in Europe, Morton and Martin (1979) in Australia, and Herrera and Jaksic (1980), Jaksic and Yanez (1980), and Jaksic et al. (1982) in South America, Europe, and North America. Birds and reptiles seldom comprise more than a few percent of the prey items of *Tyto*, although Otteni et al. (1972) found that the frequency of mammals in pellets of *T. alba* in southern Texas varied year to year from 65.5% to 98.9%, while the frequency of birds varied from 1.1% to 34.3%. Davis (1959), Vernon (1972), and Ruprecht (1979) also reported individual cases of birds making up more than 10% of the prey items of continental barn owls.

The food habits of *T. punctatissima* in the Galápagos are better known than for most insular barn owls. Salvin (1876:494) and Gifford (1919:194) reported grasshoppers in the stomachs of barn owls collected on Santa Cruz and perhaps other islands. Snodgrass and Heller (1904:266) reported rats (*Mus* = *Rattus*) as the main food of barn owls on Isabela. Niethammer (1964) reported only the mammals in pellets of *T. punctatissima* and *Asio flammeus* from the Cascajo Mountain region of Santa Cruz, although he did not distinguish which of these two owls was responsible for which pellets, if indeed he knew. The mammalian prey items were as follows: 2 bats (1 *Lasiurus borealis*, 1 *Lasiurus cinereus*) and 382 rodents (145 *Rattus rattus*, 230 *Mus musculus*, 1 *Megaoryzomys curioi*, 5 *Nesoryzomys indefessus*, 1 *N. darwini*). Abs et al. (1965, including the authors' subsequent manuscript corrections in reprints) reported on pellets of *T. punctatissima* from two localities on Santa Cruz (3 km from Academy Bay, and Cascajo Mountain). Most of these pellets appear to be the same as those reported by Niethammer (1964). Abs et al. (1965) recorded from these pellets 119 *Rattus rattus*, 224 *Mus musculus*, 1 *Megaoryzomys curioi*,

TABLE 6.—Faunal summary of Barn Owl Cave (E = extinct; 1 = introduced by man; for each taxon, first number = number of specimens; number in parentheses = minimum number of individuals represented by specimens (MN1); introduced species not considered in calculation of totals and percentages).

Species	Room 1: surface	Room 2, floor: surface	Room 2, talus slope: surface	Room 3: surface	Excavation 1: surface
Osteichthyes, sp. indet.					
Geochelone elephantopus (E)	319(20)	61(7)	558(10)	23(5)	15(2)
Phyllodactylus baurii	2(2)	2(1)			
Tropidurus grayii	102(16)	14(2)	5(2)	6(2)	4(1)
Alsophis biserialis (E)	144(3)		1(1)	2(1)	1(1)
Pterodroma phaeopygia					
Oceanodroma castro					
Nyctanassa violacea	1(1)				
Ardeidae, sp. indet.					
Non-passerine Aves, sp. indet.					
Zenaida galapagoensis	129(9)	29(4)	26(5)	32(5)	9(2)
Tyto punctatissima (E)	2(1)			1(1)	
Pyrocephalus nanus					
Myiarchus magnirostris	1(1)				
Mimus trifasciatus (E)	65(8)	11(2)	23(4)	11(3)	3(1)
Geospiza nebulosa (E)	1(1)	1(1)			
G. fuliginosa	5(4)	1(1)		1(1)	
G. fortis	3(2)		2(1)	1(1)	1(1)
G. magnirostris (E)	186(16)	149(12)	276(26)	69(7)	75(7)
G. crassirostris	2(1)		1(1)	1(1)	
G. scandens			1(1)	1(1)	
G. parvula					
G. pauper		1(1)			
G. olivacea	1(1)				
Geospiza, sp. indet.	2(0)			1(0)	
Passeriformes, sp. indet.	64(0)	14(0)	17(1)	9(0)	8(3)
Aves, sp. indet.	19(0)	11(0)	11(0)		9(0)
Lasiurus borealis	2(1)	2(1)			
Mus musculus (1)	1(1)	2(2)			
Rattus rattus (1)	2(1)	cf.3(2)			cf.1(1)
Felis domesticus (1)	1(1)				
Sus scrofa (1)	16(1)				
Total	1050(87)	296(32)	921(52)	158(28)	125(18)
Percentage of total	9.4(16.7)	2.7(6.2)	8.3(10.0)	1.4(5.4)	1.1(3.5)

6 Oryzomys species (= Nesoryzomys indefessus and/ or N. darwini), 1 Lasiurus borealis, 1 Lasiurus cinereus, 2 Zenaida galapagoensis, 1 Myiarchus magnirostris, 2 Mimus parvulus, 8 Dendroica petechia, 4 Geospiza fuliginosa, 4 G. fortis, 1 G. scandens, 3 G. pallida, 12 G. olivacea, and 1 undetermined bird. Thus birds made up 9.7% of the prey remains listed by Abs et al. (1965). Harris (1974:121; 1982:121) summarized the food of T. punctatissima as "mainly rats and mice, some small birds. Eats more crickets, grasshoppers and scorpions than the Short-eared Owl." The very rich fossil site at Cueva de Kubler, Santa Cruz, is derived from prey remains of T. punctatissima (Steadman, 1981). This fossil fauna is dominated by native rodents, but also includes many species

Excavation 1: test pit	Excavation 1: Unit A	Excavation 1: Unit B	Excavation 1: Unit C_1	Excavation 1: Unit C_2	Total	Percentage of total
	2(1)				2(1)	0.0(0.2)
102(6)	175(3)	40(4)	49(1)	1(1)	1343(59)	12.1(11.3)
114(18)	242(39)	79(10)	73(8)		512(78)	4.6(15.0)
559(17)	778(17)	1372(16)	1428(20)	5(2)	4273(95)	38.5(18.3)
254(5)	446(9)	90(2)	109(3)	13(1)	1060(26)	9.5(5.0)
1(1)					1(1)	0.0(0.2)
			1(1)		1(1)	0.0(0.2)
					1(1)	0.0(0.2)
			cf.1(1)		1(1)	0.0(0.2)
			29(0)	560(1)	589(1)	5.3(0.2)
64(11)	60(5)	12(4)	34(4)	7(1)	402(50)	3.5(9.6)
	2(1)	3(1)	2(1)		10(5)	0.1(1.0)
			1(1)		1(1)	0.0(0.2)
	3(1)		12(4)	1(1)	17(7)	0.2(1.3)
31(10)	17(2)	68(5)	56(3)		285(38)	2.6(7.3)
1(1)	2(1)				5(4)	0.0(0.8)
4(3)	5(3)		2(1)		18(13)	0.2(2.5)
1(1)		1(1)	1(1)	3(1)	13(9)	0.1(1.7)
66(7)	86(6)	46(3)	52(5)	22(2)	1027(91)	9.2(17.5)
			cf.1(1)		5(4)	0.0(0.8)
					2(2)	0.0(0.4)
	1(1)				1(1)	0.0(0.2)
	1(1)				2(2)	0.0(0.4)
1(1)	1(1)		1(1)		4(4)	0.0(0.8)
4(0)	6(0)	6(1)	11(2)	5(3)	35(6)	0.3(1.2)
75(8)	51(0)		173(0)	14(0)	425(12)	3.8(2.3)
239(0)	256(0)	230(0)	263(0)	28(0)	1066(0)	9.6(0.0)
1(1)	2(1)	1(1)	2(1)	2(1)	12(7)	0.1(1.3)
32(5)					35(8)	
cf.1(1)	cf.1(1)				8(6)	
					1(1)	
					16(1)	
1517(90)	2136(92)	1948(48)	2301(59)	661(14)	11113(520)	
13.7(17.3)	19.2(17.7)	17.5(9.2)	20.7(11.3)	6.0(2.7)		

of birds and reptiles. On islands such as Floreana that lacked rodents, however, *T. punctatissima* was obliged to eat small reptiles, birds, and insects, at least until *Rattus* and *Mus* were introduced. Using "weight %" and not "% individuals," Groot (1983) reported that barn owls on Santa Cruz ate 12.03% insects, 0.01% spiders, 3.42% birds, and 84.54% mammals, the last category represented almost entirely by introduced *Rattus* and *Mus*. Unfortunately, the species-level identifications of birds in Groot (1983) are not reliable, based upon my own examination of the specimens involved.

Few studies have been made of the modern feeding habits of barn owls on islands outside of the Galápagos. The West Indian species of *Tyto*

TABLE 7.—Faunal summary of all localities (E = extinct; I = introduced by man; for each taxon, first number = number of specimens; number in parentheses = minimum number of individuals represented by by specimens (MNI); introduced species not considered in calculation of totals and percentages).

Species	Cueva de Post Office (Inferior)		Cueva de Post Office (Superior)		Finch Cave Surface	Barn Owl Surface
	Surface	Excavations	Surface	Excavations		
Osteichthyes, sp. indet.		1(1)				
Geochelone elephantopus (E)	1900(71)	1974(32)	202(26)	1054(57)	77(17)	976(44)
Phyllodactylus baurii		47(18)	2(2)	30(9)	2(1)	4(3)
Tropidurus grayii	3(2)	144(21)	31(7)	35(9)	45(10)	131(23)
Alsophis biserialis (E)	646(4)	118(13)	2(1)	79(10)	40(2)	148(6)
Pterodroma phaeopygia						
Puffinus lherminieri	1(1)	141(1)				
Oceanodroma castro						
Nyctanassa violacea	2(1)					1(1)
Ardeidae, sp. indet.						
Non-passerine Aves, sp. indet.						
Zenaida galapagoensis	128(21)	34(13)	26(7)	11(6)	71(15)	225(25)
Tyto punctatissima (E)						3(2)
Pyrocephalus nanus						
Myiarchus magnirostris					1(1)	1(1)
Mimus trifasciatus (E)	58(11)	8(6)	71(10)	13(6)	11(4)	113(18)
Geospiza nebulosa (E)		2(2)				2(2)
G. fuliginosa	2(2)			1(1)	3(2)	7(6)
G. fortis				1(1)	24(2)	7(5)
G. magnirostris (E)	132(17)	24(9)	469(47)	535(34)	482(31)	755(68)
G. crassirostris						4(3)
G. scandens						2(2)
G. parvula						
G. pauper					1(1)	1(1)
G. olivacea		3(3)				1(1)
Geospiza, sp. indet.		1(1)		2(2)		3(0)
Passeriformes, sp. indet.	3(1)	24(2)	13(3)	29(5)	11(1)	112(4)
Aves, sp. indet.	22(0)	32(0)	39(0)	102(0)	20(0)	50(0)
Lasiurus borealis					47(4)	4(2)
Mus musculus (I)	1(1)	1(1)	2(1)	3(1)		3(3)
Rattus rattus (I)	121(3)		1(1)	1(1)	10(2)	6(4)
Felis domesticus (I)						1(1)
Sus scrofa (I)						16(1)
Equus asinus (I)	1(1)					
Mammalia, sp. indet. (I)	1(1)				1(1)	
Total	2897(131)	2553(122)	855(103)	1892(140)	835(91)	2550(217)
Percentage of total	14.4(11.8)	12.7(11.0)	4.2(9.3)	9.4(12.6)	4.1(8.2)	12.6(19.6)

also eat a higher percentage of birds and reptiles than their continental counterparts. Wetmore and Swales (1931:234–236) reported a variety of small birds, lizards, and bats in pellets of *T. glaucops* from Hispaniola. Elsewhere in the West Indies, Buden (1974) and Johnston (1974; 1975:299) reported a fair diversity of birds, lizards, and bats in pellets of *T. alba* from the Bahamas and Grand Cayman, respectively. In each of these Antillean samples, the percentage

Barn Owl Excavation	Total			Percentage of total		Percentage of grand total	Rank in abundance (based on MNI)
	Surface	Excavations	Grand total	Surface	Excavations		
2(1)		3(2)	3(2)	0.0(0.0)	0.0(0.4)	0.0(0.2)	19
367(15)	3155(158)	3395(104)	6550(262)	44.3(29.2)	26.1(18.4)	32.5(23.7)	1
508(75)	8(6)	585(102)	593(108)	0.1(1.1)	4.5(18.0)	2.9(9.8)	5
4142(72)	210(42)	4321(102)	4531(144)	2.9(7.7)	33.2(18.0)	22.5(13.0)	3
912(20)	836(13)	1109(43)	1945(56)	11.7(2.4)	8.5(7.6)	9.6(5.0)	7
1(1)		1(1)	1(1)	0.0(0.0)	0.0(0.2)	0.0(0.1)	20
	1(1)	141(1)	142(2)	0.0(0.2)	1.1(0.2)	0.7(0.2)	19
1(1)		1(1)	1(1)	0.0(0.0)	0.0(0.2)	0.0(0.1)	20
	3(2)		3(2)	0.0(0.4)	0.0(0.0)	0.0(0.2)	19
1(1)		1(1)	1(1)	0.0(0.0)	0.0(0.2)	0.0(0.1)	20
589(1)		589(1)	589(1)	0.0(0.0)	4.5(0.2)	2.9(0.1)	20
177(25)	450(68)	222(44)	672(112)	6.2(12.5)	1.7(7.8)	3.3(10.1)	4
7(3)	3(2)	7(3)	10(5)	0.0(0.4)	0.0(0.5)	0.0(0.4)	16
1(1)		1(1)	1(1)	0.0(0.0)	0.0(0.2)	0.0(0.1)	20
16(6)	2(2)	16(6)	18(8)	0.0(0.4)	0.1(1.1)	0.1(0.7)	13
172(20)	253(43)	193(32)	446(75)	3.5(7.9)	1.5(5.7)	2.2(6.8)	6
3(2)	2(2)	5(4)	7(6)	0.0(0.4)	0.0(0.7)	0.0(0.5)	15
11(7)	12(10)	12(8)	24(18)	0.2(1.8)	0.1(1.4)	0.1(1.6)	9
6(4)	31(7)	7(5)	38(12)	0.4(1.3)	0.0(0.9)	0.2(1.1)	10
272(23)	1838(163)	831(66)	2669(229)	25.8(30.1)	6.4(11.7)	13.2(20.7)	2
1(1)	4(3)	1(1)	5(4)	0.0(0.6)	0.0(0.2)	0.0(0.4)	17
	2(2)		2(2)	0.0(0.4)	0.0(0.0)	0.0(0.2)	19
1(1)		1(1)	1(1)	0.0(0.0)	0.0(0.2)	0.0(0.1)	20
1(1)	2(2)	1(1)	3(3)	0.0(0.4)	0.0(0.2)	0.0(0.3)	18
3(3)	1(1)	6(6)	7(7)	0.0(0.2)	0.0(0.1)	0.0(0.6)	14
32(6)	3(0)	35(9)	38(9)	0.0(0.0)	0.3(1.6)	0.2(0.8)	12
313(8)	139(9)	366(15)	505(24)	2.0(1.7)	2.8(2.6)	2.5(2.2)	8
1016(0)	131(0)	1150(0)	1281(0)	1.8(0)	8.8(0.0)	6.4(0.0)	–
8(5)	51(6)	8(5)	59(11)	0.7(1.1)	0.1(0.9)	0.3(1.0)	11
32(5)	6(5)	36(7)	42(12)				–
3(2)	138(10)	3(3)	142(13)				–
	1(1)		1(1)				–
	16(1)		16(1)				–
	1(1)		1(1)				–
	2(2)		2(2)				–
8563(303)	7137(542)	13008(565)	20145(1107)				
42.5(27.4)	35.4(49.0)	64.6(51.0)					

of reptiles and birds was lower than in the Floreana fossil sites because of a dominance of man-introduced rodents (*Rattus, Mus*). The relative scarcity of *Rattus* and *Mus* in the deposits from Floreana suggests that *T. punctatissima* became extinct there very shortly after the introduction of these rodents, for *T. punctatissima* preys heavily on *Rattus* and *Mus* elsewhere in the Galápagos (Niethammer, 1964; Abs et al., 1965; Groot, 1983; personal observation). Had barn owls be-

TABLE 8.—Percentages of MNI of native vertebrates in fossil sites on Floreana, derived from data in Table 7, to attempt to determine past food habits of *Tyto punctatissima*. For *Geochelone elephantopus*, the numbers in this table include only 10% of the MNI from surface deposits, and only 25% of the MNI from excavations. For birds, the numbers in this table do not include *Pterodroma phaeopygia*, *Nyctanassa violacea*, "Ardeidae, species indeterminate," "Non-passerine Aves, species indeterminate," and *Tyto punctatissima*, because these taxa are unlikely to be food items of *T. punctatissima*. See text for additional explanation.

Location	Reptiles	Birds	Bats
Cueva de Post Office (Inferior)			
Surface	19.7	80.3	–
Excavation	61.8	38.1	–
Cueva de Post Office (Superior)			
Surface	16.2	83.8	–
Excavation	43.3	56.7	–
Finch Cave			
Surface	19.7	75.0	5.3
Barn Owl Cave			
Surface	20.7	78.2	1.1
Excavation	60.0	38.2	1.8
Total			
Surface	19.4	79.0	1.5
Excavation	57.0	42.0	1.0

come extinct on Floreana in this century, for example, one would expect to find more remains of *Rattus* and *Mus* in the caves.

Volcanic activity is one last remote possibility for accumulation of fossils in the lava tubes. Mearns (1903) found 16 species of passerine birds dead in caves in Yellowstone National Park, Wyoming, which he attributed to poisonous gas and heat associated with geothermal activity. Similarly, the heat and gas of volcanic eruptions could kill animals in the Galápagos, perhaps especially birds that entered the lava tubes to escape the danger on the surface, only to die when conditions became deadly in the cave as well.

Excavations 3 and 4 of Cueva de Post Office (Superior) represent an attempt to test the importance of screening cave sediments. These excavations were adjacent to each other in a gravely

talus slope that lacked any natural stratigraphic units (Figure 9). The sediment of Excavation 3 was screened outside of the cave in standard fashion, whereas that of Excavation 4 was not screened, but was very meticulously hand-picked in situ for several hours by slowly churning the top 0.2 m of sediment, and collecting any bones that appeared. By digging to a depth of 0.3 m in Excavation 3, we determined that essentially all of the fossils in this talus slope occurred in the uppermost 0.1 m of sediment. Because both Excavations 3 and 4 were deeper than 0.1 m, all of the fossils contained in their sediments were potentially obtainable during our operations. Excavation 3 had an area (in m) of 1.2 × 0.6, or 0.72 m^2, while Excavation 4 had an area of 3.5 × 0.7, or 2.45 m^2. Thus their effective volumes of fossiliferous sediment were 0.072 m^3 and 0.245 m^3, respectively. Therefore, Excavation 4 would be expected to yield approximately 3 times as many fossils as Excavation 3, if both methods of collection were equally efficient in recovering available fossils. Table 4 shows that this was not the case; the screened sediments of Excavation 3 yielded more specimens than the larger volume of unscreened sediments from Excavation 4. Furthermore, all common taxa except *Geospiza magnirostris* were underrepresented in Excavation 4, both in numbers of specimens and in MNI. The bones of *Geospiza magnirostris*, and to a lesser extent, the immature *Geochelone elephantopus*, were relatively conspicuous and easily collected by hand (no large individuals of tortoises were present in these excavations). The small reptiles (snakes and lizards) were very much underrepresented, with a total of 52 specimens (7 MNI) in Excavation 3 versus only 9 specimens (2 MNI) in Excavation 4. Extremely small bones, such as those of *Phyllodactylus baurii*, are collected only very rarely without the use of screens. Therefore, the relative abundances of animals from the surface collections are not truly representative of the entire fossil fauna. Compared to hand-collecting, screening also yields more fossils per MNI, and more unidentifiable fragmentary specimens.

Systematic Paleontology

Mollusks, insects, and vertebrates were recovered from the Floreana caves. Each group will be discussed separately.

Phylum MOLLUSCA

Class GASTROPODA

A detailed account of the land snails from the Floreana caves has been prepared (Chambers and Steadman, in press), from which the following is abstracted. *Helicina* cf. *nesiotica* was found only in Excavation 1 of Barn Owl Cave. *Naesiotus galapaganus* was by far the most abundant species in all of the sites, but this species has been collected alive only very rarely.

Mollusks from the Floreana Caves

Order ARCHAEOGASTROPODA
  Family HELICINIDAE
    Helicina cf. *nesiotica* Dall
Order STYLOMMATOPHORA
  Family PUPILLIDAE
    Gastroprocta clausa (Reibisch)
  Family BULIMULIDAE
    Naesiotus galapaganus (Pfieffer)

Phylum ARTHROPODA
Class INSECTA

Insects are represented by at least 143 individuals of some 21 species. Scott E. Miller, of the Museum of Comparative Zoology, Harvard University, has coordinated the study of these insects. His report, which I have edited, follows.

Although most of the insect specimens have been identified at least to genus, only limited conclusions can be drawn for the following reasons.

1. Modern insects of Floreana (and the Galápagos in general) are poorly known. Although the insect fauna was listed by Linsley and Usinger (1966) and Linsley (1977), many species are poorly known and not recognizable from literature alone, and many taxa have not been sampled adequately.

2. While most of the insects that were identified are endemic to the Galápagos Islands, most are widespread within the Galápagos, and not enough is known of their modern ecology to comment on the fossils. Most species are present in a small modern collection made on Floreana in 1970 by R.S. Silberglied (now in the Museum of Comparative Zoology).

3. Most of the specimens are from surface layers. The few specimens from sub-surface layers are generally poorly preserved.

The dominant group of insects here, as in most Quaternary deposits, is the Order Coleoptera (beetles). The Family Carabidae (ground beetles) is most abundant, especially *Calosoma granatense*, a species widespread within, but confined to, the Galápagos (Basilewsky, 1968). Other beetles represented are Bostrichidae (wood borers), Tenebrionidae (darkling ground beetles), and Curculionidae (weevils).

Oothecae (egg-cases) that are apparently from the cockroach *Periplaneta americana* occur in several deposits, as do leg fragments probably from the same species. This cosmopolitan cockroach is generally thought to have originated in Africa (Roth, 1982), in spite of Durden's (1978) suggestion that it may have originated in Central America. As indicated by specimens in shipwrecks, *P. americana* was being spread by man in the New World at least as early as the sixteenth century (Durden, 1978; Roth, 1982). Man probably brought *P. americana* to the Galápagos as well, since it occurs only in surface layers of Floreana caves (and also in fossil sites on Isla Santa Cruz; Miller, unpublished data). A few fragments of this cockroach are found in sub-surface layers of test pits, but these specimens are probably the result of contamination. In Cueva de Post Office (Superior), a specimen of Evaniidae (an ensign wasp) occurs along with the oothecae of *Periplaneta*, some of which show parasitic holes. Evaniids, which are parasitic on cockroach oothecae, have not been reported previously from the Galápagos.

Insects from the Floreana Caves

Order ORTHOPTERA
  Family BLATTIDAE (cockroaches)
    Periplaneta sp., near *P. americana* (Linnaeus)—cosmopolitan
  Family unknown (not Blattidae)
    species unknown (mandible and miscellaneous parts)
Order HEMIPTERA
  Family CYDNIDAE (burrower bugs)
    Dallasiellus murinus (Van Duzee)—Galápagos and Ecuador
Order COLEOPTERA
  Family CARABIDAE (ground beetles)
    Calosoma granatense Gehin—Galápagos
    Pterostichus [=*Feronia* of Van Dyke 1953] sp., maybe *P. waterhousei* (Van Dyke)—Galápagos
    species unknown (not same as above species?)
  Family BOSTRICHIDAE (wood borers)
    Amphicercus galapaganus Lesne—Galápagos
  Family TENEBRIONIDAE (darkling ground beetles)
    Ammophorus sp. A, probably *A. cooksoni* C. Waterhouse—Galápagos
    Ammophorus sp. B
    Ammophorus sp. C
    Stomion sp., probably *S. galapagoense* C. Waterhouse—Galápagos
    two unknown species (not same as above species)
  Family CURCULIONIDAE (weevils)
    Gerstaeckeria galapagoensis Van Dyke
    Pantomorus sp., probably *P. caroli* Van Dyke
Order DIPTERA
  Family CALLIPHORIDAE (blow flies)
    unidentified species (probably this family)
Order HYMENOPTERA
  Family EVANIIDAE (ensign wasps)
    Evania sp.
  Family FORMICIDAE (ants)
    Camponotus sp.
    Odontomachus bauri (Emery)—Neotropical
    Solenopsis geminata (Fabricius)—Neotropical and southern Nearctic

Phylum VERTEBRATA

Class OSTEICHTHYES

Order through species indeterminate

(Unknown Bony Fish)

MATERIAL.—3 specimens, representing at least 2 individuals (Tables 3, 6, 7). CPOI: USNM 338446 (vertebra). BOC: USNM 338115 (2 vertebrae).

These three small, undiagnostic vertebrae are from one or more species of bony fish. *Tyto punctatissima* is not known to eat fish, so these remains probably entered the caves as undigested food of another bird. Of the species recorded as fossils from the caves, *Pterodroma phaeopygia*, *Puffinus lherminieri*, *Oceanodroma castro*, and *Nyctanassa violacea* eat fish, and perhaps *Mimus trifasciatus* once scavenged fish from the nearby shores of Floreana.

Class REPTILIA

Order CHELONIA

Family TESTUDINIDAE

Geochelone elephantopus (Harlan)

(Galápagos Tortoise)

MATERIAL.—6550 specimens, representing at least 262 individuals (Tables 3–7). All skeletal elements, as well as eggshell fragments, are represented. CPOI: USNM 284647, 284648, 284671, 284673, 284682–284695, 330570, 330577, 330581, 330583, 330586, 330589, 330594, 330595, 330599, 338247, 338253, 338259, 338264, 338264, 338268, 338275, 338279, 338286, 338291, 338294, 338298, 338464–338475. CPOS: USNM 284473, 284477, 284500, 284595, 284641, 284645, 338193, 338207, 338211, 338212, 338218, 338219, 338222, 338223, 338228, 338231–338233, 338238, 338239, 338244, 338245, 338441. FC: USNM 331472, 331502, 331557, 331561, 331564, 331579, 331582. BOC: USNM 331186, 331187, 331213, 331214, 331281, 331285, 331313, 331352, 331414, 331431, 331441, 331608, 331610, 338118, 338152, 338166, 338171, 338476.

Geochelone elephantopus is the most common fossil taxon, yet tortoises have been extinct on Floreana since approximately 1850 (see "Extinction"), resulting in a paucity of well-documented specimens from this island. I regard all Galápagos tortoises as conspecific under the name *elephantopus*, based on *Testudo elephantopus* Harlan

1827. This treatment is supported by the very high levels of genetic similarity in all extant forms of Galápagos tortoises, based on starch gel electrophoresis (Marlow and Patton, 1981) and their relatively uniform cranial morphometry (Crumly, 1984). Gunther (1877b) and Van Denburgh (1914:244–259) wrote detailed summaries of the troubled history of nomenclature and systematics of tortoises throughout the Galápagos, and much of my account of the Floreana tortoise is extracted from these sources. Harlan (1827) stated no specific island locality for the holotype (an immature animal) of *T. elephantopus,* but Van Denburgh (1914:245–249) reasoned that it probably was from Floreana. If so, the Floreana tortoise would be known as *Geochelone elephantopus elephantopus. Testudo ephippium* Gunther 1875, was based on a specimen of unknown locality or date of collection, but was regarded by Gunther (1875) to be from Floreana because it resembled a description of the Floreana tortoise by Porter (1822). Gunther (1877b:11, 62, 82) later regarded *T. ephippium* to be from Santa Cruz as well as Floreana, but Baur (1889) believed that it was from Pinta. Finally, Gunther (1896) and Van Denburgh (1914:252) believed that *T. ephippium* was from Pinzón.

The first adequate descriptions of the Floreana tortoise were those of Gunther (1902:185–192, pls. 16–21) and Van Denburgh (1914:317, pls. 55, 56), but all specimens involved were only probably, but not certainly, from Floreana. *Testudo galapagoensis* Baur 1889, is the first name based on a specimen regarded by the describer as being certainly from Floreana. The holotype of *T. galapagoensis* is a skeleton taken on Floreana in 1833 by Commodore John Downes of the U.S. frigate *Potomac,* and presented to the Boston Society of Natural History. Under the name *T. galapagoensis,* Gunther (1902) described and compared this and two other specimens supposedly from Floreana. One of the two "other" specimens, taken by a whaling ship in the 1830's, may actually be from Floreana, whereas the other was purchased on Floreana in 1871 by A. Agassiz, and thus probably was transported by local residents to Floreana from another island. Van Denburgh (1914:255, 256, 316, 317) regarded *T. galapagoensis* as a synonym of *T. elephantopus,* whereas Broom (1929) disagreed, stating that *T. elephantopus* was not from Floreana. If Harlan's holotype is not actually from Floreana, the Floreana tortoise would be known as *Geochelone elephantopus galapagoensis,* a treatment followed by Pritchard (1967:168). However, only leg bones remain of Harlan's holotype according to Van Denburgh (1914:247), while Rothschild (1902) reported the specimen to be lost. To summarize, the history of nomenclature of Galápagos tortoises, particularly that of Floreana, is confused by the uncertain collection localities for various type specimens. This nomenclatorial mess may never be untangled satisfactorily. The Floreana tortoise may be best regarded merely as *Geochelone elephantopus,* conspecific with all other tortoises in the Galápagos.

The morphology of the Floreana tortoise has not been thoroughly documented, and this fact is largely responsible for the problems of nomenclature just discussed. The first specimens of tortoises unquestionably from Floreana were skeletons (including essentially complete carapaces, plastrons, and skulls) from Cueva de Post Office (Inferior) reported and figured by Townsend (1928), and described by Broom (1929). These authors did not name the cave from which the tortoise bones were collected, but the description of the region, the cave itself, and the tortoise bones (Townsend, 1928; see quote in "The Fossil Fauna"), leave little doubt that this cave was the one named Cueva de Post Office (Inferior) by Montoriol-Pous and Escolá (1975), who also reported the presence of tortoise bones. The Crane Expedition of 1929 (Shurcliff, 1930:104) and the Hancock Expedition of 1933 (Banning, 1933:4, 5) also found bones of tortoises near Post Office Bay, probably in the same cave. Strauch (1936:84) mentioned that Dr. Friedrich Ritter entered a cave that contained tortoise bones, near Post Office Bay, in 1930. Again, this cave was probably Cueva de Post Office (Inferior), the most easily accessible of the fossiliferous caves on Floreana.

I do not know how many tortoise bones were removed by these and other unknown parties before my own visits to Cueva de Post Office (Inferior), but the number probably was considerable. There is no evidence that bones of species other than tortoises were removed by any of these explorers. I have stored in the CDRS museum additional tortoise bones from this cave that could not be transported to NMNH because of space limitations. Because of these specimens and those removed in the 1920's and 1930's (and perhaps thereafter), the MNI's and overall relative abundances of *Geochelone* in Tables 3 and 7 are too low by an unknown quantity. Most or all of the tortoises taken from Cueva de Post Office (Inferior) prior to our visits in 1978 and 1980 were large individuals, so their removal has little or no effect on the calculated past feeding habits of *Tyto punctatissima* (Table 8). No intact carapaces or plastrons remained when we first visited the cave in 1978, whereas the fossils in the three other caves sampled seem to have been undisturbed prior to our collections. As mentioned previously, it seems remarkable that none of the 20th century explorers ever reported (or noticed?) that the floor of Cueva de Post Office (Inferior) was strewn with hundreds of bones of animals other than tortoises.

Most of the tortoises that I collected from the caves had been trapped after falling through a roof collapse. Cueva de Post Office (Inferior) was an especially effective natural trap for large tortoises (Figures 7, 8, 22), many of which survived the fall through the roof collapse and wandered to the far corners of the cave before succumbing. The other three caves contained a much higher percentage of immature individuals. A complete distribution of size classes is represented by the tortoise fossils from all of the caves, ranging from hatchlings up to adults that weighed perhaps 150 kg or more. This distribution suggests that the caves were sampling a healthy population of tortoises. In Barn Owl Cave and probably in other caves as well, many of the smallest tortoises may represent prey items of *Tyto punctatissima*, which apparently can prey upon tortoises aged several

FIGURE 22.—Fossils of *Geochelone elephantopus* on floor of Room 2, Cueva de Post Office (Inferior), October 1980 (recently constructed tourist trail allowed easy access to cave, resulting in extensive damage to tortoise bones).

months or younger. I am not aware of any report of *T. punctatissima* preying upon small tortoises today, but there are no published studies of the food habits of barn owls in areas where tortoises reproduce at natural levels. That barn owls would have fed regularly on very young tortoises seems reasonable, however, especially on a rodent-free island such as Floreana. On Santa Cruz, for example, very small tortoises occur in the clearly *Tyto*-derived fossil site at Cueva de Kubler. This cave would have been ineffective as a natural trap, and thus most of the tiny tortoises there probably were prey items of *T. punctatissima*.

Order SQUAMATA

Suborder SAURIA

Family GEKKONIDAE

Phyllodactylus baurii Garman

(Gecko)

MATERIAL.—593 specimens, representing at least 108 individuals (Tables 3–7). Most major skeletal elements are represented. CPOI: USNM 284674, 330592, 330596, 338248, 338255, 338261, 338266, 338270, 338277, 338281, 338296, 338300, 338457. CPOS: USNM 284472, 284593, 338206, 338215, 338226, 338235, 338243, 338439. FC: USNM 331473. BOC: USNM 331280, 331432, 331438, 331606, 331612, 338109, 338119, 338154, 338168, 338173, 338433, 338434.

Osteological distinctions, if they exist, never have been reported for the various species of *Phyllodactylus* that occur in the Galápagos. The fossils from Floreana agree with a skeletal specimen of *Phyllodactylus* from the Galápagos, and I refer them to the species *baurii* simply because it is the only species of *Phyllodactylus* recorded on Floreana. I follow the species-level systematics of Van Denburgh (1912b), who used the name *P. baurii* for the geckos of Floreana, Gardner-near-Floreana, Champion, Enderby, Española, and Gardner-near-Española. Based upon allozyme electrophoresis, Wright (1983) has reported that *Phyllodactylus* from Floreana is most similar to those populations from Santiago, Bartolomé, and Marchena, and to be least similar to those from San Cristóbal, Santa Fé, and Fernandina. The systematic conclusions to be drawn from these findings are unclear.

Geckos were first reported from Floreana by Gunther (1877a) as *P. galapagensis* Peters, based upon specimen(s) taken in June 1875, by Commander W.E. Cookson of HMS *Peterel*. Garman (1892) regarded the geckos of Floreana, Española, and Gardner-near-Española as distinct from those of other islands, and named them as a new species, *P. baurii*, based upon a specimen collected by George Baur at Las Cuevas, Floreana, in 1891. Heller (1903) and Van Denburgh (1912b) provided descriptions and measurements of *P. baurii* and other geckos of the Galápagos. I use Garman's original spelling of the specific epithet *baurii*, although most authors since Garman (1892) have dropped the penultimate "i."

Unlike the other terrestrial reptiles of Floreana, *Phyllodactylus* has been reported to be common, even near inhabited areas such as Black Beach (Heller, 1903; Slevin, 1931). J.R. Slevin's field notes of 1905–1906 on *Phyllodactylus* (in Van Denburgh, 1912b, and Fritts and Fritts, 1982) reported these geckos to be plentiful in the lowlands under loose lava blocks, bark, and dried wood. For example, Slevin collected 125 geckos on Floreana on 11 October 1905, and 69 geckos on 23 May 1906. He also encountered eggs of geckos frequently, thus indicating apparently healthy rates of reproduction. I do not know the status of *Phyllodactylus* on Floreana today, never having looked for it. It may still be doing well, for its inconspicuous habits would make predation difficult for introduced predators such as rats, cats, and dogs.

I believe that most or all of the geckos recovered from the four caves represent prey items of *Tyto punctatissima*. Both *Phyllodactylus* and *Tyto* are active nocturnally. Like all geckos, *Phyllodactylus* is so sure-footed that it is unlikely to fall accidentally into a roof collapse and become trapped in a cave. *Phyllodactylus* is a prey item of *Tyto* on Santa Cruz as well, in both a modern and fossil context. In northern coastal Peru, Thomas and Thomas (1977) also reported remains of *Phyllodactylus* from a modern bone deposit attributed to owls, possibly to *Tyto alba*.

Had not the sediments from the caves on Floreana been sifted through a fine-mesh ($\frac{1}{16}$ inch) screen, the relative abundance of *Phyllodactylus* would have been grossly misjudged in the fossil faunas. The tiny bones of *Phyllodactylus* are never retained in coarse-mesh ($\frac{1}{4}$ inch) screens.

Family IGUANIDAE

Tropidurus grayii (Bell)

(Lava Lizard)

MATERIAL.—4531 specimens, representing at least 144 individuals (Tables 3–7). All skeletal elements are represented. CPO1: USNM 284675, 330578, 330596, 338254, 338260, 338265, 338269, 338276, 338280, 338287, 338292, 338295, 338299, 338447. CPOS: USNM 284478, 284498, 284592, 338192, 338208, 338214, 338227, 338234, 338240, 338440. FC: USNM 331474, 331503, 331504, 331560, 331563, 331580, 338326, 338436. BOC: USNM 331184, 331193, 331194, 331209, 331216, 331279, 331286, 331312, 331353, 331416, 331433, 331439, 331605, 331611, 338120, 338153, 338167, 338172.

These fossils compare favorably with a skeletal specimen of *Tropidurus* from the Galápagos. There are no known osteological distinctions among the various species of *Tropidurus* in the Galápagos, except perhaps for size. My referal of the fossil material to the species *grayii* is based purely upon geography, as *T. grayii* is the only species of *Tropidurus* known from Floreana. Bell (1843:24) originally described *T. grayii* as *Leiocephalus grayii*, from "numerous specimens" collected on Floreana and San Cristóbal by Charles Darwin in September 1835. It is not known how many of the specimens came from Floreana, or how many there were altogether. A synonymy of generic names applied to *T. grayii* is listed in Baur (1892). I follow the species-level systematics of Van Denburgh and Slevin (1913), who restricted *T. grayii* to Floreana and its satelite islets of Gardner-near-Floreana, Champion, and Enderby. In addition, I observed two males and one female of *T. grayii* on Isla Caldwell on 26 December 1980. Surprisingly, Wright (1983) found the *Tropidurus* from Floreana to be most similar to those from far-away Pinta, and least similar to those from Marchena and San Cristóbal, based on allozyme electrophoresis. These findings were not interpreted in a strict systematic manner.

On most islands in the Galápagos, *Tropidurus* thrives in the face of natural predation by hawks (*Buteo*), owls (*Tyto, Asio*), mockingbirds (*Mimus*), and snakes (*Alsophis*). There is no reason to doubt that the same was once true on Floreana. However, *Tropidurus* on Floreana apparently has suffered greatly from predation by feral mammals, especially rats, cats, and dogs. Baur (1895:70) reported *Tropidurus* as "exceedingly rare" on Floreana in 1891. Heller (1903) blamed this rarity on predation by domestic animals, especially cats. The Webster-Harris Expedition found no *Tropidurus* on Floreana during a week in 1897 (Rothschild and Hartert, 1899:99, 100). In May 1899, Heller found no *Tropidurus* during three days of collecting in the western and central parts of Floreana. Van Denburgh and Slevin (1913) regarded *Tropidurus* as almost extinct on Floreana, based upon the California Academy of Sciences Expedition taking only 16 specimens of this lizard during 28 days on this island in 1905–1906. This compares to their capture of 15 specimens in only two hours on Gardner-near-Floreana, 16 on Champion in 1½ hours, and 31 on Enderby in one hour. Slevin (1931:40, 1935:20; and in Fritts and Fritts, 1982:17, 18) stated that cats have nearly exterminated *Tropidurus* on Floreana, with the last population occurring in low numbers near the northeastern coast. My own field work on Floreana has been mostly on the northern coast near Post Office Bay, Punta Cormorant, and Bahia de las Cuevas. *Tropidurus* is extremely rare in the first two regions. It is not excessively rare at Bahia de las Cuevas (i.e., a few of them can be found with little difficulty), but still is much less common here than in comparable dry lowlands elsewhere in the Galápagos.

The small body size of *Tropidurus* on Floreana is as striking as its rarity. To assess whether or not this small body size may also be an artifact of the unnatural conditions that exist now on Floreana, I visited Isla Champion, a tiny islet 0.7 km north of Floreana, with pristine native vegetation and no introduced mammals. On 26 October 1980 and 24 May 1983, I was very impressed by how much larger (especially males) and more

abundant *Tropidurus grayii* is on Champion than on nearby Floreana. My conservative field estimates of snout-vent length of *T. grayii* on Champion range from 100 to 120 mm for males, and 90 to 110 mm for females, compared to 50 to 60 mm for individuals of either sex on Floreana. Some published snout-vent lengths for *T. grayii* from Floreana are as follows: Boulenger (1891), 59–65 mm for Darwin's five specimens (four males, one female); and Van Denburgh and Slevin (1913:165), 65 mm for an adult male taken in 1905–1906. The status of *Tropidurus* on Champion versus Floreana is paralleled by that reported by P.R. Grant (1975) on Hermanos III, a small island off the southeast coast of Isabela. He found the *Tropidurus* on Hermanos III to be much larger than those from Isabela. Likewise, P.R. Grant (1975) reported that Dagmar Werner found the *Tropidurus* on the small island of Elizabeth to be larger than those from the adjacent islands of Fernandina and Isabela. Certain lizards in the West Indies show similar trends of size and survival. Baskin and Williams (1966) reported that the teiid lizard *Ameiva polops* of St. Croix was exterminated by the introduced mongoose (*Herpestes auropunctatus*), but survived on two small islets near St. Croix that were mongoose-free. Likewise, we observed only one medium-sized individual of *Ameiva griswoldi* during four weeks on mongoose-ridden Antigua in 1980 and 1983, but found very large individuals of *A. griswoldi* to be common on the nearby small islet of Great Bird Island (Steadman et al., 1984).

The fossil material of *Tropidurus* includes many individuals that are larger than any modern specimens from Floreana, and are approximately the size of modern individuals from Champion. Again, similar situations have been reported from the West Indies. Among Puerto Rican lizards, Pregill (1981) found a larger size in late Quaternary fossils of the iguanids *Anolis cuvieri* and *A. occultus* and the anguid *Diploglossus pleei* than in any modern specimens. In the Bahamas, late Quaternary fossils of *Anolis sagrei* are also larger than modern specimens (Pregill, 1982).

The larger size of fossil *Tropidurus*, along with the examples of large individuals surviving on small, nearby, predator-free islets, suggests that the small size of today's *Tropidurus* on Floreana is the result of excessive predation by introduced cats, dogs, and rats.

Among the diagnostic characters reported for *Tropidurus* on Floreana are its small size (especially in males), its low amount of sexual dimorphism in color and mid-dorsal crest development, and its reversed sexual dimorphism in size, with males slightly smaller than females (Van Denburgh and Slevin, 1913; Carpenter, 1966, 1970). I believe that these characters do not represent the natural condition in *T. baurii*. The small size arises because individuals are never given the chance to reach full size. In any organism with indeterminate growth, a sharp increase in rate of predation will reduce mean body size of the population, particularly in a lizard such as *Tropidurus* that becomes more conspicuous to predators as its size increases. The average size of *Ameiva polops* in St. Croix decreased this century from 6–7 inches to 4–5 inches as their population was being reduced by mongoose predation (Baskin and Williams, 1966). The reduced levels of sexual dimorphism in size, color, and mid-dorsal crest development in *T. grayii* of Floreana can also be explained by the artificially high rate of predation they now experience, which does not allow males to attain fully any of the normal adult male characteristics. The differences in display movements between males and females of *Tropidurus* in the Galápagos (described by Carpenter, 1966) may make males somewhat more conspicuous than females. This would result in males being preyed upon at an earlier average age and thus accentuate the artificially low levels of sexual dimorphism. That there may be an abnormal sex ratio in *Tropidurus* on Floreana is suggested by the collection of 14 females versus only 1 male by the California Academy of Sciences Expedition in 1905–1906.

In conclusion, I would suggest that size can be used as taxonomic character for insular reptiles only with great caution. Inter-island comparisons

of size in closely related reptilian taxa should consider historical information on predation, such as the introduction of alien predators or the extinction of natural predators.

Suborder SERPENTES

Family COLUBRIDAE

Alsophis biserialis (Gunther)

(Floreana Snake)

MATERIAL.—1945 specimens, representing at least 56 individuals (Tables 3–7). All skeletal elements are represented. CPOI: USNM 284649, 284676, 330574, 330575, 330591, 330593, 330597, 338249, 338256, 338262, 338267, 338271, 338278, 338282, 338288, 338301, 338450, 338458, 338460. CPOS: USNM 284479, 284499, 284594, 338213, 338220, 338221, 338225, 338229, 338236, 338241, 338242, 338438. FC: USNM 331475, 338327. BOC: USNM 331185, 331192, 331210, 331217, 331434, 331440, 331607, 331613, 338121, 338169, 338174, 338431, 338432.

These fossils compare favorably with a skeletal specimen of *Alsophis* from the Galápagos. No osteological descriptions exist for the snakes of Galápagos; I assume that the fossils are conspecific with *A. biserialis*, the only snake known from Floreana. The snakes of the Galápagos are xenodontine colubrids, a complex assemblage of neotropical snakes in which generic level systematics is very unsettled (John E. Cadle, pers. comm.). Traditionally, snakes of the Galápagos are placed in the genus *Dromicus*, but I follow Maglio (1970) in placing them in *Alsophis*, a genus that otherwise occurs on mainland South America and in the West Indies. For species-level systematics, I follow Van Denburgh (1912a), in realization that a paucity of specimens leaves this question unsettled. Until the description of *A. biserialis eibili* from San Cristóbal (Mertens, 1960), *A. biserialis* was known only from Floreana, Gardner-near-Floreana, and Champion. Thus the snake of Floreana and its satellites is

now known as *A. biserialis biserialis*.

Snakes are apparently extinct on Floreana (see "Extinction"). The only snake ever collected from life on Floreana was a young specimen taken by Charles Darwin in September 1835, which Gunther (1860) described as *Herpetodryas biserialis*. Dr. A. Habel secured a snake in 1868 that supposedly came from Floreana, but Van Denburgh (1912a) stated that this specimen came from either Santa Cruz or Rábida. Heller (1903) mentioned, without any details, that the *Hassler* Expedition of 1872 took a snake on Floreana. However, Steindachner (1876:305) reported that the *Hassler* Expedition found (but did not collect) only 1 snake in all of the Galápagos, this being on Rábida. The only other specimen of *A. b. biserialis* is an adult female collected on Gardner-near-Floreana on 3 October 1905, by the California Academy of Sciences Expedition (Van Denburgh, 1912a; Slevin, 1931). Snakes are found commonly today, but not collected, on Champion and Gardner-near-Floreana (De Ridder, 1976; B. Voigt, 1977a,b; P.R. Grant, 1980; B.R. Grant, 1981).

Snakes seem unlikely to fall into natural traps with any frequency. Instead I believe that most of the snakes recovered from the caves of Floreana were prey items of *Tyto punctatissima*. Judging from their occurrence as fossils in Cueva de Kubler, Santa Cruz, snakes were eaten regularly but in rather low numbers by *T. punctatissima*. Floreana lacks native rodents, so barn owls may have eaten snakes there more frequently than on Santa Cruz, although confirmation of this suggestion awaits completion of the study of the fossil fauna from Cueva de Kubler. The small size of *T. punctatissima* would make a fully adult snake difficult to procure. Therefore, snakes in the Galápagos fossil deposits may not include the largest individuals in the population.

Class AVES

The standard references for the distribution and/or systematics of birds within the Galápagos are Salvin (1876), Ridgway (1897), Rothschild and Hartert (1899, 1902), Snodgrass and Heller

(1904), Gifford (1913), Loomis (1918), Swarth (1931), and Harris (1973, 1974, 1982). Herein I will follow my own systematic judgements, which often agree with those of one or more of the authors cited above. I have used trinomials only when subspecies can be distinguished osteologically.

Order PROCELLARIIFORMES

Family PROCELLARIIDAE

Pterodroma phaeopygia (Salvin)

(Dark-rumped Petrel)

MATERIAL.—1 specimen, representing 1 individual (Tables 6, 7). BOC: USNM 331599 (alar phalanx).

Pterodroma phaeopygia is larger than any other procellariid that occurs regularly in the Galápagos. This petrel may be too large to be a regular prey item of *Tyto punctatissima*, although Groot (1983) reported it from barn owl pellets on Santa Cruz. *Pterodroma phaeopygia* nests and roosts today in caves, crevices, and burrows in the highlands of larger islands in the group, including Floreana. Coulter (1982) reviewed the current status of *P. phaeopygia* on Floreana, finding it to be declining rapidly in numbers, with most individuals confined to Cerro Pajas. Barn Owl Cave, although in the lowlands, may have served as a former roosting or nesting area for *P. phaeopygia*. In October 1980, we found bones of *P. phaeopygia* of little apparent antiquity in the shallow caves of the Bahia de la Cuevas region on the northeast coast of Floreana. These bones provide additional evidence that *P. phaeopygia* once was much more widespread on Floreana than today. *Pterodroma phaeopygia* is also known from late Quaternary fossils in the Hawaiian Islands (Olson and James, 1982b:32).

Puffinus lherminieri Lesson

(Audubon's Shearwater)

MATERIAL.—142 specimens, representing at least 2 individuals (Tables 3, 7). CPOI: USNM

284678 (carpometacarpus), 330587 (partial associated skeleton).

This species is distinguished from all other procellariids in the Galápagos by its small size. It is, however, larger than any species of oceanitid. *Puffinus lherminieri* is a very common resident bird in the Galápagos, nesting in holes and crevices on shoreline cliffs on Floreana and many other islands. It may have been incorporated into the fossil fauna as prey of *Tyto punctatissima*. Quaternary fossils of *P. lherminieri* have been reported from the Hawaiian Islands (Olson and James, 1982b:33), many islands in the West Indies (Brodkorb, 1963:246; Olson and Hilgartner, 1982), and St. Helena Island (Olson, 1975:20).

Family OCEANITIDAE

Oceanodroma castro (Harcourt)

(Harcourt's (Madeiran) Storm Petrel)

MATERIAL.—1 specimen, representing 1 individual (Tables 6, 7). BOC: USNM 338323 (mandibular articulation).

I compared this specimen to all species of oceanitids that occur in the Galápagos except *Fregetta grallaria*, which is a very rare non-breeding visitor. Most species that occur anywhere in the eastern Pacific were considered as well. The fossil is larger than in *Oceanites gracilis, O. oceanicus, Oceanodroma tethys, O. leucorhoa,* or *Halocyptena microsoma,* and smaller than in *Oceanodroma markhami* or *O. tristrami.* It is approximately the size of *Fregetta tropica, Pelagodroma marina, Oceanodroma castro, O. furcata, O. homochroa, O. hornbyi, O. melania,* or *O. monorhis,* but resembles the mandible of *O. castro* and differs from all others of similar size in having a shorter and stouter Proc. mandibulae medialis.

Oceanodroma castro nests in many localities in the Galápagos, the nearest to Post Office Bay being Isla Champion. This storm-petrel is nocturnal on its breeding grounds, and its occurrence in Barn Owl Cave is undoubtedly due to predation by *Tyto punctatissima.* Predation on storm-petrels by barn owls is not without prece-

dent, for Bonnott (1928) reported that *T. alba* fed heavily on *O. leucorhoa* at Castle Rock, coastal California. Late Quaternary fossils of *O. castro* are known from the Hawaiian Islands (Olson and James, 1982b:33), Ascension Island (Ashmole, 1963; Olson, 1977), and St. Helena Island (Olson, 1975).

Order Incertae Sedis
(following Olson, 1979)

Family ARDEIDAE

Nyctanassa violacea (Linnaeus)

(Yellow-crowned Night Heron)

MATERIAL.—3 specimens, representing at least 2 individuals (Tables 3, 6, 7). CPOl: USNM 330568 (radius, tarsometatarsus). BOC: USNM 331208 (vertebra).

Nyctanassa violacea is unique in size among herons in the Galápagos, all other taxa being either larger or smaller. It is resident on Floreana and many other islands in the archipelago. Night-herons are too large to be preyed upon by *Tyto punctatissima*, but they may have died in Cueva de Post Office (Inferior) and Barn Owl Cave while searching for large insects. *Nyctanassa violacea* commonly occurs well inland in arid low-land areas of the Galápagos (Gifford, 1913:59; Harris, 1974:82, 1982:83; personal observation). It is recorded only from surface levels, so another possibility is that the remains of a dead individual were carried into the cave by a feral scavenger, such as a cat, dog, or pig. Quaternary fossils of *N. violacea* have been reported from Florida and the West Indies (Brodkorb, 1963:285; Olson and Hilgartner, 1982).

Ardeidae, species indeterminate

(Unknown Heron)

MATERIAL.—1 specimen, representing 1 individual (Tables 6, 7). BOC: USNM 331372 (ungual phalanx).

This specimen is from an immature, medium-sized heron. It is likely to represent either *Ardea alba* (Great Egret) or *Nyctanassa violacea*, but is not sufficiently diagnostic to allow specific identification.

Non-passerine Aves, order indeterminate

(Unknown Non-Passerine Bird)

MATERIAL.—589 specimens, representing at least 1 individual (Tables 6, 7). BOC: USNM 331366, 338170 (elements uncertain).

These shattered, very fragmentary fossils dominated the lowest unit (C_2) of Excavation 1, Barn Owl Cave. They are of an indeterminate large bird, but are too incomplete to reveal any diagnostic features. Because these fossils are associated stratigraphically and are all preserved similarly, they probably belong to a single individual.

Order COLUMBIFORMES

Family COLUMBIDAE

Zenaida galapagoensis Gould

(Galápagos Dove)

MATERIAL.—664 specimens, representing at least 112 individuals (Tables 3–7). All skeletal elements are represented. CPOl: USNM 284646, 284677, 284696, 330569, 330576, 330579, 330580, 330584, 330585, 330590, 330600, 330759, 338258, 338263, 338272, 338283, 338293, 338297, 338302, 338449, 338454. CPOS: USNM 284474, 284576, 284597, 284644, 338194, 338209, 338216. FC: USNM 331468, 331501, 331556, 331578, 331585. BOC: USNM 330690, 330701, 330715–330717, 330728, 330735, 330736, 330741, 331183, 331195, 331206, 331219, 331277, 331287, 331311, 331318, 331351, 331355, 331365, 331412, 331428, 331590, 331600, 338103, 338110, 338124, 338155, 338175, 338306.

These fossils agree in detail with a skeleton of

Z. galapagoensis, the only columbid that occurs in the Galápagos. Males of this dove are significantly larger than females in external measurements (Ridgway, 1897:617, 618; Gifford, 1913:11, 111) and likewise the fossils fall into two distinct size categories. Sundevall (1871) proposed the genus *Nesopelia* for *Z. galapagoensis*, but neither osteology nor plumage support generic separation of this dove.

Zenaida galapagoensis is a ground-dwelling dove that occurs throughout the Galápagos, although it usually avoids the moist highlands on larger islands except Floreana. The concentration of dove bones in the Floreana caves is undoubtedly due to predation by *Tyto punctatissima*. This statement is corroborated by the large number of immature individuals represented. *Zenaida galapagoensis* is common also in the *Tyto*-derived fossil site at Cueva de Kubler, Santa Cruz.

In pristine times, *Z. galapagoensis* was abundant and conspicuous throughout all dry regions of the Galápagos. Early accounts of the islands mention the tameness and great numbers of these doves, which were slaughtered and eaten regularly by the crews of passing ships. For example, Darwin (1871:173, 174) stated:

Cowley (in the year 1684) says, that the "turtle-doves were so tame, that they would often alight upon our hats and arms, so as that we could take them alive: they are not fearing man, until such time as some of our company did fire at them, whereby they were rendered more shy." Dampier also, in the same year, says that a man in a morning's walk might kill six or seven dozen of these doves. At present, although certainly very tame, they do not alight on people's arms, nor do they suffer themselves to be killed in such large numbers. It is surprising that they have not become wilder; for these islands during the last hundred and fifty years have been frequently visited by buncaniers [sic] and whalers; and the sailors, wandering through the woods in search of tortoises, always take cruel delight in knocking down the little birds.

These birds, although now still more persecuted, do not readily become wild: in Charles Island, which had then been colonized about six years, I saw a boy sitting by a well with a switch in his hand, with which he killed the doves and finches as they came to drink. He had already procured a little heap of them for dinner; and he said that he had

constantly been in the habit of waiting by this well for the same purpose.

Galápagos doves are still remarkably tame today on islands such as Genovesa, Santa Fé, Rábida, and Fernandina that are not populated by humans or feral predators. They are reluctant to fly and can be baited with seeds to feed from a person's hand. As much as any species in the Galápagos, doves represent the extreme tameness characteristic of insular birds.

The rarity of doves on Floreana in 1905–1906 was attributed to predation by feral cats, dogs, and humans (Gifford, 1913:6, 8). I agree that feral predation is probably a major cause of the rarity of doves on Floreana, but other factors may be involved as well. For example, P.R. Grant and K.T. Grant (1979) showed that approximately 50% of the dove nests they studied on Genovesa were located in old mockingbird nests, and these nests had a higher rate of fledgling success than those not using old mockingbird nests. Thus the extinction of *Mimus trifasciatus* on Floreana may have removed many prime nesting sites for the doves. Further, P.R. Grant and K.T. Grant (1979) noted that doves on Genovesa fed on the flowers, seeds, and pulp of *Opuntia*. The unnatural scarcity of *Opuntia* on Floreana has depleted an important source of food, as well as nesting sites.

The future of doves on Floreana is not promising; I doubt if they will survive this century. The only doves that I saw during 4 weeks on Floreana were a pair that frequented ledges on the deep, vertical walls of the entrance to Finch Cave in 1978, where they were apparently protected from predators. A similar situation exists on Santa Cruz, where Gifford (1913:6) found doves to be common or abundant in 1905–1906. Since that time, cats, dogs, and people have populated Santa Cruz, and doves are rare there today (personal observation). The survival of doves in the entire archipelago depends upon islands like Genovesa, Santa Fé, Rábida and Fernandina being maintained free of human residents and feral predators.

Order STRIGIFORMES

Family TYTONIDAE

Tyto punctatissima (Gray)

(Galápagos Barn Owl)

MATERIAL.—10 specimens, representing at least 5 individuals (Tables 6, 7). BOC: USNM 331189 (vertebra), 331288 (coracoid), 331316 (manus phalanx), 331371 (2 pedal phalanges), 338114 (2 vertebrae), 338156 (3 pedal phalanges).

The coracoid (Plate 1) and vertebrae agree with a partial skeleton of *Tyto punctatissima* from Santa Cruz, while the phalanges (not available in the partial skeleton) agree qualitatively with those of the nearly cosmopolitan *T. alba,* and differ from those of the only other owl in the Galápagos, *Asio flammeus* (Family Strigidae). *Tyto punctatissima* has been regarded as a subspecies of *T. alba* by most authors of the past two decades, but I recognize *T. punctatissima* as a full species, very distinct from the races of *T. alba* in mainland North, Central, and South America. *Tyto punctatissima* is smaller in all external measurements than *T. alba,* and every skeletal element of *T. punctatissima* (best known from numerous fossils from Cueva de Kubler, Santa Cruz) is easily distinguished from that of *T. alba,* being only approximately ⅔ as large. Furthermore, the plumage in *T. punctatissima* is much darker than in *T. alba.*

Tyto punctatissima is known from San Cristóbal, Santa Cruz, Baltra, Santiago, Isabela, and Fernandina, but is extinct on Floreana (see "Extinction"). Harris (1973) regarded barn owls on Floreana as "probably extinct" (p. 270), and "probably once resident, now not present" (p. 274). I am aware of no evidence for the former occurrence of *T. punctatissima* on Floreana, however, other than the fossils I found in Barn Owl Cave. Groot (1983:169) reported "only one doubtable record of Barn Owl pellets found on Floreana by J. Hatch (Brosset 1963) came to my knowledge." Brosset (1963), in fact mentioned no such record.

The fossils from Barn Owl Cave include at least one immature individual, thus establishing that barn owls nested as well as roosted on Floreana.

Order PASSERIFORMES

Various passerine birds dominate the modern terrestrial avifauna of the Galápagos. Each species is small enough to be preyed upon by *Tyto punctatissima,* and I believe that by this method they were incorporated into the fossil deposits.

Family TYRANNIDAE

Pyrocephalus nanus Gould

(Galápagos Vermilion Flycatcher)

MATERIAL.—1 specimen, representing 1 individual (Tables 6, 7). BOC: USNM 338382 (humerus).

This specimen agrees qualitatively with the humerus of *Pyrocephalus rubinus* of mainland North, Central, and South America. It is distinguished from the humerus of other Galápagos passerines except *Myiarchus magnirostris* in lacking the medial Fossa pneumotricipitalis. It is smaller than the humerus of *M. magnirostris.*

Ridgway (1894) described a new species, *Pyrocephalus carolensis,* on the basis of specimens from Floreana. I agree with Swarth (1931:88, 93) in regarding *P. carolensis* as a synonym of *P. nanus.* Most authors since Swarth (1931) have regarded *P. nanus* as a subspecies of *P. rubinus,* but I believe that the differences in osteology and adult plumage between these two taxa warrant species-level recognition. The wings and tail of *P. nanus* are much shorter than in *P. rubinus.* Bones of the wing are much smaller in *P. nanus* than in *P. rubinus,* while the reverse is true for bones of the leg. Reduction of the pectoral girdle and enlargement of the pelvic girdle are common phenomena in insular birds. It seems unlikely that *P. nanus* could undergo any further reduction of the pectoral assemblage, for such would render it flightless or very nearly so. I cannot think of any selective advantage for flightlessness

in an arboreal flycatcher such as *Pyrocephalus,* which catches insects on the wing. The male plumage of *P. nanus* is a lighter and duller red than in *P. rubinus.* The female plumage of *P. nanus* is very unlike that of *P. rubinus,* being yellow below with slight or no streaking, while *P. rubinus* is more or less cream-colored below, suffused with varying amounts of pink, and with prominent brown streaks. DeBenedictis (1966) noted differences between the songs and song flights of *P. nanus* compared to those of *P. rubinus* of the mainland (California, Arizona, Colombia).

Two species of *Pyrocephalus* have evolved in the Galápagos (*P. dubius* from San Cristóbal, and *P. nanus* from nearly all other islands), thus providing additional evidence that the Galápagos forms have been distinct genetically from the ancestral *P. rubinus* for quite some time. *Pyrocephalus dubius* differs from *P. nanus* mainly in size and female plumage. Like *P. nanus,* it is very distinct from *P. rubinus* of the mainland.

Pyrocephalus nanus is most common on islands such as Floreana that have moist highlands. On these islands it seldom if ever nests in the arid lowlands, occurring there mainly in the nonbreeding season. Thus its rarity in the fossil fauna is easily understood.

Myiarchus magnirostris (Gould)

(Large-billed Flycatcher)

MATERIAL.—18 specimens, representing at least 8 individuals (Tables 5–7). FC: USNM 331477 (humerus). BOC: USNM 330718 (quadrate), 330761 (quadrate), 338113 (humerus), 338305 (mandible), 338311–338314 (4 mandibles), 338377–338381 (5 humeri), 338420 (4 quadrates).

Each of these fossils agrees with a skeleton of *M. magnirostris,* and differs from all other Galápagos passerines, except *P. nanus,* as follows: quadrate, in ventral aspect, with entire mandibular articulation more rectangular (less triangular) in outline, and with a relatively shallow

depression or notch in the central portion; mandible, with relatively small retroarticular process, the internal articular process nearly horizontal in posterior aspect, the ramus relatively straight and weak, and the symphysis broad and flat. *Myiarchus magnirostris* is distinguished from *Pyrocephalus nanus* by its larger size.

Ridgway (1893) proposed a new genus *Eribates* for *M. magnirostris,* but few subsequent authors have recognized this taxon. The placement of *M. magnirostris* in *Myiarchus* seems well substantiated by morphology and behavior (Lanyon, 1978:603–609).

This species is found throughout the Galápagos, at nearly all elevations. It is common today in the lowlands of Floreana.

Family MIMIDAE

Mimus trifasciatus (Gould)

(Floreana Mockingbird)

MATERIAL.—446 specimens, representing at least 75 individuals (Tables 3–7). All skeletal elements are represented. CPO1: USNM 284358–284366, 284651, 284651, 284681, 330670, 330671, 338290, 338456. CPOS: USNM 284367–284373, 284475, 284575, 284586, 284639, 284643. FC: USNM 331467, 331476, 331499. BOC: USNM 330686, 330729, 330744, 330748, 331177–331180, 331196, 331205, 331220, 331276, 331289, 331310, 331317, 331354, 331369, 331411, 331427, 331593, 331601, 338104, 338111, 338125, 338157, 338419.

Mimus trifasciatus is easily recognized osteologically as the largest passerine bird that occurs in the fossil sites. The fossils agree qualitatively and quantitatively (Table 9) with skeletons of *M. trifasciatus* from Champion. They are consistently much larger than all skeletal elements of *M. parvulus* (Plate 2), while they are slightly smaller than *M. macdonaldi* in the rostrum and mandible, but similar in size to *M. macdonaldi* in most postcranial elements. Skeletons of *M. melanotis* were

TABLE 9.—Osteological measurements of adult *Mimus* (in mm), comparing Floreana fossils with modern skeletons from other Galápagos islands (all means rounded to nearest 0.1 mm because of small sample sizes).

Specimens	Length of rostrum	Length of mandible	Maximum depth of mandible	Width of mandibular articulation	Length of humerus	Proximal width of humerus	Distal width of humerous	Length of ulna
Mimus trifasciatus (Floreana)								
mean	28.3	42.8+	3.2	5.2	29.4	7.5	6.4	33.4
range		42.8±42.9	3.1–3.4	4.9–5.4	28.7–30.2	7.3–7.7	6.0–6.8	31.4–34.7
number	1	2	2	5	9	5	15	9
Mimus trifasciatus (Champion)								
mean	29.0	42.8	3.1	5.0	29.0	7.3	6.2	32.8
range	29.0–29.1	42.0–43.6	3.0–3.2	4.9–5.2	28.4–29.6	6.9–7.7	5.9–6.6	31.8–33.9
number	2	2	2	2	2	2	2	2
M. macdonaldi (Española, Gardner-near-Española)								
mean	32.2	46.1	3.1	5.4	28.4	7.5	6.5	32.6
range	31.2–34.1	44.7–47.1	2.9–3.3	5.1–5.5	27.2–29.4	7.1–7.9	5.9–6.9	30.9–33.8
number	5	5	5	5	5	5	5	5
M. parvulus barringtoni (Santa Fé)								
mean	25.4	39.0	2.8	4.2	24.2	6.3	5.3	26.9
number	1	1	1	1	1	1	1	1
M. p. bauri (Genovesa)								
mean	28.2	42.2	2.8	4.6	27.0	7.0	6.0	31.1
range	27.6–28.8	40.3–43.6	2.6–2.9	4.4–4.8	25.9–27.8	6.7–7.2	5.8–6.2	29.4–32.2
number	4	4	4	4	3	3	2	3
M. p. parvulus (Santa Cruz)								
mean	21.5	34.8	2.4	4.1	24.9	6.0	5.0	27.9
number	1	1	1	1	1	1	1	1
M. p. personatus (Rábida, Pinta)								
mean	24.5	38.4	2.6	4.6	25.1	6.6	5.7	28.7
range	22.3–26.8	35.8–41.8	2.5–2.7	4.3–4.7	23.7–26.4	6.4–6.9	5.3–6.0	26.9–30.1
number	3	3	3	3	3	3	3	3

not available, but this species, confined to San Cristóbal, is similar in all external measurements to *M. parvulus* and thus its skeleton would be smaller than the fossils from Floreana. X-rays provide the only means of comparing the fossils with the holotype of *M. trifasciatus*, taken on Floreana in October 1835 by Captain Robert Fitzroy of the *Beagle*. When compared directly to the x-rays, the Floreana fossils (especially the rostrum and mandible) are more similar in size to the three specimens of *M. trifasciatus* than to any other species of *Mimus* in the Galápagos.

Mimus trifasciatus lives today on the small offshore islands of Champion and Gardner-near-

TABLE 9.—Continued

Length of carpometa-carpus	Proximal depth of carpometa-carpus	Length of coracoid	Length of femur	Distal width of femur	Length of tibiotarsus	Distal width of tibiotarsus	Length of tarsomet-atarsus	Proximal width of tarso-metatarsus	Distal width of tarso-metatarsus
18.9	4.6	22.5	27.3	5.4	52.8+	4.3	41.6	4.8	3.6
17.8–19.9	4.0–5.0	21.5–23.2	26.7–28.0	5.0–5.8	51.2±54.2+	4.0–4.6	40.1–42.7	4.4–5.1	3.5–3.7
9	8	7	7	13	9	19	7	14	14
18.6	4.5	22.3	27.2	5.2	53.4	4.3	40.6	4.8	3.4
18.1–19.1	4.4–4.6	21.5–23.1	26.8–27.7	5.0–5.4	52.7–54.1	4.2–4.4	39.9–41.3	4.6–4.9	3.2–3.5
2	2	2	2	2	2	2	2	2	2
19.2	4.5	23.2	26.8	5.2	50.1	4.3	38.6	4.7	3.7
18.3–20.0	4.2–4.7	22.0–23.9	25.5–27.7	4.6–5.4	47.6–52.0	4.2–4.5	36.3–40.5	4.5–4.9	3.4–3.9
5	5	4	5	5	5	5	5	5	5
15.4	3.9	18.6	22.7	4.4	43.4	3.5	33.0	4.0	3.0
1	1	1	1	1	1	1	1	1	1
17.6	4.3	20.9	25.1	4.9	46.8	4.0	35.7	4.6	3.3
17.0–18.1	4.2–4.3	20.2–21.5	24.3–25.8	4.8–4.9	43.9–49.1	3.9–4.1	33.5–37.0	4.4–4.7	3.2–3.4
3	3	3	3	3	3	3	3	3	3
15.9	3.7	19.3	24.0	4.2	45.2	3.5	34.9	4.0	3.2
1	1	1	1	1	1	1	1	1	1
16.3	4.0	19.8	24.0	4.5	45.6	3.7	35.8	4.3	3.1
15.2–17.1	3.8–4.2	18.7–20.8	22.8–25.6	4.2–4.8	43.3–48.4	3.6–3.8	33.5–37.8	4.2–4.3	2.9–3.2
3	3	3	3	3	3	3	3	3	3

Floreana, but is extinct on Floreana. The ecology and behavior of this species are covered in the section on extinction. Unfortunately, Gould (1837b) named no specific island as the type-locality of *M. trifasciatus*, although the data on the two *Beagle* specimens seem to indicate clearly that they were taken on Floreana. The holotype was collected by Darwin, and the other was taken by Fitzroy. Sulloway (1982b) gives additional information on these specimens.

Mimus trifasciatus is one of 4 species of mockingbirds in the Galápagos according to Swarth (1931:104–131) and most subsequent authors. Davis and Miller (1960) united all Galápagos

mockingbirds under the name *trifasciatus* (not *melanotis*, as stated by I. Abbott and L.K. Abbott, 1978), restricting the nominate subspecies to Floreana and its satelites. Even if one were to follow Davis and Miller (1960) in lumping all of the Galápagos mockingbirds into a single species, none of which is sympatric, the name *trifasciatus* would still apply to the Floreana mockingbird because of priority. Sundevall (1871) listed the mockingbirds from San Cristóbal, Santa Cruz, Santiago, and Floreana all as "*Mimus melanotis.*" On this basis, Salvin (1876:466) and Ridgway (1890:119, 122) erroneously reported that two species of mockingbirds, *M. trifasciatus* and *M. melanotis*, occurred on Floreana.

Recently, I. Abbott and L.K. Abbott (1978) analyzed variation in length of the bill, wing, and tarsus in all populations of mockingbirds in the Galápagos, but reached no firm systematic conclusions other than recommending that *M. melanotis* of San Cristóbal be lumped with the widespread *M. parvulus*. *Mimus trifasciatus* is distinguished from other species of mockingbirds in the Galápagos as follows (based upon my own examination and measurements of skins and skeletons, supplemented by the data in Ridgway, 1907:245–248; Swarth, 1931:111–117; Bowman and Carter, 1971:248; and I. Abbott and L.K. Abbott, 1978): larger size (much larger in all respects than *M. melanotis* or *M. parvulus*, slightly larger than or equal to *M. macdonaldi* of Española in all external and skeletal measurements except those of the bill); entire dorsum darker with little or no streaking; less white in the tail; auricular region lighter in color than crown (other species have a dark facial patch); brown breast band present (breast white with varying amounts of streaking in other species). Gifford (1919:207) noted that the song of *M. trifasciatus* is different from that of other Galápagos mockingbirds. Bowman and Carter (1971) were unable to hybridize captive *M. parvulus* with either *M. trifasciatus* or *M. macdonaldi*. Further, a canonical analysis of three external measurements (I. Abbott and L.K. Abbott, 1978) clustered *M. trifasciatus* as far from other Galá-

pagos populations as it was from *M. longicaudatus* of the mainland.

The Floreana mockingbird was first described by Gould (1837b) as *Orpheus trifasciatus*, but thereafter most authors reported it as *Mimus trifasciatus* (see Sharpe, 1881:346, and references therein) until Ridgway (1890) named the new genus *Nesomimus* for all Galápagos mockingbirds. Rothschild and Hartert (1899:142; 1902:381) questioned the validity of the genus *Nesomimus*, but still recognized it, as have most other authors since. I agree with I. Abbott and L.K. Abbott (1978) that the distinctions between mockingbirds of the mainland and the Galápagos do not warrant generic recognition. Designating the species *melanotis* as the type of his new genus, Ridgway (1890:102) diagnosed *Nesomimus* as follows: "Similar to *Mimus* BOIE, but bill longer and much more compressed basally, and tarsus much longer (nearly twice as long as middle toe instead of only about one-third longer)." These characters do not hold. Although *M. trifasciatus* and *M. macdonaldi* do have longer bills than any of their non-Galápagos congeners, this is not the case for *M. parvulus* or *M. melanotis*, where bills of equal length may be found in *M. longicaudatus* and *M. saturinus* of mainland South America. Even when all Galápagos mockingbirds are included in the genus *Mimus*, the variation in length and curvature of the bill in *Mimus* is no greater than in *Toxostoma*, another genus of Mimidae. Also, the bill may be as "compressed basally" in *M. polyglottos*, *M. gundlachii*, or *M. gilvus* as in the Galápagos birds. The tarsus of Galápagos mockingbirds is not relatively longer than that of *M. gundlachii*, *M. thenca*, or *M. longicaudatus*. In fact, mockingbirds of the Galápagos are similar enough to *M. longicaudatus* to suggest very strongly that the latter is their direct ancestor. To separate these species in different genera masks their relationships. The relatively shorter tail in the Galápagos birds presents no problem systematically, for reduction in relative tail length has occurred in other passerines of the Galápagos (flycatchers, finches) when compared with their nearest relatives on the mainland.

Family FRINGILLIDAE

Subfamily EMBERIZINAE

Genus *Geospiza* Gould

(Darwin's Finches)

Darwin's finches consist of 13 living species in the Galápagos and 1 species on Cocos Island, Costa Rica. Among the major islands in the archipelago (Figure 1), 3 to 8 species of Darwin's finches are recorded from each of the relatively small, dry islands, and 9 to 11 species from each of the larger, more environmentally diverse islands. Floreana had 11 species of *Geospiza*, among which only *G. pallida* has not been shown to be resident. The evolution of Darwin's finches is an interesting topic that lies beyond the scope of this paper. P.R. Grant (1981) and Steadman (1982) review the origin and adaptive radiation of this fascinating group of small, tame birds.

I follow the generic classification of Steadman (1982) and the species-level classification of Lack (1945, 1947). For distributional data, I follow Lack (1969) and Harris (1973, 1974, 1982), except where stated otherwise. Identifications of fossil Darwin's finches are based on my own unpublished osteological diagnoses and interspecific comparisons. Identification of post-cranial specimens usually was possible only for *G. magnirostris*, which is larger than any of the other species of Darwin's finches. All other identifications are based on cranial elements, especially the rostrum, mandible, and quadrate.

Geospiza nebulosa Gould

(Sharp-beaked Ground Finch)

MATERIAL.—7 specimens, representing at least 6 individuals (Tables 3, 6, 7). CPOI: USNM 330675 (mandible), 338459 (pterygoid). BOC: USNM 330694 (mandible), 330708 (rostrum), 330712 (mandible), 330721 (quadrate), 330743 (rostrum).

This finch has been recorded historically from San Cristóbal, Floreana, Santa Cruz, Isabela, Fer-

nandina, Santiago, Pinta, Genovesa, Culpepper, and Wenman. Today, *G. nebulosa* is either extinct, very rare, or of uncertain status on the first four or five of these islands (see "Extinction").

Lack (1945, 1947) united all populations of the Sharp-beaked Ground Finch under the name *G. difficilis*, a treatment followed by all subsequent authors until Sulloway (1982a,b) showed that the earlier name *G. nebulosa* Gould (1837a) is based on an extinct population from Floreana, and therefore *G. difficilis* Sharpe (1888) is a synonym of *G. nebulosa* for reasons of priority. Sulloway (1982a,b) has also determined the specific island localities for most of the *Beagle* specimens of Darwin's finches. His measurements of these specimens reveal slightly larger bill dimensions for the Floreana birds than for any other populations of *G. nebulosa*. This large size is corroborated by the fossils reported herein, which are also larger than the cranial elements of other forms of *G. nebulosa*, but differ both qualitatively and quantitatively from those of *G. nebulosa*'s closest relatives (*G. fuliginosa*, *G. fortis*, and *G. scandens*).

As is also the case with *G. magnirostris*, the fossils from Floreana of *G. nebulosa* represent more individuals than are known from skins. *Geospiza nebulosa* is known from Floreana by four skins whose history has been studied by Sulloway (1982b). Two of these specimens, collected by Fitzroy in 1835 and Kinberg in 1852, are known to be from Floreana because of their associated field data. The other two, collected by Darwin in 1835, most probably came from Floreana because of circumstantial evidence of the chronology and geography of Darwin's collecting, and because these specimens, one of which is now lost, agree closely with the other two specimens.

Geospiza nebulosa occurs as a fossil with about the same frequency as *G. olivacea*. On large islands such as Santa Cruz and presumably Floreana, both of these species tend to be more common, and do most or all of their nesting, above the arid coastal region. They occur regularly in the lowlands only in the non-breeding season (Gifford, 1919:238). *Geospiza nebulosa* oc-

curs more commonly as a fossil than other finches, such as *G. crassirostris, G. parvula,* and *G. pauper,* that are regarded as characteristic of areas more humid than the region surrounding the caves. Therefore, *G. nebulosa* probably was once rather common in the middle and higher elevations of Floreana. It may even have nested in the lowlands, where it was at least a regular visitor.

Geospiza fuliginosa Gould

(Small Ground Finch)

MATERIAL.—24 specimens, representing at least 18 individuals (Tables 3–7). CPOI: USNM 330669 (mandible), 330672 (mandible). CPOS: USNM 330679 (mandible). FC: USNM 330681 (skull with rostrum), 330683 (mandible), 330684 (mandible). BOC: USNM 330689 (mandible), 330693 (mandible), 330697 (mandible), 330704 (mandible), 330705 (mandible), 330706 (mandible), 330709 (rostrum), 330713 (mandible), 330714 (mandible), 330725 (mandible), 330731 (mandible), 330737 (rostrum), 330739 (rostrum), 330742 (mandible), 331188 (mandible), 338303 (rostrum), 338304 (rostrum), 338309 (mandible).

Geospiza fuliginosa occurs nearly throughout the Galápagos. It is the second most common fossil finch on Floreana, and almost certainly its numbers would be augmented if some of the specimens relegated to "*Geospiza,* species indeterminate" were less fragmentary. Now that *G. magnirostris* no longer dominates the finch fauna of Floreana, *G. fuliginosa* has become by default the most common finch of the lowlands surrounding Post Office Bay, vying with *Dendroica petechia* as the most common land bird in this region today, at least during my observations in June and July 1978, and October 1980.

Geospiza fortis Gould

(Medium Ground Finch)

MATERIALS.—38 specimens, representing at least 12 individuals (Tables 4–7). CPOS: USNM

330678 (rostrum). FC: USNM 330685 (rostrum), 330680 (associated partial skeleton; jugal, palatine, quadrate, rostrum, mandible, and major elements of the wing and leg; 23 total specimens). BOC: USNM 330688 (mandible), 330692 (mandible), 330699 (mandible), 330700 (mandible), 330702 (jugal), 330711 (mandible) 330745 (quadrate), 330752 (mandible), 330753 (mandible), 330757 (mandible), 331199 (jugal), 33810 (mandible), 338370 (pterygoid).

The partial associated skeleton of *G. fortis* from Finch Cave represents the only positively identified post-cranial fossils of any Darwin's finch except *G. magnirostris.* Because of this associated skeleton, *G. fortis* has a higher number of specimens, relative to MNI, than in any other finches except *G. magnirostris. Geospiza fortis* is very widespread in the Galápagos. It is the third most common fossil finch, and only *G. fuliginosa* is more common today in the lowlands of Floreana. *Geospiza fortis* is extremely variable in size on Floreana (Lack, 1947, Pl. IV, tables XXIV, XXIX), as corroborated by the fossils.

Geospiza magnirostris Gould

(Large Ground Finch)

MATERIAL.—2669 specimens, representing at least 229 individuals (Tables 3–7). All skeletal elements are represented. CPOl: USNM 284459–284471, 284652–284670, 284672, 284679, 284680, 338462, 338250, 338251, 338273, 338284, 338289, 338462. CPOS: USNM 284374–284450, 284452–284458, 284480–284497, 284501–284574, 284579–284591, 284600–284638, 284640, 284642, 338182–338189, 338195–338204, 338246, 338442–338444. FC: USNM 331442–331466, 331478–331498, 331505–331555, 331558, 331559, 331562, 331565–331571, 331573–331577, 331586–331588. BOC: USNM 330722, 330724, 330762–330767, 331114–331176, 331198, 331202–331204, 331221–331275, 331290–331309, 331319–331350, 331356–331361, 331373–331410, 331419–331426, 331589, 331591, 331592, 331596–

331598, 338105, 338106, 338126–338149, 338158–338163, 338176–338179, 338308, 338369, 338372–338375, 338410–338418, 338424, 338435.

Geospiza magnirostris is recorded from each site. It is the most common avian taxon in the fossil fauna. The fossils include several nearly complete associated skeletons (e.g., Figure 23). Both cranially and post-cranially, its large size distinguishes *G. magnirostris* from all other Darwin's finches (Figure 24; Plates 3, 4).

Geospiza magnirostris, like *G. nebulosa,* is now extinct on Floreana. These two finches resemble each other further in having been major sources of controversy among ornithologists of the past century. The basic questions have been: (1) did *G. magnirostris* ever occur on Floreana?; and (2) if so, why did it become extinct there? Sulloway

(1982a,b) has answered the first of these questions in the affirmative, just as he did for *G. nebulosa.* In addition, the paleontological evidence (2669 fossils) for the occurrence of *G. magnirostris* on Floreana is unequivocal. By combining paleontological evidence with data from modern ecological studies, the second question now can also be addressed (see "Extinction").

Wherever it occurs, *G. magnirostris* is restricted mainly to the arid lowlands. This finch occurs, or did occur, on most of the major islands in the Galápagos, but it is seldom as abundant as at least 2 or 3 smaller sympatric finches. Based on MNI, *G. m. magnirostris* is more than 12 times as common in the Floreana fossil deposits as the 2nd most abundant finch, *G. fuliginosa.* Barring the unlikely possibility that *Tyto punctatissima* on Floreana was a highly specialized feeder on *G. m.*

FIGURE 23.—Associated skeleton of *Geospiza magnirostris* from Finch Cave (USNM 331573; approximately life size).

FIGURE 24.—Adult male skins of *Geospiza magnirostris* (in lateral aspect): top, *G. m. magnirostris*, BM(NH) 1885.12.14.280, Floreana; bottom, *G. m. strenua*, BM(NH) 1899.9.1.171, Genovesa (individuals from Genovesa are largest of any surviving populations of *G. magnirostris*; specimens × 0.4 life size).

magnirostris, there is little doubt that this large finch was the most common lowland bird on Floreana before human contact.

Geospiza crassirostris (Gould)

(Vegetarian Finch)

MATERIAL.—4 specimens, representing 4 individuals (Tables 6, 7). BOC: USNM 330691 (mandible), 330698 (quadrate), 330707 (mandible), 338387 (tarsometatarsus), 338426 (quadrate).

Geospiza crassirostris has been recorded from all of the large, biologically diverse islands in the Galápagos. It nests no lower than the transition zone on islands such as Floreana, but descends into the lowlands in the non-breeding season. In February and March 1906, Gifford (1919:243) found *G. crassirostris* on Floreana only above 1000 feet elevation. I have never seen this species in the arid zone of Floreana. It is surprising that as many as four individuals of *G. crassirostris* were preserved as fossils, but if Darwin's three specimens of *G. crassirostris* actually came from Floreana, as Sulloway (1982b) has suggested, then this finch may have been more common on this island in pristine times than today.

Geospiza scandens (Gould)

(Cactus Finch)

MATERIAL.—2 specimens, representing 2 individuals (Tables 6, 7). BOC: USNM 330696 (rostrum), 330703 (jugal).

Geospiza scandens occurs on most islands in the archipelago. It is generally characteristic of arid lowlands, although Gifford (1919:239) reported *G. scandens* to occur at higher elevations on Floreana, particularly when introduced oranges were ripe. In the lowlands of Floreana, Gifford (1919:239) found *G. scandens* to be most common near the localized stands of cactus. Today, *G. scandens* seem to be fairly common in the Post Office Bay region, but it is decidedly less common than *G. fuliginosa* or *G. fortis*. The rarity of *G. scandens* as a fossil is puzzling, especially when one considers the former abundance of cactus on Floreana. The overwhelming prehistoric abundance of *G. magnirostris* may have affected the numbers of *G. scandens*.

Geospiza parvula (Gould)

(Small Tree Finch)

MATERIAL.—1 specimen, representing 1 individual (Tables 6, 7). BOC: USNM 330730 (mandible).

Geospiza parvula is the smallest and most widespread of the tree finches. It is common on the larger, higher islands, including Floreana, and nests mainly in the transition and *Scalesia* zones; it occurs regularly, sometimes commonly, in the arid zone, especially outside of the breeding season. Tentatively, I would rate *G. parvula* as the fourth most common finch in the lowlands of Floreana today, behind *G. fuliginosa*, *G. fortis*, and *G. scandens*. I have seen up to 5 or 6 individuals in a single day (26 June 1978) in the Post Office Bay region. Based on its modern abundance, one might expect *G. parvula* to have occurred as a fossil in slightly greater numbers. The actual relative abundance of *G. parvula* in the fossil record may be masked, however, be-

cause this species is difficult to distinguish osteo-logically from *G. fuliginosa*. Certain of the frag-mentary fossils reported as "*Geospiza*, species in-determinate" may pertain to *G. parvula*.

Geospiza pauper (Ridgway)

(Medium Tree Finch)

MATERIALS.—3 specimens, representing 3 in-dividuals (Tables 5–7). FC: USNM 330682 (man-dible). BOC: USNM 330695 (rostrum), 330738 (rostrum).

Geospiza pauper is endemic to Floreana, nest-ing in and above the transition zone. In the non-breeding season, *G. pauper* regularly occurs in the arid lowlands. Gifford (1919:249) reported that it was seldom encountered below 1000 feet elevation in 1906, although a few specimens were taken in the lowlands. I found *G. pauper* to be common at low elevations near Bahia de las Cue-vas on 23 October 1980, and observed a single individual near Post Office Bay on 26 June 1978. The relative abundance of *G. pauper* in the fossil fauna seems to be more or less as expected.

Geospiza olivacea (Gould)

(Warbler Finch)

MATERIAL.—7 specimens, representing 7 in-dividuals (Tables 3, 6, 7). CPOI: USNM 330673 (mandible), 330676 (quadrate), 338285 (frontal). BOC: USNM 330726 (mandible), 331200 (cran-ium), 338423 (quadrate), 338425 (quadrate).

Surprisingly, *G. olivacea* is the fourth most common fossil finch on Floreana. The relative abundance of *G. olivacea* may be biased somewhat by its very small size, which greatly facilitates identification. Nevertheless, *G. olivacea* seems to be decidedly uncommon in the northern low-lands of Floreana today, where I have never observed it in spite of looking for it outside of the nesting season (June, July, October). Gifford (1919:220, 223) found *G. olivacea* to occur un-commonly in the "wooded interior and on the south slope" of Floreana in 1906, with breeding

records in February and May. The fossils suggest that *G. olivacea* occurred in the arid lowlands of Floreana more commonly in the past than today, although my observations of its present status were limited.

Geospiza, species indeterminate

(Unidentifiable Darwin's Finches)

MATERIAL.—38 specimens, representing at least 9 individuals (Tables 3, 4, 6, 7). CPOI: USNM 330674. CPOS: USNM 330677, 338210. BOC: USNM 330687, 330710, 330719, 330720, 330732–330734, 330740, 330746, 330749–330751, 330754–330756, 330758, 330760, 331201, 338150, 338307, 338315–338322, 333871, 338376, 338427–338430.

Indeterminate species of *Geospiza* are repre-sented by 3 cranial fragments, 2 rostra, 2 jugals, 1 pterygoid, 11 quadrates, and 19 mandibles. Each of these fragmentary fossils is smaller than *G. magnirostris* and larger than *G. olivacea*, but cannot be distinguished from two or more other species of Darwin's finches. Most of these speci-mens agree in size with *G. fuliginosa* or *G. par-vula*, and very likely belong to one of these species.

Passeriformes, family through species indeterminate

(Unknown Passerine Birds)

MATERIAL.—505 specimens, representing at least 24 individuals (Tables 3–7). CPOI: USNM 284650, 330582, 330598, 338252, 338257, 338274, 338406–338409, 338451, 338461. CPOS: USNM 284577, 284599, 338190, 338224, 338230, 338237, 338404, 338405. FC: USNM 331572, 331584, 338402, 338403. BOC: USNM 331181, 331367, 331368, 338112, 338383–338401.

This category consists of passerine post-cranial elements that clearly are not from *Mimus trifas-ciatus* or *Geospiza magnirostris* because of their

small size, or are too fragmentary to determine accurately even their size. Most of the specimens fall into the first category, and of these, the great majority undoubtedly represent Darwin's finches. As stated previously, the smaller species of *Geospiza* seem to be impossible to distinguish on the basis of post-cranial elements.

AVES, order through species indeterminate

(Unknown Birds)

MATERIAL.—1281 specimens, representing no new individuals (MNI) because sufficient numbers of diagnostic avian fossils were recovered from each of the same sites and levels (Tables 3–7). CPOI: USNM 338445, 338452, 338453, 338455. CPOS: USNM 284578, 338181, 338191, 338205. FC: USNM 331469, 331500, 338437. BOC: USNM 330727, 331182, 331197, 331207, 331218, 331278, 331362, 331363, 331370, 331413, 331429, 331430, 331594, 331595, 351602, 331603, 338107, 338108, 338122, 338123, 338164, 338165, 338180, 338325.

This material consists of avian post-cranial elements that are too fragmentary for identification even to order. From their size, however, all or nearly all of these specimens represent birds no larger that *Zenaida galapagoensis*. Very likely these specimens pertain mainly to the three most common fossil species—*Geospiza magnirostris*, *Zenaida galapagoensis*, and *Mimus trifasciatus*.

Class MAMMALIA

Order CHIROPTERA

Family VESPERTILIONIDAE

Lasiurus borealis (Muller)

(Red Bat)

MATERIAL.—59 specimens, representing at least 11 individuals (Tables 5–7). Nearly all skeletal elements are represented. FC: USNM 331470, 331581, 331583. BOC: USNM

331282, 331315, 331364, 331604, 338117, 338151, 338324.

Lasiurus borealis is a very widespread species that occurs in much of North, Central, and South America. The form of *L. borealis* that occurs in the Galápagos was originally described as a new species, *Atalapha brachyotis*, by Allen (1892:47), who noted that "this insular form closely resembles *A. varia* [= *L. borealis*] in coloration, size and proportions, except that it has much smaller ears." Allen's holotype and only specimen was from San Cristóbal. Most authors since Allen (1892) have regarded *L. brachyotis* as a valid species, although Niethammer (1964) noted that *brachyotis* may be only a race of *borealis*. While I have not made a critical study of the external morphology of *L. "brachyotis"* versus *L. borealis* of the mainland, I have examined the skulls, dentaries, and other bones of these forms, finding no justification for recognition of *brachyotis* as a species distinct from *borealis*. In the absence of a series of skins from the Galápagos, Allen's character of smaller ears in *"brachyotis"* cannot be evaluated. The Galápagos form may deserve recognition as a subspecies of *borealis*, but the paucity of specimens prevents any decision in this regard. *Lasiurus borealis* from the Galápagos is larger than most races of *L. borealis* from the mainland, although it is the same size as certain continental races.

To my knowledge, no specimens of *L. borealis* have ever been taken before on Floreana. Without providing the date or exact locality, Brosset (1963) noted a sight record of *Lasiurus* (species undetermined) from Floreana, this being the only evidence of the occurrence of bats on Floreana until the fossils reported herein. I never saw bats during my field work on Floreana. The only other bat in the Galápagos is *L. cinereus*, which is significantly larger than *L. borealis*. Specimens of *L. cinereus* from the Galápagos have been reported only from Santa Cruz.

What little is known of the biology of bats in the Galápagos has been reviewed by Brosset (1963), Orr (1966), Vanalek (1982), and Clark (1984). Brosset (1963) noted that *Tyto punctatis-*

sima will prey upon *L. borealis,* and probably this is how the fossils from Floreana were deposited in the caves, for *L. borealis* roosts in vegetation, not in caves. 1 have also identified fossils of *L. borealis* from Cueva de Kubler, Santa Cruz, these bones certainly being derived from prey items of *T. punctatissima.*

Introduced Mammals

The remaining mammals have been introduced on Floreana by man. Because they are not a part of Floreana's natural fauna, 1 have not included these species in any of the totals in Tables 3–7. None of these specimens is likely to be older than A.D. 1832, the year that General Jose Villamil established the first large human settlement on Floreana (see "Human History"). For nomenclature, 1 follow Corbet (1978).

Order RODENTIA

Family MURIDAE

Subfamily MURINAE

Mus musculus Linnaeus

(House Mouse)

MATERIAL.—42 specimens, representing at least 12 individuals (Tables 3, 4, 6, 7). Most major skeletal elements are represented, including maxillae and dentaries. CPOI: USNM 330573, 338448. CPOS: USNM 284598, 338217. BOC: USNM 331190, 331283, 331435, 331437, 331609.

Although we collected this introduced rodent from excavations as well as surface deposits, a critical look at its occurrence in the excavations reveals no evidence for great antiquity of *Mus musculus* on Floreana. From Cueva de Post Office (Inferior), it is represented by 1 pelvis in the 0–3 cm level. From Cueva de Post Office (Superior), it occurs again only in the 0–3 cm level

(1 premaxilla, 2 dentaries). From Excavation 1 in Barn Owl Cave, *M. musculus* was found only in the test pit, in the form of 26 specimens (3 MNI) from the 0–10 cm level, 5 specimens (1 MNI) from the 10–20 cm level, and 1 specimen from the 30–40 cm level. The stratigraphy of test pits is never fool-proof, and the six specimens of *M. musculus* from below 10 cm are undoubtedly contaminants that dribbled into lower levels during excavation of the test pit. After completion of the test pit, we enlarged Excavation 1 horizontally in a much more controlled manner, according to its stratigraphic units. *Mus musculus* was not present in the stratigraphically controlled excavation. This little rodent is discussed further in "Introduced Mammals."

Tyto punctatissima probably was the main or sole agent for deposition of *Mus musculus* in the caves. The rarity of both *Mus musculus* and *Rattus rattus,* however, suggests that these two introduced rodents co-existed on Floreana with *T. punctatissima* for only a very short time.

Rattus rattus (Linnaeus)

(Black Rat)

MATERIAL.—142 specimens, representing at least 13 individuals (Tables 3–7). All skeletal elements are represented. CPOI: USNM 330571, 330572, 330588. CPOS: USNM 284451, 284476. FC: USNM 331471. BOC: USNM 331211, 331284, 331415, 331436, 338116.

As with *Mus musculus,* the specimens of *Rattus rattus* from excavations cannot be considered as evidence of its prehistoric occurrence on Floreana. From Excavation 3 of Cueva de Post Office (Superior), this introduced rodent is represented by a single humerus from the uppermost 10 cm of sediment, which therefore could have been on the surface originally. From Excavation 1 of Barn Owl Cave, *R. rattus* occurs only as one upper incisor and one dentary from the 0–10 cm level of the test pit, and one vertebra from Unit A, the highest unit. *Rattus rattus* is discussed further in Introduced Mammals.

Order CARNIVORA

Family FELIDAE

Felis catus Linnaeus

(Domestic Cat)

MATERIAL.—1 specimen, representing 1 individual (Tables 6, 7). BOC: USNM 331191 (radius).

Felis catus is recorded only from the surface of Room 1 in Barn Owl Cave. Cats are too large to be prey items of *Tyto punctatissima*. (Instead, cats may have preyed upon *T. punctatissima* during the barn owl's last days on Floreana.) *Felis catus* thrives today in the lowlands of Floreana.

Order ARTIODACTYLA

Family SUIDAE

Sus scrofa Linnaeus

(Domestic Pig)

MATERIAL.—16 specimens, representing at least 1 individual (Tables 6, 7). BOC: USNM 331212 (13 post-cranial elements), 331215 (skull, mandible), 331314 (radius).

These bones were scattered over an area approximately 4 m in diameter on the surface of Room 1 of Barn Owl Cave. They likely belong to one individual of *S. scrofa* because of their similarity in preservation, and because they all represent a very young pig. Until very recently, feral pigs were common on Floreana.

Order PERISSODACTYLA

Family EQUIDAE

Equus asinus Linnaeus

(Donkey)

MATERIAL.—1 specimen, representing 1 individual (Tables 3, 7). CPOI: USNM 338477 (keratinous hoof sheath).

The lack of any other donkey remains makes me question that the entire donkey was ever in the cave. Instead, a dog, cat, pig, or rat may have brought the hoof sheath of *E. asinus* into the cave. Donkeys are common today in the lowlands of Floreana.

Mammalia, order indeterminate

(Unknown Mammal)

MATERIAL.—2 specimens, representing 2 individuals (Tables 3, 5, 7). CPOI: USNM 338478 (fused thoracic vertebrae). FC: USNM 338463 (cranial fragment).

The first of these surface remains is from an immature individual, dog-sized or larger. The cranial fragment is approximately the size of *Capra* or *Sus*, but lacks any diagnostic features.

Discussion

HUMAN HISTORY.—An understanding of Floreana's human history is crucial to this study, for all vertebrate extinction on Floreana is related temporally to human arrival. Many accounts of the settlements on Floreana are vague and conflicting, and that which follows is my best attempt to piece together briefly the major historical events on this island.

Except for the dubious possibility of limited, temporary Amerindian encampments (Heyerdahl and Skjolsvold 1956; Heyerdahl 1963), the discovery of the Galápagos Islands is credited to Fray Tomás de Berlanga, the Bishop of Panama, in 1535. The particular islands that he visited cannot be determined with certainty from his writings. Privateers and pirates frequented the Galápagos, including Floreana, in the late 17th and early 18th centuries. Here these sailors could make repairs and obtain food (especially tortoises) and water in between raids on Spanish ships and coastal towns of Latin America. In the late 1700s, Galápagos waters became the focus of whaling ships from the United States and Britain. Initially, Floreana was visited often because it offered both tortoises and fresh water,

as well as good anchorage. When tortoises became very rare in approximately 1840 (see "Extinction"), Floreana became a little less popular with the whalers, who were drawn there nevertheless by the fresh water and vegetables.

In 1807, Patrick Watkins became Floreana's first long-term resident. This Irish sailor was probably the first settler anywhere in the entire archipelago. Slevin (1959:105) and others have summarized Watkins' harsh life on Floreana, based upon the diary, written in 1813, of Midshipman William W. Feltus of the U.S. frigate *Essex*, and upon the journal of Captain David Porter of the *Essex* (Porter, 1822). Watkins lived on Floreana for approximately 2 years before hijacking a boat to mainland South America.

In 1832, General Jose Villamil established a sizeable colony on Floreana with the permission of the newly formed Ecuadorean government. This colony was the first significant human settlement anywhere in the Galápagos. Villamil's colony is described by Darwin (1871:141, 142), who noted the presence of introduced plants and animals there in 1835. Villamil's settlement lasted only until 1845 or 1846, after which Floreana was sporadically inhabited (although rather frequently visited) until 1929, when two Germans, Dr. Karl Friedrich Ritter and Frau Dore Strauch, settled in the highlands, remaining there until Ritter's death in 1934, when Strauch returned to Germany (Strauch, 1936). The Wittmer family, also of Germany, moved to Floreana in 1932. The Wittmer's initially consisted of Heinz, his wife Margret, and a son. Another son and a daughter were born subsequently. Frau Wittmer, who now lives at Black Beach (the family originally settled in the highlands), has recounted her family's experiences on Floreana (Wittmer, 1961). Later in 1932, Baroness Antoinette (Eloise) von Wagner-Bousquet moved to Floreana with three men. Controversy and mistrust filled the lives of the Baroness and her companions, as well as Ritter, Strauch, and the Wittmer's, as one can easily discern from the conflicting accounts in Strauch (1936), W.A. Robinson (1936), Conway and Conway (1947), and

Wittmer (1961). The ensuing tragic events that occurred on Floreana in 1934 still rate as the most popular of unsolved mysteries in the Galápagos (Treherne, 1983).

Various persons have moved to Floreana since the 1930's, the most prolific being the Cruz family, some of whose 11 children still live on Floreana (Gayle Davis, pers. comm.). Wittmer (1961:221, 234) reported that approximately 50 persons lived on Floreana during the period of 1956–1959. Floreana's population today is still around 50 (Gayle Davis, pers. comm.), living both in the highlands and at Black Beach.

INTRODUCED MAMMALS.—"We may infer from these facts what havoc the introduction of any new beast of prey must cause in a country before the instincts of the indigenous inhabitants have become adapted to the stranger's craft or power" (Darwin 1871:176).

Perhaps more than any other island in the Galápagos, Floreana has been adversely affected by mammals introduced by man. These feral mammals, which may be more harmful to native insular animals than man himself, are probably involved in the extinctions of as least six species of vertebrates on Floreana, although evidence for this accusation is no better than circumstantial. Only the extinction of the hawk *Buteo galapagoensis* is difficult to relate to the impact of feral mammals. Large animals are more vulnerable to direct human predation than smaller animals because they are more conspicuous. On Floreana, predation by man may be the chief cause of extinction for *Geochelone* and *Buteo*, but may be involved as well in the loss of *Alsophis* and *Tyto*.

Slevin (1959:7), Leveque (1963), and Thornton (1971:268) noted that the following species of feral mammals occurred on Floreana: black rat (*Rattus rattus*), house mouse (*Mus musculus*), dog (*Canis familiaris*), cat (*Felis catus*), pig (*Sus scrofa*), goat (*Capra hircus*), cow (*Bos taurus*), and burro or donkey (*Equus asinus*). Eckhardt (1972) also listed all of these species as currently inhabiting Floreana, with cats and donkeys designated either as especially abundant or particularly de-

structive. Eckhardt (1972) is an excellent reference for the ecological effects of introduced plants and animals in the Galápagos, although he makes little reference to Floreana in particular. During my field work on Floreana in 1978 and 1980, 1 noted cats, goats, and donkeys to be common in the arid northern coastal region. 1 did not observe pigs, cattle, or dogs on Floreana, but 1 have spent only part of a single day in the highlands. 1 have not seen *Rattus* on Floreana, but 1 have identified bones of both *Rattus* and *Mus* from cave deposits on Floreana as well as from modern pellets of Short-eared Owls (*Asio flammeus*) that roost on Champion but hunt mainly on nearby Floreana. The islands of San Cristóbal, Santa Cruz, Santiago, and Isabela have more or less the same species of feral mammals as Floreana (Leveque, 1963; Eckhardt, 1972), but on these four larger islands feral mammals seem to have done somewhat less damage to native vertebrates. Table 10 is a very current assessment by Bruce D. Barnett of the introduced animals on Floreana, where the low figures for dogs, pigs, and cattle are due to an effective hunting and poisoning campaign for the past several years.

Once established, most populations of feral mammals thrived on Floreana up to the present, or at least up until the past decade. Sheep, men-

tioned only by Tanner (1888) and A. Agassiz (1892:68), would be an exception. Most species of feral mammals escaped into the wilds of Floreana within 10 years after 1832, the year that Villamil established the settlement there. It is possible that buccaneers or whalers released goats on Floreana prior to 1832, but the suggestion of Wittmer (1961:32) that goats and cattle were released on Floreana by Fray Tomás de Berlanga in 1535 seems highly unlikely. Captain David Porter of the *Essex* released goats on Santiago as early as 1814 (Porter, 1822), but I know of no earlier report of feral mammals anywhere in the Galápagos. Darwin (1871:142) noted feral goats and pigs on Floreana in September 1835. By 1846, Berthold Seemann of HMS *Herald* stated (in Van Denburgh, 1914:226) that "wild dogs, pigs, goats, and cattle had increased wonderfully" on Floreana, and Villamil's settlement also owned approximately 2000 head of cattle.

Captain A.H. Markham visited Floreana in 1880 in HMS *Triumph*, finding the island to be (1880:744) "in undisturbed possession of the so-called wild cattle. . . . , donkeys, dogs, pigs, and other animals that had been left to run wild on the abandonment of the island by the former inhabitants." In 1887, Midshipman M. Estienne of the French corvette *Decres* reported (in Slevin, 1959:103) abundant donkeys on Floreana, as well as wild cattle and pigs. Captain Tanner (1888) of the *Albatross* noted large numbers of cattle, sheep, hogs, horses, and donkeys running wild on Floreana in 1888. A. Agassiz of the *Albatross* found cattle, donkeys, sheep, goats, hogs, cats, dogs, and "common fowl" in a feral state on Floreana in 1891 (A. Agassiz, 1892:68). Slevin (1931:39–43) reported cats, dogs, goats, cattle, pigs, and donkeys seen on Floreana by the California Academy of Sciences Expedition in October 1905. Strauch (1936), Conway and Conway (1947), and Wittmer (1961) collectively mentioned rats, mice, cats, dogs, pigs, goats, cattle, donkeys, and horses on Floreana between 1930 and 1960, with pigs and cattle being very destructive to their crops.

Patton et al. (1975) stated that rats occurred

TABLE 10.—Numbers of individuals of introduced vertebrates on Floreana, February 1984 (data from Bruce D. Barnett, as related to Marsha S. Cox).

Animal	Domestic	Feral
Mice	0	"Infinite"
Rats	0	"Infinite"
Dogs	25	0
Cats	20	<1000
Pigs	44	10–20
Goats	3	5000
Cattle	265	50–60
Burros	55	>1000
Horses	17	1
Ducks	12	0
Chickens	427	~150
Pigeons	2	0

on Floreana by sometime in the 1800s, noting that Darwin made no mention of rats being there in 1835. The first specimen of *Rattus* from Floreana was taken by the Hopkins Stanford Galápagos Expedition in 1898–1899 (Heller 1904). Rats may have been living on Floreana in 1835 or very shortly thereafter, but were simply overlooked. On Santa Cruz, where rats seem to be abundant today (personal observation), they can easily go unnoticed to someone who is not specifically looking for them.

While I am convinced that alien introductions triggered the extinction of native forms, the direct evidence of such is elusive. Rats may be involved in the extinction of *Geochelone* (predation on eggs and hatchlings) and *Alsophis* (predation on young). Atkinson (1977) hypothesized the potentially detrimental effects of *Rattus rattus* on birds in Hawaii, through direct predation and transmission of disease. There is, however, very little unequivocal evidence of actual predation on birds by *Rattus* (Norman 1970, 1975), or of their role in transmission of disease. Atkinson (1977) noted that avian extinction coincided with the introduction of *Rattus* on Hawaii, Lord Howe Island, and Big Smith Cape Island in New Zealand. The role of *Rattus* in the extinction of birds on Floreana is purely speculative. I am not aware of studies of any sort on *Mus* in Galápagos, nor do I know that *Mus* has had any damaging effect on the native vertebrates of Floreana or any other island in the Galápagos or elsewhere.

Certain vertebrates on Floreana probably have suffered heavily from predation by feral cats and dogs. For example, Strauch (1936:93) and Wittmer (1961:136) both owned cats on Floreana that regularly ate finches and doves. Cats and dogs may be involved in the extinctions of *Geochelone*, *Alsophis*, and perhaps *Buteo*, *Tyto*, *Mimus*, *Geospiza nebulosa*, *Geospiza magnirostris*, and perhaps in the present rarity of *Tropidurus* and *Zenaida*. Fortunately, feral dogs have been eliminated on Floreana in the past decade by poisoning and shooting (Barnett, 1982), thus ending a period of 140 years as the largest carnivores on the island.

Among the introduced ungulates of Floreana, only the pig may prey directly on vertebrates. While rooting around in the soil and ground cover, pigs probably kill small individuals and eggs of *Geochelone* and *Alsophis*. Koford (1966) noted that residents of Santa Cruz claim that pigs destroy the nests and eggs of tortoises.

Goats, cattle, and burros destroy the native vegetation by their relentless browsing and grazing. Goats are especially notorious for habitat alteration on islands, both in the Galápagos and elsewhere (Coblentz, 1978). In arid regions such as the Galápagos, succulents are preferred because of their high water content. Hamann (1975) has reviewed the damage done to vegetation by introduced herbivores, especially goats, on Santa Cruz, Santa Fé, and Pinta; the same general principles apply to Floreana. Koford (1966) mentioned that Floreana had, at that time, the densest population of donkeys in the Galápagos.

EXTINCTION.—Seven species of vertebrates from Floreana have become extinct, six of which are recorded as fossils. The fossils themselves provide no evidence concerning the cause of extinction, but the main importance of the fossils is in determining the presence or absence of a species at a given time, in this case the late Holocene. Having established that a certain species once lived on Floreana, then various kinds of independent, circumstantial evidence can be sought to suggest causes of extinction.

The chronology of extinction on Floreana suggests man's involvement; all or nearly all extinction has occurred since man's arrival. Except for the barn owl, all extinct vertebrates from Floreana are known to have survived into historic times, i.e., to A.D. 1835 or later. While the barn owl is not recorded definitely from Floreana other than from fossils, I believe that its extinction was also in historic times (see below). A fairly extensive fossil record from Floreana has disclosed no clear cases of prehistoric extinction. If man's impact is a major cause of extinction on islands, then a paucity or lack of prehistoric extinction is not unexpected on an archipelago

such as the Galápagos where prehistoric man probably never occurred, or at most visited on a very limited basis. New, dated fossil faunas from other islands in the Galápagos will provide the crucial test. I predict that most or all extinction in the Galápagos will be shown to have occurred in historic times. Radiocarbon dating is essential. For example, Steadman and Ray (1982) could say little about the extinction of the giant rat of Santa Cruz, *Megaoryzomys curioi*, because of the lack of radiocarbon dates from any of the localities from which it was collected.

Geochelone elephantopus: Presumably, extinction of tortoises on Floreana was due mainly to direct human predation, although predation on eggs and young by introduced mammals such as rats, cats, dogs, and pigs may have also contributed. Various accounts of visits to the Galápagos in the 17th, 18th, and early 19th centuries mention the tremendous numbers of tortoises that lived there, and Floreana was no exception. The buccaneers, whalers, and explorers of this time often took on board hundreds of tortoises during a single landing. As a result, tortoises became very rare or extinct on islands that initially seemed to have an inexhaustible supply. My account of the history of man-tortoise relationships in the Galápagos is taken mostly from Baur (1889), Van Denburgh (1914), Townsend (1925a), and Slevin (1935, 1959).

Floreana has not been active volcanically in historic times, so volcanic catastrophies can be eliminated as a possible cause of extinction of tortoises there. Fernandina is the only island in the Galápagos where volcanism may be involved in the extinction or rarity of tortoises. Only a single tortoise has ever been collected on Fernandina (on 6 April 1906, by Rollo Beck). Fernandina is the most active volcano in the Galápagos, and most of its area is covered with fresh, barren lava flows. If tortoises ever occurred naturally and are now extinct on Fernandina, then this extinction is undoubtedly due to natural means, i.e., volcanic activity.

Tortoises can survive for months without food or water, so they are an ideal source of fresh meat for sailors. According to Captain Benjamin Morrell (1832; in Baur, 1889:1055, 1056):

They are an excellent food, and have no doubt saved the lives of thousands of seamen employed in the whale-fishing in those seas, both American and Englishmen. I have known whale-ships to take from six to nine hundred of the smallest size of these tortoises on board when about leaving the islands for their cruising grounds; thus providing themselves with provisions for six to eight months, and securing the men against the scurvy. I have had these animals on board my own vessels from five to six months without their once taking food or water; and on killing them I have found more than a quart of sweet fresh water in the resceptacle [sic] which nature has furnished them for that purpose, while their flesh was in as good condition as when I first took them on board. They have been known to live on board some of our whale-ships for fourteen months under similar circumstances, without any apparent diminution of health or weight.

On large islands, female tortoises occur more frequently in the arid coastal regions than males, which tend to concentrate in the humid highlands (Hendrickson, 1966). Thus human predation initially took many more females than males, simply because the females were more accessible. Medium-sized tortoises (50–100 lbs.) were preferentially sought because they were not too heavy to transport, yet they could yield significant quantities of meat. Tortoises were taken mainly for their meat, but their oil was also an attractive commodity for many tortoise hunters. Residents of various islands in the Galápagos, including Floreana, killed tortoises regularly and in large numbers for their oil alone. The tortoises from Floreana and Hood Island (= Española) may have been favored above those of other islands, for Porter (1822:233) stated that those from Española "were of a quality far superior to those found on James Island. They were similar in appearance to those of Charles Island, very fat and delicious."

Rose (1924:354) reasoned that Floreana was the island where buccaneer Edward Davies of the *Batchelor's Delight* obtained many tortoises in 1687, which would be the first record of human predation on the Floreana tortoise. Through much of the 18th century, however, removal of

tortoises from Floreana probably occurred at a low rate because of the infrequency of ships passing through the Galápagos. American and British whaling ships became numerous in Galápagos waters from the late 1700's until the late 1800's. These ships were very destructive to tortoises.

By the year 1800, tortoises were still abundant on Floreana, although the whaling ships undoubtedly had already reduced their numbers. The largest decline of Floreana tortoises occurred in the last 50 years of their existence, the period from 1800 to 1850. Amasa Delano (1817) reported that tortoises were plentiful on Floreana in 1801 and several years thereafter. Known removals of tortoises from Floreana from 1812 through 1837 are compiled in Table 11, although this list is very incomplete. For example, no fewer than 31 whaling ships called at Floreana between 13 October 1832 and 30 August 1833 (Reynolds, 1835; in Baur, 1889). Reynolds (in Townsend, 1925a) estimated that each of these ships took on board 200 tortoises, whereas Townsend (1925a) reported an average of 138 tortoises taken by each of 9 whaling ships that called at Floreana in early and mid-1830s. Thirty-one ships taking 138 tortoises each over a period of 10½ months would result in the removal of 4890 tortoises per year from Floreana by ships alone, and this figure may be an underestimate. Baur (1889) stated that about 100,000 tortoises were removed from the Galápagos since their discovery, but subsequently he revised this figure (in Townsend, 1925a,b) to 10,000,000. The truth may lie somewhere in between.

E.C. Cornell (in Townsend, 1925a:95) noted the presence of hatchlings in 1816, suggesting that tortoises were still reproducing at a significant rate, which suggests further that most or all of the feral predators were absent at that time. Visits by whaling ships to Floreana increased in frequency after 1832, for General Villamil's settlement could provide passing ships with fresh fruit and vegetables. The availability of fresh water, produce, and tortoises made Floreana the most beneficial stop in the entire archipelago.

TABLE 11.—Tortoises taken from Floreana by ships (mostly American whalers) from 1812 to 1837 (data mainly from Townsend (1925a, 1928), supplemented by Porter (1822:160) and Slevin (1935; 1959:74, 128)).

Year/Ship	Number of tortoises	Number of days of tortoise hunting
1812 Sukey	250	?
1813 Essex	30	1
" "	400–500	?
" Briton	"a few"	1
1814 "	24	1
1816 Eliza	"boatloads"	1
" "	74	2
" Apollo	300	7
1820 Essex	60	?
1824 Wasp	100	?
" Loan	394	?
1828 India	100	?
1831 Magnolia	155	2
" Frances	179	5
1832 Hector	226+	7
1833 Octavia	235	?
1834 Bengal	100	2
" Moss	350	15
" Benezet	120	5
" L. C. Richmond	?	1
1835 Barclay	50	3
" Benezet	40	6
" Pioneer	?	8
1836 Ohio	?	4
" Pioneer	?	2
1837 Eliza Adams	24	4
Total	3311+	77+

Van Denburgh (1914:220) reported that the people who colonized Floreana in 1832 (see "Human History") had, with the help of their feral mammals, "reduced the number of tortoises upon Charles Island so rapidly and to such an extent that within three years [= 1835] the people were obliged to send hunting parties to other islands to procure a supply of food." In 1835, Darwin (1871:144) encountered on James Island (= Santiago) a group of men from Floreana who were hunting tortoises. Yet tortoises were still being hunted successfully on Floreana at that time, for Darwin (1871:142) noted that, "the staple article of animal food [of the people living

on Floreana in 1835) is supplied by the tortoise. Their numbers have of course been greatly reduced in this island, but the people yet count on two days' hunting giving them food for the rest of the week."

Very shortly after 1835, however, the Floreana tortoise declined to the point of no return. The combined hunting pressure from human residents, whalers, and feral mammals was simply exhaustive. The whaler's logbooks examined by Townsend (1925a, 1928) record no tortoises taken from Floreana after 1837, except for a few obtained in 1847 by the ship *Congaree* and in 1848 by the ship *Aurora*. Townsend reasoned, however, that these tortoises probably were not native to Floreana, but were imported from other islands.

Reasonable estimates of the date of extinction of the Floreana tortoise range from 1840 (Heller, 1903) to 1850 (Broom, 1929). The French frigate *La Venus* visited Floreana in 1838, just three years after the *Beagle*'s visit, and made collections of birds and plants, but made no mention of tortoises (Slevin, 1959:56). Berthold Seemann of HMS *Herald* visited Floreana in 1846 and reported the tortoise to be extinct, whereas wild dogs, pigs, goats, and cattle were abundant (Van Denburgh, 1914:226). Dr. Kinberg of the Swedish ship *Eugenie* found no tortoises on Floreana in 1852. The U.S. whaling ship *Fabius* visited Floreana for one day in 1858, sending "boats ashore after turtle" (Townsend, 1925a:82). Their results are not known. Professor Louis Agassiz, on board the U.S. steamer *Hassler*, purchased a tortoise on Floreana in 1872, and Townsend (1928) listed three tortoises taken on Floreana in 1882 by the U.S. whaler *Atlantic*. Broom (1929) rightly cautioned, however, that any tortoises collected on Floreana after 1850 were probably brought there from another island by the settlers of Floreana. The following statement of Heller (1903:45) is misleading in that it implies that Commander W.E. Cookson of HMS *Peterel* collected tortoises on Floreana in 1875: "Commander Cookson . . . collected some reptiles, chiefly tortoises, at Abingdon, Albemarle, and Charles." In fact, Cookson (1876) reported that

the Floreana tortoise had become extinct 20–30 years before 1875. (Steindachner (1876) and Gunther (1877a,b) reported on the reptiles collected by Cookson.) All subsequent explorers of Floreana have also failed to find living tortoises, including the thorough search made by the California Academy of Sciences Expedition in 1905–1906 (Slevin, 1931:5; see J.R. Slevin's herpetological field notes in Van Denburgh, 1914:317, 318, and in Fritts and Fritts, 1982). All things considered, the year 1850 is a very reasonable estimate of the date of extinction of the Floreana tortoise, although it must have been extremely rare during the last decade of its existence.

Tortoises on Floreana may have become extinct or nearly so even if direct human predation had never occurred; the 150 years of combined efforts by alien mammals may have been sufficient by itself to reduce tortoise populations beyond recovery. Rats, cats, dogs, and pigs eat young tortoises or tortoise eggs, while feral browsers and grazers (donkeys, cattle, and especially goats) are detrimental to tortoise populations through competition for food (MacFarland et al., 1974a,b). Even if the adult population were healthy, the feral predators may be capable of preventing successful recruitment. Cookson (1876) stated that dogs kill not only very young tortoises, but also those weighing up to 60 lbs. Townsend (1928) mentioned that rats and cats feed on newly hatched tortoises. Thus it may be that Floreana's feral mammals played a significant role in wiping out the tortoises; predation by seafarers and residents probably was not the unique cause of their extinction.

Alsophis biserialis: This snake is known from Floreana by only one specimen taken in 1835 by Charles Darwin. Presumably it is extinct there, but extinction is difficult to prove because of the inconspicuous habits of snakes. *Alsophis* may possibly survive on Floreana in extremely reduced numbers, simply having eluded collectors of the past 150 years. Snakes had never been collected on San Cristóbal, for example, until three specimens were taken in 1957 (Mertens, 1960). The California Academy of Sciences Expedition collected one snake on Gardner-near-Floreana Is-

land on October 1905, this specimen apparently being conspecific with the snake of Floreana itself (Van Denburgh, 1912a:337). As mentioned previously, snakes are common today on Champion and Gardner-near-Floreana. The California Academy of Sciences Expedition collected 98 snakes on other islands in the Galápagos from 24 September 1905 to 25 September 1906 (Van Denburgh, 1912a:330; Slevin, 1931:34, 150), an average of one snake for every 3.7 days in the field. They spent 28 days on Floreana (see the herpetological field notes of J.R. Slevin in Van Denburgh, 1914:317, 318, and in Fritts and Fritts, 1982), which therefore could have been expected to yield approximately 7 or 8 snakes. Instead they found none.

Scarcity or absence of snakes on Floreana can be attributed to man and his introduced mammals. Van Denburgh (1912a:338) stated:

Snakes must be very rare on Charles Island, for none were seen there by any member of our expedition [CAS], although careful search was made for them. It is probable that the ravages of the smaller kinds of mammals that have been introduced there—particularly rats and cats—have pushed them to the verge of extinction, as they have the *Tropidurus*. It is probable that a longer search would show that snakes are still to be found on Champion and Enderby as well as on Gardner, for *Tropiduri* [sic] still are fairly abundant on all these islets.

Presumably the predatory actions of rats, cats, dogs, and pigs, as well as humans, have been devastating to the Floreana snake. Humans are particularly fond of killing snakes of any sort, out of simple fear and loathing.

The vegetational damage wrought by goats, cattle, pigs, and donkeys on Floreana may also have been detrimental to snakes. Goats alone may not be very damaging to snakes in the short run because snakes are still common today on Santiago, Española, and Sante Fé, three islands that are, or have been until recently, heavily populated by goats. Discussing modern tropical situations, Janzen (1976:372) stated:

Through intensive grazing, browsing, and trampling, especially near watercourses during severe dry seasons, large herbivores should greatly reduce the cover available for reptiles, the small vertebrate prey of snakes, and the insects available to reptiles.

Similar damages by large herbivores on Floreana may have been very detrimental to *Alsophis biserialis* as well as the lizard *Tropidurus grayii*.

Judging from the size of collections from individual islands of the California Academy of Sciences Expedition (Van Denburgh, 1912a: 330), snakes were common in 1905–1906 on Española, Santa Cruz, and Santa Fé, and were reasonably common on Santiago, Fernandina, Baltra, and Rábida. At that time, only Santiago of the above islands had rats (Patton et al., 1975) and pigs, and probably none of these islands had feral cats or dogs. Isabela, San Cristóbal, and Floreana were the large islands where snakes were rare or non-existent in 1905–1906; each of these islands already had been settled by people and had obtained a variety of feral mammals, including rats. The effect of introduced mammals on snakes can be inferred further from the case of Santa Cruz. As noted above, snakes were common on Santa Cruz when this island lacked introduced mammals. Since the 1920's, Santa Cruz has been colonized intensively by people, and now it boasts a full complement of rats, cats, dogs, pigs, goats, cattle, and donkeys, not to mention several thousand people. Snakes are very rare on Santa Cruz today; I have never seen a snake there in over four months of field work. Snakes are common today in the Galápagos only on Española, Santa Fé, Seymour Norte, Pinzón, Rábida, Santiago, and Fernandina (Robert P. Reynolds, pers. comm.; personal observation). Each of these islands except Santiago lacks introduced mammals. Santiago is heavily populated by goats, pigs, and rats, so the abundance of snakes there is difficult to explain.

To summarize, the decline and probable extinction of snakes on Floreana is more speculative than that of the Floreana tortoise. It is much easier to say that an island has no tortoises than to say that it has no snakes. Most or all of the introduced mammals were well established and undoubtedly affecting the snake population of Floreana by the 1830's. Snakes were probably in very low numbers by 1850, and may not have survived the close of the 19th century.

Buteo galapagoensis: Specimens of *B. galapa-*

goensis have never been reported from Floreana, nor is this hawk mentioned specifically to occur there in early accounts, such as those of Porter (1822), Darwin (1871), and Markham (1880). Nevertheless, this passage from Gould (1841:25), based upon Darwin's observations on hawks in 1835, provides fairly convincing evidence that *B. galapagoensis* did indeed once live on Floreana: "... on all islands, it [the hawk] is excessively numerous. ... It is extremely tame, and frequents the neighborhood of any building inhabited by man. ... These birds will eat all kinds of offal thrown from houses. ... They are said to kill young doves, and even chickens. ..." These statements could pertain only to Floreana, for the other three islands visited by the *Beagle* were uninhabited by people in 1835. Because it went unrecorded on Floreana by all subsequent collectors, *B. galapagoensis* must have died out or been severely depleted soon after 1835.

Providing no details, Thornton (1971:150), Harris (1973; 1974:37, 86; 1982:37, 87), Vries (1975), and Groot (1983) have noted that hawks are extinct on Floreana. This extinction may have been due to human predation because *B. galapagoensis* is very tame. On Isabela and Fernandina I have approached these hawks to within 0.5 m. This hawk can be killed easily with firearms, and in fact, is still hunted in the Galápagos (Duffy, 1981; Groot, 1983). Hawks are also presumably extinct on the settled island of San Cristóbal (Harris, 1973; 1974:37,86; 1982:37, 87), where the last specimen was taken in 1905–1906 by the California Academy of Sciences Expedition (Swarth, 1931:50). On Santa Cruz, hawks were abundant in 1905–1906 (Gifford, 1919:190), but are very rare today (Harris, 1973). Santa Cruz was first settled in the 1920's and 1930's, and now supports more people than any other island in the Galápagos.

Snodgrass and Heller (1904:265) noted that the absence of hawks on Floreana may be due to the scarcity of *Tropidurus*, but it seems unlikely that a change in availability of prey, such as the drastic reduction in numbers of snakes and lava lizards, could have caused the hawk's extinction. *Buteo galapagoensis* is an extremely opportunistic and versatile predator and scavenger (Vries, 1976), and probably could have thrived on the rats, mice, and large mammal carrion that became available on Floreana with the arrival of man. Direct human predation appears to be the most reasonable explanation for the loss of hawks on Floreana.

Tyto punctatissima: Barn owls were not recorded definitely from Floreana until I found their fossils in Barn Owl Cave. Nevertheless, I believe that barn owls died out in historic times, as with all other extinct vertebrates from Floreana. Otherwise, the remains of black rats (*Rattus rattus*) and house mice (*Mus musculus*) in the caves would be difficult to explain. The other owl in the Galápagos, *Asio flammeus*, does not roost in lava tubes.

The extirpation of *T. punctatissima* may have occurred through severe population declines in its preferred prey species, and probably was aided by direct predation on the owls by people, cats, or dogs. Rodents dominate the diet of *T. punctatissima* on other islands. Floreana has always lacked native rodents, which would have appeared in the fossil sites had they been present. Thus *T. punctatissima* never may have been as common on Floreana as it is (or was) on the rodent-bearing islands of San Cristóbal, Santa Cruz, Santiago, Isabela, and Fernandina. Groot (1983) attributed the absence of barn owls on Floreana to the lack of rodents, but the fossil record shows that barn owls did exist and breed on Floreana in the absence of native rodents. Based upon fossils, the 7 most common vertebrate prey items for barn owls on Floreana were, in descending order, *Geospiza magnirostris*, *Tropidurus grayii*, *Zenaida galapagoensis*, *Phyllodactylus baurii*, *Mimus trifasciatus*, *Alsophis biserialis*, and hatchling *Geochelone elephantopus* (Tables 7, 8). Collectively, these 7 species made up approximately 86% of the barn owl's diet. *Geospiza magnirostris*, *Mimus trifasciatus*, *Alsophis biserialis*, and *Geochelone elephantopus* are now extinct on Floreana, whereas *Tropidurus grayii* and *Zenaida galapagoensis* survive only in extremely reduced numbers. *Phyllodactylus baurii* is the only one of the 7 most common prey species that still prob-

ably occurs on Floreana in "normal" numbers. But this tiny gecko is the smallest vertebrate on Floreana and could never provide the bulk of an owl's diet. Otteni et al. (1972) noted a drastic decline in yearly reproductive rates of *T. alba* in Texas when their preferred food (in this case, small mammals) declined in numbers. Therefore, a rapid but long-term decline in preferred prey, such as occurred on Floreana, could have proved fatal to an insular population of barn owls. The major decline in prey species occurred approximately from 1830 to 1860, so *T. punctatissima* may have died out on Floreana by the 1860s or 1870s.

Killing of barn owls by people and feral mammals may also have been involved in their disappearance. Such predation may have provided only the "coup de grace," or it may have been just as important as loss of prey in wiping out *T. punctatissima*. In the absence of predation from man and feral mammals, *T. punctatissima* may have been able to adjust to the change in prey availability (i.e., fewer native animals, more introduced rats and mice) that occurred with the peopling of Floreana. Harris (1973) stated that man probably was directly involved in the loss of *T. punctatissima* from Floreana, presumably through predation. I believe that most 19th century encounters between human residents and barn owls were fatal to the latter, for this owl is amazingly tame, and can be killed very easily. As with hawks, residents still kill barn owls today on other islands in the Galápagos (Duffy, 1981; Groot, 1983). In 1906, the California Academy of Sciences Expedition collected one barn owl on Isabela with a stick, and three on Santa Cruz that were perched only 6–7 feet away (Gifford, 1919:194). On Santa Cruz, I have approached barn owls to within arm's reach without making them fly. That *T. punctatissima* could have existed on Floreana in the 19th century but eluded collectors is not unrealistic, for few ornithologists visit caves or do much collecting at night.

Mimus trifasciatus: This mockingbird has been extinct on Floreana since approximately the 1870s. It survives today only on Champion and Gardner-near-Floreana, with respective total populations (in 1980) of 48 and 150–200 individuals (P.R. Grant, 1980). Other than the fossils reported herein, only 3 specimens of *M. trifasciatus* are known from Floreana. The *Beagle* Expedition collected two specimens in September 1835 (Gould, 1837b), and Dr. Kinberg of the Swedish frigate *Eugenie* collected a single specimen in May 1852 (Sundevall, 1871). As far as I can determine, no specimens of *M. trifasciatus* have been taken on Floreana since 1852. The last record of mockingbirds on Floreana is from Dr. A. Habel, whose field notes of 1868 (in Salvin, 1876:472) reported that "the Mocking Thrushes there [Floreana] differed in their livelier and more intelligent habits, and in their superior powers of song [compared to *M. macdonaldi* of Española.]" Habel took no specimens of mockingbird from Floreana.

Baur (1895) was the first to suggest that *M. trifasciatus* was extinct on Floreana, followed by Ridgway (1897:482, 483). Ridgway was unaware of Kinberg's specimen taken in 1852, and thus stated that nobody had collected *M. trifasciatus* since Darwin's visit in 1835. Rothschild and Hartert (1899:142, 143) were next to mention the extinction of mockingbirds on Floreana, based on the failure of collectors such as Habel (in 1868), the naturalists of the *Albatross* (in 1888, 1891), Baur and Adams (in 1891), and Webster and Harris (in 1897), as well as others, to procure any specimens. (As noted above, however, Habel did observe mockingbirds on Floreana.) Since 1899, *M. trifasciatus* has been reported to be extinct or probably extinct on Floreana by Snodgrass and Heller (1904:358, 359), Rothschild (1907:xi, xii), Gifford (1919:207), Swarth (1931:114, 117), Hellmayr (1934:334), Lack (1947:23), Harris (1968, 1973, 1974:36, 37, 128; 1982:36, 128), Bowman and Carter (1971), Thornton (1971:79, 80, 157, 160), and I. Abbott and L.K. Abbott (1978). Swarth (1931:117) suggested that the mockingbirds collected by the *Beagle* Expedition may have been taken on Gardner-near-Floreana instead of Floreana itself. This caution was reiterated by Thornton (1971:160) and Bowman and Carter (1971).

As mentioned previously, *M. trifasciatus* still

occurs on Floreana's satellite islands of Champion and Gardner-near-Floreana. I have not visited Garner-near-Floreana, so I will confine my discussion to the mockingbirds living on Champion. The flora of Champion seems to be pristine (Figure 25; also see plant lists in B. Voigt and A. Voigt, 1977; P.R. Grant, 1980). We are fortunate that this small offshore island has preserved a flora that probably resembles that which existed on the adjacent lowlands of northern Floreana before the arrival of man. During visits to Champion on 4 July 1978, 26 October 1980, and 24 May 1983, I observed at least 12 different mockingbirds, each of which was either on the ground or in an arborescent prickly pear cactus (*Opuntia megasperma* var. *megasperma*). Although other trees and shrubs were common, such as *Bursera graveolens, Croton scouleri, Jasminocereus*

thouarsii, Parkinsonia aculeata, and *Prosopis juliflora,* I did not observe the mockingbirds to use these plants in any way. The only time that I saw a mockingbird on Champion use any plant other than *Opuntia* was a single bird that landed briefly in a shrub (*Cordia lutea*) on 24 May 1983. My observations are corroborated by those of several other authors. Gifford (1919:207) reported finding mockingbirds on Champion near *Opuntia,* with "a nest or two . . . in nearly every good-sized cactus tree." Harris (1974:128) reported the nest of *M. trifasciatus* to be "usually a substantial mass of twigs placed in a cactus." B. Voigt (1977b) noted: "Old nests found only in cacti, about 2 m above ground." Mockingbirds from other islands in the Galápagos also use *Opuntia* frequently as a nesting site (Rothschild and Hartert, 1902:383; Gifford, 1919:209–214; Harris,

FIGURE 25.—Gayle Davis among the abundant cactus, *Opuntia megasperma* var. *megasperma* (Champion Island, May 1983).

1974:126, 128; P.R. Grant and N. Grant, 1979), but they are not as completely dependent upon *Opuntia* as is *M. trifasciatus.*

Opuntia may also be important to *M. trifasciatus* as food, although no quantified food studies exist. *Mimus trifasciatus* feeds on flowers and fruits of *Opuntia*, as well as grasshoppers, ants, moths, spiders, and centipedes from the ground and rotting *Opuntia* pads, eggs of *Sula nebouxii*, and flowers of the prostrate vine *Convulvulus* (Hatch, 1965; Bowman and Carter, 1971; De Ridder, 1976; B. Voigt, 1977a,b; B. Voigt and A. Voight, 1977; B.R. Grant, 1981; Harcourt, 1982).

To summarize, *M. trifasciatus* feeds, nests, and roosts exclusively in or near *Opuntia*, a plant that is essential to the survival of *M. trifasciatus* on Champion. A major vegetational difference between Champion and Floreana is Champion's much greater density of *Opuntia*. One would expect to find *Opuntia* commonly in the arid lowlands of Floreana just as on other islands in the Galápagos, but in fact both species of columnar cactus (*Jasminocereus thouarsii* var. *thouarsii*, Fig. 46A of Dawson, 1962; and *Opuntia megasperma* var. *megasperma*, Figure 25) survive on Floreana mainly on steep, inaccessible, rocky outcrops, such as on the tops of dikes or vertically eroded tuff cones. Floreana's small, offshore islets are the only places left in the Floreana region where cacti are still more or less as they existed before human contact (Figure 25). Porter (1822:162) found "prickly pears in great abundance" on Floreana in 1813, so there is no reason to doubt that cactus was not abundant on Floreana before 1832, the initial year of major human occupation. The botanist Hugh Cuming visited Floreana in 1829 (Howell, 1941), three years before Villamil settled the island, but I am unaware of any notes describing the cactus he presumably found there.

The destruction of cactus on Floreana was caused by feral ungulates. The arid lowlands of Floreana lack fresh surface water, so the succulent stems and pads of cactus provide a very good source of moisture for large introduced herbi-vores. Townsend (1930) and Dawson (1962) blamed feral donkeys and cattle for the scarcity of *Opuntia* on Floreana. Koford (1966) and Hamann (1975) discussed damage to *Opuntia* in the Galápagos by feral goats, an extreme example of which is found by comparing figures 1 and 6 of Hamann (1975). According to Dawson (1962) and Andre De Roy (pers. comm.), donkeys are stronger and therefore more destructive to cactus than are goats, so that goats alone are less effective in destroying cactus than is the combination of goats and donkeys. Beginning in the 1830's, I believe that goats and donkeys heavily damaged the cactus of Floreana. As the *Opuntia* disappeared, so did the mockingbirds.

The extinction of *M. trifasciatus* on Floreana was not as rapid as that of *Geospiza magnirostris*, another bird whose loss I attribute to the rarity of *Opuntia* in the lowlands of Floreana. I doubt that the longer survival of *M. trifasciatus* was due to its being any less dependent on *Opuntia* than was *G. magnirostris*. Instead, *M. trifasciatus* may have been slightly better at avoiding predation from feral cats and dogs. Such predation may have added the final touches to wiping out both *G. magnirostris* and *M. trifasciatus*, once they were localized because of loss of habitat.

Predation by dogs and especially cats has been suggested as the sole cause of extinction of *M. trifasciatus*, although Swarth (1931:117), who questioned whether or not *M. trifasciatus* ever occurred on Floreana, doubted that such predation was an important factor. Swarth pointed out that the northern coast of Floreana, adjacent to Champion, lacked cats and dogs early in the 20th century according to J.R. Slevin. Swarth's suggestion seems unlikely, however, for cats and dogs were certainly established elsewhere on Floreana at this time, as indicated by Slevin himself (1959:7; see "Introduced Mammals"). Harris (1974; 1982:36, 37) also doubted that cats were responsible for the loss of *M. trifasciatus* on Floreana. On Santa Cruz and southern Isabela, *M. parvulus* appears to thrive today in the presence of cats and dogs, and the same is true for *M. melanotis* on San Cristóbal. Behavioral differ-

ences, however, may have made *M. trifasciatus* more vulnerable to predation than *M. parvulus* or *M. melanotis*. By leading a rather specialized life that involves spending essentially all of its time either in cactus or on the ground, *M. trifasciatus* may have been much easier to prey upon than *M. parvulus* or *M. melanotis*, which are not so dependent upon *Opuntia*. Lastly, Duffy (1981) suggested that pathogens, perhaps introduced by domestic fowl, may have been involved in the loss of *M. trifasciatus*.

If feral ungulates were removed from Floreana, the vegetation of the arid lowlands may regenerate toward what it was like before the 19th century. If *Opuntia* increased in abundance, *M. trifasciatus* might be able to live once again on Floreana, if feral carnivores were eradicated. Re-colonization of Floreana would probably require transplanting individuals from Champion or Gardner-near-Floreana, for I. Abbott and L.K. Abbott (1978) noted that no stray mockingbirds from these nearby islands have ever been recorded on Floreana. Captain David Porter (1822:163) found mockingbirds in great numbers on Floreana in 1813. To restore their former abundance would seem to be a worthy goal of future conservation efforts in the Galápagos.

Geospiza nebulosa nebulosa: Lack (1945:9, 10, 14, 15) was the first author to suggest that *G. nebulosa* may be extinct on Floreana. Until Lack's discovery that *G. nebulosa* was a large form of *G. "difficilis*," ornithologists since Salvin (1876) had regarded *G. nebulosa* as a synonym of *G. fortis* (see account of *G. nebulosa* in "Systematic Paleontology"). This synonymy not only masked the true relationships of *G. nebulosa*, but also covered up the fact that nobody had collected *G. nebulosa* on Floreana since 1852. *Geospiza fortis*, on the other hand, had been collected regularly on Floreana since the *Beagle's* visit in 1835, and is still common there today. By regarding *G. nebulosa* as synonymous with *G. fortis*, ornithologists had no clue that they were ignoring an extinct, morphologically recognizable population. Subsequent to Lack (1945), the following authors have noted that an extinct form of *G. "difficilis"* may

have occurred on Floreana: Lack (1947:23, 120; 1969), Bowman (1961:270), Paynter (1970:162), Harris (1973; 1974:36, 144; 1982:36, 145), Sulloway (1982a,b, who resurrected the name *nebulosa*), and Schluter and P.R. Grant (1982).

Geospiza nebulosa was either extinct or very rare on Floreana by the 1860s or 1870s. It was last collected in 1852 by Dr. Kinberg of the Swedish frigate *Eugenie*. Floreana was visited rather frequently from the 1860s onward, yet no specimens of *G. nebulosa* were procured. Almost certainly it was extinct no later than the turn of the century, for the California Academy of Sciences Expedition found none during their intensive collecting effort on Floreana in 1905–1906. That the *Beagle* crew took 3 specimens of *G. nebulosa* from Floreana in 1835 suggests that it was not a rare bird at that time. This was just three years after the initial settlement of Floreana, so *G. nebulosa* may not yet have been affected greatly by human habitation. Nevertheless, total extinction of *G. nebulosa* may have occurred rapidly once its population began to decline. On Santa Cruz, *G. nebulosa* was common in 1905–1906 (Gifford, 1919:238), but apparently had vanished by the late 1930's (Lack, 1945:13), within a decade after the highlands of Santa Cruz began to be cleared extensively for cattle grazing.

Referring to the history of Santa Cruz, Lack (1945:9, 10, 13), Bowman (1961:270), Harris (1974, 1982:36), and Sulloway (1982b) postulated that habitat destruction in the highlands may have been responsible for the extinction of *G. nebulosa* on Floreana as well. Bowman (1961:270) noted that predation from feral cats may have been another factor. I. Abbott et al. (1977:170) cited "lack of preferred habitat or food" and "competition" as reasons for the absence of *G. nebulosa* from Floreana. If "lack of preferred habitat" can be taken to mean habitat destruction, then the reasons of I. Abbott et al. (1977) seem compatible with those of Sulloway (1982b), who discussed the extinction of *G. nebulosa* more thoroughly than any previous author. Sulloway stated (1982b:89):

Although once found on all of the larger islands in the archipelago, *G. difficilis* has definitely become extinct on several of them, probably owing to ground clearing and cultivation in the humid zone. It is hardly surprising, then, that *G. difficilis* may have encountered this same fate on Charles Island, which was the first island to be settled, in 1832. Within just a few years, ecological disturbances associated with the settlement were already manifesting themselves. Darwin [see Barlow, 1963:264] specifically noted that the larger species of ground finches, which normally prefer the arid lowlands, were extremely common on Charles Island near the cleared tracts as the highlands settlement. Indeed, these ground finches had become quite troublesome to the settlers, eating seeds buried up to six inches in the cultivated fields. Thus, by the mid-1830s any endemic Charles Island population of *G. difficilis* would have been faced with two threats to its continued existence: a diminishing habitat and increased competition from other species of Darwin's finches that are normally restricted to the lower altitudes.

To summarize, I believe that the extinction of *G. nebulosa* on Floreana, as well as on Santa Cruz and perhaps San Cristóbal and Isabela, can be attributed to a combination of habitat destruction (probably affecting both nesting and feeding), predation by feral cats and possibly dogs, and perhaps competition from newly invading finches such as *G. fortis* and *G. fuliginosa*. Schluter and P.R. Grant (1982) concluded that interspecific competition is the best available explanation for the nearly mutually exclusive distributions of *G. nebulosa* and *G. fuliginosa*. This would seem to support competition as an important factor in the extinction of *G. nebulosa* on Floreana and elsewhere.

On Genovesa and Pinta, P.R. Grant and B.R. Grant (1980) and Schluter and P.R. Grant (1982) studied in detail the food habits of *G. nebulosa acutirostris* and *G. n. difficilis*, respectively, but to extrapolate these results to Floreana would be risky because the bill in *G. n. nebulosa* of Floreana is so much larger than in *G. n. difficilis* and especially *G. n. acutirostris*. Our information on the habits of *G. nebulosa* in the highlands of large islands is from Gifford (1919:238), who found them commonly on Santa Cruz in 1905–1906

in the thickly vegetated region of the lower humid belt, usually feeding on the ground under bushes, often in flocks. More than once we shot at one, mistaking it for a rail, so skulking were its habits. . . . in the arid region below 75 feet elevation . . . they were found, as formerly in the humid belt, under bushes, digging vigorously in the grass and dry leaves.

Gifford found *G. nebulosa* to feed on the ground also on Santiago, and summarized their habits by stating that (p. 239) "it is strictly terrestrial and does not feed in the trees as do the other species." Its terrestrial habits may have made *G. nebulosa* more vulnerable to predation by feral carnivores than other small finches.

Geospiza magnirostris magnirostris: This finch is almost certainly extinct on Floreana. Claims to its existence after the *Beagle* collections are refuted in Steadman (1984). Based on its abundance as a fossil, *G. m. magnirostris* must have been an extremely common bird prior to the arrival of humans. It makes up 75% of the total fossil finch fauna, being over 12 times more numerous than any other species of Darwin's finch. *Geospiza m. magnirostris* constitutes 86% of the finches from surface deposits, and 65% of the finches from excavations. Probably the last figure more closely approximates the actual relative abundance of this large finch as a fossil, for, as stated previously, the surface collections were biased by the size of *G. magnirostris*. Regardless, the fossil evidence suggests that *G. m. magnirostris* was once very abundant in Floreana's lowlands.

In 1813, Porter (1822:163) found on Floreana great numbers of "a small black bird, with a remarkably short and strong bill, and a shrill note." Porter's bird was probably *G. m. magnirostris*. This species was still common on Floreana in 1835, three years after the establishment of Villamil's colony. The *Beagle* Expedition collected 15 specimens of Darwin's finches on Floreana in 1835, of which five, or 33%, were *G. m. magnirostris*. If we assume the likelihood that the *Beagle* specimens of *G. m. magnirostris* were collected in the lowlands of Floreana, whereas at least some of the *Beagle* specimens of *G. nebulosa* and *G. crassirostris* (which total five specimens) were from the highlands of Floreana, then *G. m. magnirostris* would constitute up to 50% of the lowland finch fauna collected by the *Beagle* crew.

This figure is not too far from the 65% derived from paleontological data, although the relative abundances of the *Beagle* specimens are at best a crude approximation of relative density because of small sample size, collectors' biases, and the possibility of lost specimens.

Geospiza m. magnirostris probably disappeared from Floreana within a decade or two after the only historic specimens were collected. That no additional specimens were taken after 1835 is significant negative evidence, for *G. m. magnirostris* was probably rather conspicuous in life, and by necessity all trips to Floreana had to pass through its habitat in the arid lowlands. The earliest post-*Beagle* collecting efforts on Floreana were those of Adolphe-Simon Neboux and Charles-Rene-Augustin Leclancher of the French frigate *Venus* in 1838, Thomas Edmonston of HMS *Herald* in 1846, and Dr. Kinberg of the Swedish frigate *Eugenie* in 1852. Collectively, these three expeditions spent more than 13 days (perhaps as many as 20 days) on Floreana and obtained specimens of *Geospiza nebulosa*, *G. fuliginosa*, *G. fortis*, *G. scandens*, and *G. parvula*, but not *G. magnirostris* (Sundevall, 1871; Sharpe, 1888; Sulloway, 1982b). It is particularly noteworthy that the *Venus* collectors obtained no specimens of *G. m. magnirostris* during their 11 days on Floreana in 1838, only three years after the *Beagle*'s visit. The *Beagle* crew may have collected *G. m. magnirostris* during its final several years of abundance.

Salvin (1876:479) specifically noted that Dr. A. Habel did not encounter *G. magnirostris* during his visit to Floreana from 27 July to 12 August 1868. Gifford (1919:225) reported that the California Academy of Sciences Expedition took specimens of *G. magnirostris* on Floreana, but Swarth (1931:147) pointed out that Gifford was actually referring to *G. fortis* and not *G. magnirostris*. Bowman (1961:20, 271) cited a specimen he collected as evidence of the modern and past occurrence of *G. magnirostris* on Floreana. This specimen is much too small, however, to represent the large Floreana race of *G. magnirostris* (Steadman, 1984).

As on Floreana, *G. m. magnirostris* has not been recorded from San Cristóbal since the *Beagle*'s visit in 1835 (Sulloway, 1982b). Ridgway (1890:121) noted that the *Albatross* Expedition recorded it there in 1888, but he cited no specimens or other details of this record. 1 have searched in vain for such a specimen in the USNM collection, where the *Albatross* specimens are housed. San Cristóbal was settled approximately a decade after Floreana, so perhaps *G. m. magnirostris* survived there a little longer than on Floreana.

Rothschild and Hartert (1899) were the first to suggest that *G. m. magnirostris* may be extinct on Floreana.

On Charles Island ... probably at least one or two thick-billed finches have become extinct. As the earliest settlement of men has been on Charles Island, and as we know that they had no regard for the birds—sailors, finding the tameness of the birds strange and novel, used to take a cruel pleasure in knocking them down with sticks—we are probably right in ascribing these disappearances merely to human influence [p. 142].

It is probable that *G. magnirostris* [on Floreana] is exterminated or extremely scarce. This is quite possible when we consider that *Nesomimus trifasciatus* has disappeared from Charles Island, and that these finches, according to Darwin [see Gould, 1841:100], did "much injury by digging up roots and seeds from a depth of even six inches." It is therefore to be supposed that they were killed by the colonists, who complained of their injuries, and who first settled on Charles Island about 1830 [p. 154].

Townsend (1928:168; 1930:154) suggested that the loss of *G. m. magnirostris* was due to predation by cats and rats. Lack (1947:23) said that its extinction probably was due indirectly to the human settlement on Floreana, which may mean habitat destruction or predation by feral mammals. Duffy (1981) mentioned introduced pathogens as a possibility. The following authors have regarded *G. m. magnirostris* as possibly, probably, or certainly extinct on Floreana, without proposing any specific cause: Ridgway (1901:493, 496), Lack (1946, 1969:253, 254, 261), Paynter (1970:161), Harris (1973, 1974:143; 1982:144), and Sulloway (1982a,b).

To summarize the story up to this point, *G. m.*

magnirostris was once a very common bird in the lowlands of Floreana, but its extinction occurred rapidly, perhaps within a decade after the *Beagle*'s visit to Floreana in 1835. This extinction has been attributed to human agency through predation by introduced cats and rats, as well as humans themselves. The fossil record sheds no new light on the extinction problem, but does demonstrate the former abundance of *G. m. magnirostris*.

By itself, predation from alien animals does not seem to be sufficient to cause the rapid decline and extinction of *G. m. magnirostris* on Floreana. Other ground finches, such as *G. fuliginosa* and *G. fortis*, were probably less common initially than *G. m. magnirostris*. Why should these species survive such predation while *G. m. magnirostris* did not? If predation, especially by cats and humans, could act this rapidly by itself, then one might expect that *Zenaida galapagoensis* would have become extinct first. Yet this extremely tame and tasty, ground-dwelling dove has survived (although just barely) 150 years of predation on Floreana from man and his feral mammals.

As with *Mimus trifasciatus*, I believe that the severe depletion of *Opuntia* on Floreana by feral ungulates is related to the extinction of *G. m. magnirostris*. This idea has recently been put forth by B.R. Grant and P.R. Grant (1982:653), but requires additional evidence and explanation. Both the bill of *G. m. magnirostris* and the seed of *Opuntia megasperma* var. *megasperma* are extremely large. In fact the seed of *O. m.* var. *megasperma* is much larger and harder than in any other *Opuntia* in the Galápagos, including *O. m.* var. *orientalis* of San Cristóbal and Española (Howell, 1933; Dawson, 1962, fig. 65A–C, 1966; Wiggins and Porter, 1971:545; B.R. Grant and P.R. Grant, 1982). Howell (1934:516) described the seed of *O. m.* var. *megasperma* as "like small, somewhat compressed marbles about a half inch in diameter." No finch of ordinary strength could crack such a seed.

I. Abbott et al. (1977) formulated a composite index of size (depth) and hardness (kg of force) of seeds to evaluate the ability of Darwin's finches to feed on different types of seed. B.R. Grant and P.R. Grant (1982:653) report that the size-hardness index for seeds of *O. m.* var. *megasperma* from Champion is greater than 20, compared to 10.9 for *O. m.* var. *orientalis* from Española and a range of 2 to 7 for other forms of *Opuntia* in the Galápagos. The size-hardness index of *Opuntia* seeds appears to be correlated positively with the bill size of *G. magnirostris* from the same island; Floreana simply represents the highest values for each of these characters: These large sizes evolved together on Floreana, resulting in a dependence of *G. m. magnirostris* on *Opuntia* for much of its food. In addition, Racine and Downhower (1974, table 4) reported that *O. m.* var. *megasperma* produces a much greater volume of seeds than any other *Opuntia* in the Galápagos. *Opuntia m.* var. *orientalis* from San Cristóbal has the second greatest seed volume, but has the greatest fruit volume of all. B.R. Grant and P.R. Grant (1981, 1982) noted that the fruit surrounding the seed is fibrous in *O. megasperma*, whereas it is fleshy in *O. echios*, *O. helleri*, and *O. galapageia*. Thus both the seed and fruit of *O. megasperma* are tougher than in other species of *Opuntia*.

Geospiza magnirostris feeds not only on the seeds of *Opuntia*, but also the flowers, pollen, fruit, and pad fibers (P.R. Grant and B.R. Grant, 1980; B.R. Grant and P.R. Grant, 1981). *Opuntia* occupied 22.5% of the foraging time of *G. magnirostris* on Rábida in June (I. Abbott et al., 1977:181). On Genovesa in November, *G. magnirostris* spent 64.6% of its foraging time on *Opuntia* seeds on the ground, as well as 4.5% on *Opuntia* pad fiber (P.R. Grant and B.R. Grant, 1980, table 18). *Geospiza m. magnirostris* may also have depended heavily upon *Opuntia* for nesting sites, for 28 of 46 nests of *G. m. strenua* on Genovesa were in *Opuntia* (P.R. Grant and B.R. Grant, 1980, table 12).

If *G. m. magnirostris* was dependent upon *Opuntia* for feeding and nesting, then a cause of its extinction on Floreana can be proposed. Beginning in the 1830's, feral goats and donkeys

severely reduced the *Opuntia* in the lowlands of Floreana, thereby destroying the major source of food and nesting sites for *G. m. magnirostris*. Feral herbivores may also have competed with *G. m. magnirostris* for the relatively few remaining fruits of *Opuntia*. By itself, reduction of *Opuntia* may not have completely wiped out *G. m. magnirostris*, but the small, localized groups that survived may have succumbed to predation by rats, cats, dogs, or humans. Thus I suggest that the extinction of both *Mimus trifasciatus* and *G. m. magnirostris* was due mainly to the loss of *Opuntia*. The apparently more rapid extinction of the latter species of bird may be attributed either to a need for larger territories (i.e., a greater inability to survive in small, localized patches of *Opuntia*), or to a greater vulnerability to feral predators, or both.

The extinction of *G. m. magnirostris* on San Cristóbal may have occurred in the same manner as on Floreana because, as mentioned above, the *Opuntia* on San Cristóbal also has large, hard seeds and tough fruit. B.R. Grant and P.R. Grant (1982) have recently suggested that *G. magnirostris* (subspecies unknown) may once have occurred on Española, but became extinct before it was recorded by scientific collectors. This interesting idea awaits verification by the discovery of fossils on Española, which might be difficult because no lava tubes have ever been reported there.

In discussing extinction on Floreana I have taken the position that all faunal losses are due to the impact of man or his introduced mammals. My position is supported by the fossil record, which discloses no clear-cut losses in the last few thousand years before human arrival. This raises several questions. For example, to what degree are insular extinctions random events? By documenting extinctions, can the Holocene fossil record be used to illuminate studies of island biogeography? Can human impact or other causes of extinction be related to the observed differences in intensity and chronology of extinction on different groups of islands?

THEORETICAL BIOGEOGRAPHY AND FOSSILS.—

The past 20 years have witnessed an explosion of publications on the diversity and distribution of insular biotas. Stimulated mainly by the theoretical models of Preston (1962a,b) and MacArthur and Wilson (1963, 1967), researchers have analyzed the floras and faunas of many islands and archipelagos, attempting to support, modify, or refute these models, which are part of an all-encompassing "equilibrium theory of island biogeography." My main intention here is to demonstrate the importance of paleontological evidence in understanding patterns of insular biogeography. I will preface this, however, with some non-paleontological criticisms of theoretical island biogeography.

The species-area equation, $S = CA^z$, is one model of MacArthur and Wilson (1967:8, 9) that has received an enormous amount of attention. "S" is the number of species of a particular taxonomic group on an island, "A" is the area of the island, "C" is a constant "that depends on the taxon and biogeographic region, and in particular most strongly on the population density determined by these two parameters," and "z" is a constant "that changes very little among taxa or within a given taxon in different parts of the world." Both C and z are fitted to the data available for S and A. For a related set of insular floras or faunas, a log-log plot of S (Y-axis) versus A (X-axis) will yield a fitted regression line of supposed predictive abilities whose slope is z and whose Y-intercept is C. Preston (1962a) expressed the species-area equation as $N = KA^z$, but since most workers follow the terminology of MacArthur and Wilson (1967), I will do the same.

The species-area equation, as well as other aspects of the equilibrium theory of island biogeography, has enjoyed great popularity; the few serious attempts to point out its shortcomings have generally been ignored. For example, Haas exposed several major flaws in the species-area equation, stating (1975:371):

In fitting data of any sort there is bound to be some error, which may produce uncertainty about the fitted constants [C, z] and thus the conclusions based on them. The reader

should not be forced to program the data anew himself in order to judge how much to trust these fitted constants. ... wide confidence intervals are not untypical and should be considered more fully before any discussion of the differences between particular z values, which may have been influenced very strongly by a few data points. ... the confidence intervals have a tendency to flare as they move away from the mean, the most stable point on the regression line. Errors or poor fits about the data points will tend to "rock" the regression line about the mean, affecting the end points of the curve most. For this reason, the confidence intervals flare. This means that if one has a species-area curve and wishes to use it to predict the number of species on a nearby island, he must be ready to accept almost any number as fitting his prediction (making it meaningless) if the island is very much smaller or larger than those already considered.

Haas (1975:372) also noted that the theory behind the interpretation of the constants C and Z is poorly understood (and therefore ignored), but that this

really should come as no surprise, since many factors affecting species abundance influence and, in turn, are absorbed by these two constants. This is especially so with C, which is affected variously by the density of the organisms, number of species in the taxa, degree of isolation (MacArthur and Wilson, 1967), and the scale with which the area is measured. In fact, so much variation is sopped up by C that particular values of it are hardly ever discussed. Although used primarily as an index of isolation or "islandness," the parameter z must also be influenced by other factors.

A biogeographic analysis of Hawaiian birds by Juvik and Austring (1979, fig. 2) is a good example of the shortcomings of the species-area equation discussed by Haas. Juvik and Austring do not give confidence intervals, and their data for the two smallest islands are essentially meaningless, or at least are not readily comparable to those of the six larger islands, because the numbers of species of birds and the areas of the islands include drastic changes in magnitude (from 1 to 20 species and from 0.77 to 10,464 km², respectively). Further, their graph has only 8 points per regression line. Finally, as I will discuss further, their biogeographic analyses failed to anticipate how much richer the Hawaiian avifauna was in prehistoric times.

Sauer (1969) made another detailed critism of the equilibrium theory of MacArthur and Wilson

(1967) that deserves more attention than it has received. He wrote (1969:590, 591, 593):

In short, the equilibrium model and its derivatives suffer from extreme oversimplification by treating islands as functional units with no attention to internal habitat diversity and by treating species as interchangeable with no allowance for genetic or geographical diversity. This is not even good as a first approximation, because it filters out the interpretable signal instead of the random noise. The authors are in such a hurry to abandon the particulars of natural history for universal generalization that they lose the grand theme of natural history, the shaping of organic diversity by environmental selection. A model that visualizes various sizes of assemblages of characterless species on various sizes of featureless plains is essentially absurd, since it excludes the very basis of genesis and continued coexistence of multiple species.

MacArthur and Wilson recognize the impracticality of measuring immigration and extinction rates in their models but suggest that these rates might be deduced from variation among islands in equilibrial species number and species composition. They are also hopeful about direct measurement of colonization rates. However, all these approaches require synoptic tabulations of entire biotas. Available tabulations, including most of those the authors cite, are usually accumulations of observations over extended periods of time and, even so, omit parts of the biotas. For an island of any size and complexity, a complete census-type enumeration would be a fantastic undertaking, particularly if the criterion of species presence were based on propagules rather than on established populations. The whole approach smacks of ornithology and is reasonable enough for creatures that fly about advertising their presence, especially if they are identifiable by a body of volunteer watchers. However, enumerating the entire biota would require a massive collecting job to be undertaken by specialists. The entire biomass would have to be screened, the forests felled, and the soil sifted for seeds, spores, and whatnot, with each tested for viability and cultured until mature enough to be identified. Each census would produce the suggested artificial Krakatoa and whatever was left of the biota could hardly be pursued to the next census as an equilibrium system.

At present, I believe, biogeography would accomplish more by using its concepts and tools than by redesigning them. No matter how cleverly derived, our models will remain soft and amorphous until calibrated with real values. We need to work out enough solid cases of species patterns and the processes shaping them to get beyond vague banalities and isolated details. This is a grand enterprise in which any number can join. Eventually, work will have to be pushed with some taxonomically difficult organisms in some unpleasant habitats. At the moment there are still plenty of easily recognized species and many beautiful islands that no bio-

geographer has claimed. There are good practical reasons for continuing to draw on islands for case studies, though there is no longer any excuse for segregating them from continents in biogeographical theory

Sauer's criticisms are no less valid today than they were in 1969.

The species-area relationship has recently been criticized from another standpoint by Connor and Simberloff (1978), who discussed inadequacies in studies of species-area relationships of Galápagos plants and birds. They noted (p. 219): "Generalizations about factors determining species numbers that are based on multiple regression and correlation are precarious." Further, Connor and Simberloff (1978) stated that the values used for numbers of species may be faulty for the following reasons, which are more or less the same as some of Sauer's criticisms: all species are treated equally, when in fact some are much more abundant or otherwise biologically important than others; criteria for residency are ambiguous (for example, is a single propagule enough to be counted, or must there be a breeding population?); and different islands have not been collected as thoroughly as others, so that species lists vary in their levels of completeness (see the example below on bats of St. Bartholomew). Connor and Simberloff justifiably criticized previous attempts to model the biogeography of the Galápagos, but then they went ahead and proposed their own, admittedly inadequate, alternative models.

Connor and McCoy (1979) analyzed the data used in 100 species-area curves from all over the world in reviewing the statistics and biology of the species-area relationship. Their conclusions (pp. 814, 815) should be sobering to many theoretical biogeographers:

Our discussion of the theoretical basis of the species-area relationship was basically inconclusive. The two most frequently proposed hypotheses, habitat diversity and area per se are both possibly correct, yet the results of either mechanism is neither qualitatively nor quantitatively different. One virtually always observes a positive correlation between species number and area, regardless of the mechanism. . . .

In general, we have found that published predictions and interpretations concerning both the slope and intercept pa-

rameters [z and C] are not supported by the available evidence. Many other predictions and interpretations are either logically untestable or require additional data for an adequate test. Because of these results, we are skeptical that any biological significance can be attached to these parameters and recommend that they be viewed simply as fitted constants devoid of specific biological meanings.

1 do not believe that the findings of Connor and McCoy (1979) were as inconclusive as they claimed. Rather, 1 believe that they corroborated the thesis of Sauer (1969) and Haas (1975), namely that biogeographers have yet to blend quantitative theory satisfactorily with empirical data.

To summarize thus far, the criticisms by Sauer (1969), Haas (1975), Connor and Simberloff (1978), and Connor and McCoy (1979) cast much doubt on the significance of modern quantified island biogeography. The derivations of C and z are simply too vague and shallow to permit quantitative comparisons of insular biotas that are based on the calculated values of these constants, which cannot account for all of the factors that actually do influence the number of species on islands. Common sense tells us that both area and habitat diversity are related to the number of species of organisms on islands, but neither is sacred in itself.

That Sauer's suggestions have been ignored is particularly unfortunate; instead of rigorous surveys of insular biotas, many biogeographers do little if any field work and thus are not familiar with the methodology and validity of the data sets that they manipulate. Most workers still operate with the illusion that the systematics and distribution of vertebrates are so well known that one can go merely to check-lists and find definitive data to be analyzed. For the past 10 years, various field parties from the Smithsonian Institution have been surveying the vertebrates of the West Indies. We have visited over 40 islands altogether, and in nearly every case we have added species to the island's faunal list, whether amphibians, reptiles, birds, or mammals. Much of this information is still unpublished, but our findings clearly show that the distribution of

vertebrates (considered to be the best-known group of animals) in the West Indies (considered to be one of the best-known groups of islands) is in fact too poorly known to attempt any detailed, quantitative analyses.

For example, Fleming (1982) studied several aspects of the distribution of birds and bats in the West Indies; his computations depended upon knowing how many resident species occur on each island considered. There is such scatter in the points of his species-area graphs (Fleming's figs. 1, 2) that any line drawn through these points has confidence intervals so large as to be meaningless or very nearly so, sensu Haas (1975). One reason why these points are so scattered is the inconsistency of the data-gathering process, exemplified as follows. In October 1982, our field party (R.I. Crombie, L.K. Gordon, G.K. Pregill, and I) collected three species of bats (*Brachyphylla cavernarum, Artibeus jamaicensis,* and *Molossus molossus*) on St. Bartholomew that had not been recorded there previously, thereby raising the number of species of bats known from this island from one to four. If three nights (six net-nights) of suburban mist-netting can quadruple an island's chiropteran fauna, we should not be surprised that the points in Fleming's graphs are so scattered. Nevertheless, typical of ecologists, Fleming laments that (1982:59) "all that is known about them [the bats] is their geographic distribution." Only through much more field work can we piece together the distribution and species-level systematics of West Indian vertebrates, and the same could be said for just about any other group of islands.

P.R. Grant has recently stated (in Lewin, 1983:1411): "There are so many factors influencing the morphology and distribution of organisms that it has been very difficult to generate general theories of community structure." This statement is certainly true, but should we be concerned that functional generalizations are difficult to formulate? As pointed out by Sauer (1982:62, 63), generalized models are seriously flawed because "they eliminate the environmental variables that are the basic causes of such

[biogeographic] patterning." Whether islands or continents or somewhere in between, each region of the world is biologically unique because its geography, geology, and climate, both past and present, have interacted with plants and animals. The potential complicating factors are innumerable, so why should generalization be our main goal if each situation is unique? Comparisons are usually informative, but our efforts should not focus solely upon the search for similarities. Instead we should evaluate each set of data on its own merit, in realization that we will never solve all of the mysteries, nor will generalized models explain specific situations.

For example, we should not be surprised that Darwin's finches "fail to conform" to species-area relationships as predicted by the MacArthur and Wilson model. Yet Juvik and Austring (1979) were concerned and puzzled by this "failure." They claimed that the earliest reliable distributional data on birds of the Galápagos were those compiled by the California Academy of Sciences Expedition in 1905–1906, before which time Juvik and Austring regarded the extent of man's influence on avian distribution in the Galápagos to be (p. 212) "only a matter of speculation." By finding and studying fossils, I have shown that it is possible to reconstruct the avifauna of the Galápagos well before 1905, and to reveal the nature of the fauna before human impact. More than previously realized, we can determine the extent of man's influence on insular life.

Most biogeographical studies, from MacArthur and Wilson up to the present, have ignored the prehistoric and historic factors that have influenced insular biotas. To some degree, man has had an impact on the biota of nearly every island in the world before the initial collection of data that could be used in quantified insular biogeography. We must attempt to determine the severity of these influences if our goal is a realistic comparison of truly natural biotas. Written documentation exists in varying levels of accuracy and completeness for man's activities of the past several hundred years on many islands, and these writings should be an important

source of information for the biogeographer. For information that precedes written records, we must turn to the fossil record, which is the only way to determine which species occurred at a given locality at any time that predates written accounts. ("Fossil" herein refers to bones found in either a paleontological or archaeological context.)

Admittedly, most biogeographers prefer to analyze today's floras and faunas, not those of the past. But such studies are meaningless if the fauna of a relatively undisturbed island is compared to that of another island that has been greatly altered by man. The modern vegetation may not reveal the history of habitat disturbances and associated extinctions, for habitat destruction that occurred hundreds or thousands of years ago can be masked completely by successional recovery of the vegetation. Nor does the present number of human inhabitants necessarily reflect past numbers. (For example, several hundred people lived on Floreana in the 1830's, compared to approximately 50 today. Henderson Island, in the Pitcairn Group, has been uninhabited in historic times and is often cited as one of the few examples of a "pristine" island. However, Fosberg et al. (1983) reported Polynesian archaeological sites from Henderson, in which occur four species of birds that no longer live on this island (Steadman and Olson, 1985). Even Henderson Island, therefore, can no longer be regarded as "pristine.") In his critique of the MacArthur and Wilson equilibrium theory, Williamson (1981:83) also noted that this theory does not consider historical factors. But Williamson then stated that historical phenomena are frequently unimportant in studying modern distributions. I believe that any biogeographical analyses, whether on continents or islands, are unreliable if they are not backed by historical information.

Although the arguments in this paper are applicable in concept to any group of organisms, they pertain in practice only to those groups for which a significant fossil record is obtainable, such as vertebrates, mollusks, and certain groups of insects. This discussion will deal mainly with terrestrial avifaunas for several reasons.

1. The number of species of birds on an island may be high enough to have at least some mathematical potential for quantitative manipulation. These analyses would be less well suited for insular mammals, for example, because of their lower species diversity.

2. Birds are an easily accessible group to study, and living insular avifaunas thus are often relatively well known compared to other groups of organisms (as Sauer stated, 1969:591: "The whole approach smacks of ornithology. . ."). Nevertheless, as noted previously, more thorough distributional data are needed even for birds.

3. Deposits of vertebrate fossils on islands usually include many birds.

In the few instances where the fossil record of a particular island is well documented, one can reconstruct that island's past avifauna in a manner that at least approaches the natural situation. The best-documented is in Hawaii, where Olson and James (1982a, 1982b, 1984) have shown that late Quaternary extinction of birds occurred at a much greater rate than ever before suspected. They have collected rich deposits of avian fossils from most of the major Hawaiian islands. These fossils document for the first time the occurrence of many new species, as well as many new records of species otherwise known only from other islands in the archipelago. Altogether, fossils have more than doubled the number of previously known species of terrestrial Hawaiian birds (1982a, table 1; 1982b, table 5), and new species are still being discovered. Olson and James' fossil record includes many species that apparently became extinct through hunting and habitat destruction of the past 1000 years by Polynesians. It is still uncertain how much of this extinction occurred in prehistoric times (i.e., before A.D. 1780) versus early historic times (ca. A.D. 1780 to 1880), because few specimens were collected during the first hundred years after European contact. Regardless, the wave of extinction among Hawaiian birds during the past century

was not a unique event within or outside of Hawaii. Elsewhere in Polynesia, levels of extinction in birds as great or greater than those in Hawaii are now being discovered for the Cook Islands (Steadman, 1985) and the Marquesas (Steadman, personal observation of previously unstudied archaeological bones). The prehistoric record is even more important than the historic record in determining the natural avifauna of Polynesia. Biogeographic studies of the Polynesian avifauna that do not consider the fossil record are not only incomplete, they are downright misleading.

Turning to Floreana, we see that late Holocene fossils from the Post Office Bay region have confirmed that *Tyto punctatissima*, *Mimus trifasciatus*, *Geospiza nebulosa*, and *G. magnirostris*, each of which is now extinct on Floreana, were once resident there. These findings should not be unexpected, for Floreana has suffered as much or more human-related biological disturbance than any other island in the Galápagos (see "Human History," and "Introduced Mammals"). The fossil record of Floreana differs from that of Polynesia, however, in two major ways—the chronology and the extent of the extinction. The extinctions on Floreana occurred later in time than those in Polynesia. So far, no prehistoric extinctions are surely known from Floreana, whereas numerous prehistoric (= before European contact) extinctions occurred in Polynesia. As noted above, many extinct birds are associated with Polynesian cultural sites, and therefore must have became extinct within the last 1000 years. Thus the chronology of extinction in Polynesia, as in the Galápagos, is related to the arrival of man. The Galápagos lacked pre-European inhabitants, and we find little if any prehistoric extinction there. Note that this discussion is confined to the Holocene, thereby eliminating any effects of climatic change near the Pleistocene-Holocene boundary.

Aside from the chronological difference, the extent of extinction was much greater in Polynesia than in the Galápagos. Several factors may be involved here. One is the much greater human population of Polynesia both in prehistoric and historic times. The climate and soil in most of Polynesia are generally much better suited for human occupancy than that of the Galápagos. It follows that higher human populations will tend to have a greater impact on an area than smaller populations. For example, essentially all of the remaining native forest in Hawaii is in humid, mountainous regions. The Polynesians had destroyed essentially all of the lowland forest before the arrival of Europeans in the late 1700s, and in doing so they wiped out numerous species of birds. The human population of the Galápagos measured only in the hundreds from its beginning in 1832 until the 1940s. Today approximately 7000 persons live in the Galápagos, more than ever before, but nevertheless a relatively low figure. Many of the islands in the Galápagos retain pristine or nearly pristine lowland habitats. Another factor is how long the islands have been inhabited. Human residency in the Galápagos spans only 150 years, although these islands have been visited sporadically for over 400 years, whereas most of Polynesia, including Hawaii, Marquesas, and Cook Islands, has supported people for at least 1000 years. Lastly, certain Polynesian birds were more vulnerable to extinction simply because of what they were. It is easy to imagine flightless geese, ibises, and rails being hunted to extinction by Polynesians. The only flightless birds in the Galápagos are marine species—*Spneniscus mendiculus* (Galápagos Penguin) and *Phalacrocorax harrisi* (Flightless Cormorant), both of which are confined to the shorelines of Fernandina and Isabela in places that are too inhospitable to be colonized by humans. Nevertheless, feral dogs are now a threat to Galápagos penguins, at least on Isabela (Barnett, 1982).

The Galápagos fauna has suffered extinction without replacement; human impact seems to have wiped out more species than have been replaced by natural colonization. This same phenomenom has occurred in the West Indies (Steadman et al., 1984), as well as in Polynesia and other oceanic islands. As noted by Johnson (1983) for the Channel Islands, the concept of

natural turnover (if such exists) is not applicable to islands that have been significantly disturbed by man. Olson and James (1982b:53) point out that: "Data [on numbers of species] from islands that have suffered from human disturbance, which would include most of the islands in the world, should not be relied upon for numerical studies of island biogeography unless the impact of such disturbance is known." I would add that the fauna of the Galápagos is nowhere near "equilibrium" (if such exists), regardless of the extent of historic extinctions. The Galápagos lack species from most families of Neotropical land birds. For example, I see no reason why the Galápagos could not support indigenous populations of falcons, goatsuckers, woodpeckers, cotingas, wrens, or tanagers, just to mention a few possibilities. Cuckoos and warblers were probably unrepresented in the Galápagos until only hundreds or at most thousands of years ago (see below). Thus faunal diversity in Galápagos birds largely depends upon availability of colonists. These islands are large enough and diverse enough environmentally to support many more species than exist now.

Another problem in analyzing numbers of species of land birds on islands is deciding which resident birds should be included. For instance, should one include aquatic birds such as ducks (*Anas bahamensis*), gallinules (*Gallinula chloropus*), or shorebirds (*Himantopus mexicanus, Phoenicopterus ruber*)? Are certain rails (*Laterallus jamaicensis, Neocrex erythrops*) non-aquatic enough to be considered among the land birds? Is *Geospiza pallida*, known from only a single historic Floreana specimen, to be included? For Floreana, Harris (1973) listed 16 species as "breeding now" and 22 species as "ever recorded." The two rails were not included in Harris' numbers, but I have included them in my own analysis of the land birds of Floreana (Table 12) because these rails occur mainly in the moist highlands and because they are preyed upon by barn owls (Groot, 1983; personal observation).

Concerning Darwin's finches, B. R. Grant and

TABLE 12.—Status of resident land birds of Floreana (23 species either breed now, have bred in the past, or may have bred in the past, on Floreana).

Species	Occurs as a fossil	Extinct on Floreana	Recent colonizer of Galápagos
Buteo galapagoensis		X?	
Laterallus jamaicensis			
Neocrex erythrops			X
Zenaida galapagoensis	X		
Coccyzus melacoryphus			X
Tyto punctatissima	X	X	
Asio flammeus			X?
Pyrocephalus nanus	X		
Myiarchus magnirostris	X		
Progne modesta			
Mimus trifasciatus	X	X	
Dendroica petechia			X
Geospiza nebulosa	X	X	
G. fuliginosa	X		
G. fortis	X		
G. magnirostris	X	X	
G. scandens	X		
G. crassirostris	X		
G. parvula	X		
G. pauper	X		
G. psittacula		X?	
G. pallida		X?	
G. olivacea	X		
Total	14	4 to 7	3 or 4

P.R. Grant stated (1982:654):

Extinctions are not likely to be observed, but they can be inferred from extrapolations of observed fluctuations. To understand the absence of species on islands and the ecological and morphological differences between those present, there is no real substitute for direct studies of food availability and use by coexisting species over a long period of time.

I do not deny the importance of direct food studies; indeed such studies, as well as studies of nesting habits, have helped in suggesting causes of extinction for *Geospiza nebulosa* and *G. magnirostris* on Floreana. Reciprocally, ecologists need the fossil record to document the chronology and extent of the extinctions in the first place.

Hamilton and Rubinoff (1963, 1964, 1967)

studied factors (area, isolation, plant diversity) that are potentially related to number of species and degree of endemism in Darwin's finches. They cited Lack (1947) and Bowman (1961) in recognizing 9 species of Darwin's finches to be native to Floreana. But Lack (1947, table XVII) listed only 8 resident species, noting that if *G. difficilis* (= *nebulosa*) and *G. magnirostris* were found to have been once resident on Floreana, this figure would increase to 10. Bowman (1961, table 7) recognized 9 species, omitting *G. nebulosa* because of apparent uncertainties in its locality of collection (discussed in Lack, 1945:14, 15). (Contrary to Hamilton and Rubinoff (1963), Bowman (1961) did not follow the taxonomic conclusions of Swarth (1931), who recognized 28 species of Darwin's finches in the Galápagos as compared to Bowman's 13 species.) Hamilton and Rubinoff (1963) produced an equation to predict the number of Darwin's finches on any island in the Galápagos. For Floreana, this equation predicted 6.2 species, far short of the 10 or 11 species now known to have ocurred there (Sulloway 1982a,b; this study). Harris (1973:274) listed 8 species of Darwin's finches as currently resident on Floreana, with *G. nebulosa* regarded as "probably once resident, now not present" *G. magnirostris* regarded as "has been recorded, probably stragglers." Power (1975), Connor and Simberloff (1978), and Alatalo (1982) used the data of Harris (1973) for their quantitative analyses of the Galápagos avifauna. Unavoidably, these data were compiled in the absence of paleontological information, so they do not represent the undisturbed fauna of the Galápagos.

To summarize, biogeographical equations look good only when they produce results that are consistent either with previously known empirical data or with the researcher's preconceptions. When these circular equations fail to "predict" the desired numbers, the unfortunate results are written off as being due to such things as statistical errors, inadequate data, or "unknown factors." In effect, these reasons only represent an admission of our ignorance of biological phenomena. Even on islands, biogeogra-

phy is too complex to be explained by a few magic numbers.

After 20 years of emphasis on theoretical research in the field of island biogeography, the emerging paleontological record may spark a return to empiricism. Fossils permit us to determine the natural fauna of Floreana and other islands with more confidence than ever before. The fossil record from Floreana seems to be too young to reveal evolutionary changes; instead, its forte is in revealing extinctions and past relative abundances. As fossil records emerge from other islands in the Galápagos, we will be able to make more meaningful inter-island faunal comparisons.

ANIMALS NOT RECORDED AS FOSSILS.—Not included among the fossils are certain species that either still live on Floreana, once lived there, or may be suspected to have once occurred there. In order to interpret a fossil fauna as thoroughly as possible, one must attempt to account for absences in the record by answering some basic questions. Is a certain species unrepresented in the fossil fauna because it simply did not occur there at the time of deposition of the fossils? If not, are there any behavioral or ecological traits of the species that may help to explain its absence?

Cricetine rodents and land iguanas (*Conolophus*) fall into the first category. They are not known historically from Floreana, and I regard their absence as fossils as strong evidence that they in fact never occurred there. Various *Tyto*-derived fossil sites on San Cristóbal, Santa Cruz, Rábida, and Isabela are dominated by indigenous rodents; had rodents been present on Floreana, the barn owls would have preyed upon them and deposited their bones in the caves. Land iguanas occur as fossils regularly but in low numbers on Santa Cruz, Rábida, and Isabela. Young land iguanas are preyed upon and deposited in caves by barn owls, whereas adults are trapped within the caves by falling through vertical roof collapses. One of these methods probably would have entombed land iguanas in the Floreana caves, had they been present. Porter (1822:163)

noted that land iguanas were not found on Flo-reana in 1813, a time when tortoises were still abundant and before the takeover by feral mammals.

Nine of the 23 species of birds in Table 12 were not recorded as fossils. Of these, the absence of *Buteo galapagoensis* (Galápagos Hawk) and *Asio flammeus* (Short-eared Owl) may be explained by their being too large to be eaten by barn owls, as well as the fact that they do not use caves for any of their own activities. The seven other species of birds are small enough to be eaten by barn owls, so different reasons must be sought for their absence. Four of these species, *Laterallus jamaicensis* (Black Rail), *Neocrex erythrops* (Paint-billed Crake), *Geospiza psittacula* (Large Tree Finch), and *G. pallida* (Woodpecker Finch) occur mainly in the humid highlands of Floreana, outside of the hunting territory of barn owls that roosted near Post Office Bay. In addition, *N. erythrops* is undoubtedly a very recent colonizer of the Galápagos, for these reasons: it is totally undifferentiated from mainland forms; it was not recorded in the Galápagos until 1952; and it does not occur in the huge fossil sample from Cueva de Kubler, Santa Cruz. The fauna of Cueva de Kubler does include, although in small numbers, fossils of *L. jamaicensis, G. psittacula,* and *G. pallida.* The presence of these species in Cueva de Kubler but not in the fossil faunas of Floreana may only reflect the much larger number of fossils from Cueva de Kubler combined with its location farther inland and at a slightly higher elevation than the Floreana sites, although Cueva de Kubler is still in arid zone vegetation.

The situation for *G. pallida* is more complicated, for this finch is known on Floreana from only a single specimen, collected in the moist highlands on 11 October 1905 (Gifford, 1919:253, 254; Swarth, 1931:243). Thus the possibility exists that *G. pallida* never was resident on Floreana. Harris (1982:152) noted without detail a "few sight records" of *G. pallida* from Floreana, presumably within the past 20 years. Specimens are essential to document any new or

unusual island records of Darwin's finches; sight records are not reliable. Although *G. pallida* is apparently very rare or extinct today on Floreana, it probably once occurred there as a resident, only to be victimized somehow by the large-scale biotic changes that have occurred in the Floreana highlands during the past 150 years. *Geospiza pallida* is still common today in the highlands of Santa Cruz and Isabela, but the habitat destruction on these two larger islands has not been as complete as on Floreana. Lack (1969:263) attributed the absence of *G. pallida* on Floreana to "unknown reasons (but just conceivably linked with the co-existence there, and nowhere else, of *C. psittacula* and *C. pauper*)." The natural status of *G. pallida* on Floreana remains a mystery.

Progne modesta (Galápagos Martin) is a rare bird on Floreana, although it does occur in the lowlands. This martin has not been recorded from any modern or fossil barn owl roost in the Galápagos. *Progne modesta* roosts mainly along cliffs near the sea, places that make it inaccessible to barn owls.

The absence of the two remaining birds, *Coccyzus melacoryphus* (Dark-billed Cuckoo) and *Dendroica petechia* (Yellow Warbler) cannot be explained by biases of habitat or predation. These two species are common today in the lowlands of Floreana. In fact, the Yellow Warbler may be the most common lowland bird. Furthermore, both the cuckoo and warbler occur regularly in modern pellets of barn owls from Santa Cruz and Isabela. In Cueva de Kubler, Santa Cruz, for example, *C. melacoryphus* and *D. petechia* are present in fresh barn owl pellets, but are not among the thousands of avian fossils studied thus far, which were collected only 50 m away. The lack of fossil remains of cuckoos and warblers from both Floreana and Santa Cruz suggests that these two currently common species colonized the Galápagos only very recently, perhaps even in the last several hundred years. The fossil sites on Floreana range in age from modern to at least 2400 years B.P., whereas Cueva de Kubler has yielded radiocarbon ages ranging from modern

to 1750 years B.P. The ages from Cueva de Kubler are unreliable, however, because of apparent contamination from surface testing of nuclear weapons in the Pacific (Robert Stuckenrath, pers. comm.). Thus the actual age of the fossils in Cueva de Kubler is at least 1750 years B.P. and may be much older. For now, I can say only that the conspicuous absence of *C. melacoryphus* and *D. petechia* from all fossil sites on Floreana and Santa Cruz suggests that these species were not present during the time of fossil deposition.

Although both seem to be relatively recent colonizers, the cuckoo is likely to have been more recent than the warbler, based on date of first collection of historic specimens and on the level of morphological differentiation of the Galápagos populations. *Coccyzus melacoryphus* may not have colonized the Galápagos until the 19th century, for it was not collected there until 1888, on Floreana and San Cristóbal (Ridgway, 1890). Rothschild and Hartert (1902:404) described it as "somewhat rare and apparently a recent immigrant." In 1905–1906, the California Academy of Sciences Expedition recorded cuckoos from six different islands (55 specimens), suggesting a rapid increase in numbers and distribution, typical of geometrically expanding populations of a newly arrived species. Specimens of *C. melacoryphus* from the Galápagos do not differ significantly from those of mainland South America (Swarth, 1931:71, 72; personal observation), inferring that there has been very little time available for morphological changes to develop between the two populations.

Dendroica petechia was first recorded from Floreana in 1852 (Sundevall, 1871), although it must have been there in 1835, for Gould (1841) noted that warblers were common throughout the archipelago during the voyage of the *Beagle*. Yellow Warblers of the Galápagos and Cocos Island are essentially identical to each other and are traditionally regarded as forming their own subspecies, *D. p. aureola*. Salvin (1883:420) apparently regarded the birds from the Galápagos as identical to those of the mainland, for he recorded "*Dendroeca aureola*" from coastal Ec-

uador and Peru, as well as the Galápagos. Hellmayr (1935:383) and Harris (1982:129) noted that *D. p. aureola* is very similar to *D. p. peruviana* of the Pacific coast of Colombia, Ecuador, and Peru. I have compared specimens of *D. p. peruviana* with *D. p. aureola* from both Cocos Island and the Galápagos, finding the two insular populations to be indistinguishable from each other and slightly distinct from, but very similar to, the birds from coastal Peru. *Dendroica p. aureola* seems to be a barely recognizable race that is derived from *D. p. peruviana*. Additional fossil sites from other islands in the Galápagos should either strengthen or discredit my suggestion of recent colonization by cuckoos and yellow warblers.

Some historic colonization in the Galápagos may have been aided by ships travelling from the mainland, as well as within the islands. Harris (1974, 1982:120) has suggested that the several recent records of anis (*Crotophaga sulcirostris* and *C. ani*) in the Galápagos are possibly due to human agency. Other species may also be getting free rides to the Galápagos.

THE PALEONTOLOGICAL POTENTIAL OF THE GALÁPAGOS.—The opportunity to elucidate ancient and therefore undisturbed insular faunas depends upon locating suitable accumulations of fossils. The Galápagos lack calcareous dunes (aeolianites), which have yielded Quaternary faunas on Hawaii, St. Helena, and Fernando de Noronha (Olson, 1975, 1981; Olson and James, 1982b). They also lack muck deposits, known to be very rich in bird bones in parts of New Zealand (Gregg, 1972; McCulloch and Trotter, 1979), as well as phosphate deposits and fine-grained alluvium, which can be fossiliferous on Ascension and St. Helena (Olson, 1975, 1977). Limestone caves, crevices, and sinkholes often contain fossils elsewhere, e.g., Hawaii, Cook Islands, Bermuda, and the West Indies, but these weathered karst features are also absent in the Galápagos. To date, no fossil sites are known from fumaroles in the Galápagos, as have been found on Ascension Island (Olson, 1977). Fine-grained volcanic ashes, such as those containing

bird skeletons on Isla San Benedicto, Revillagi-
gedos Islands, Mexico (Brattstrom and Howell,
1956), are rare in the Galápagos and have not
been explored paleontologically. Peat bogs occur
in the highlands of the larger Galápagos islands,
but they have not been excavated for fossils.

Deposits in lava tubes are the one outstanding
opportunity for bone preservation in the Galá-
pagos, although several vertebrate fossil sites
here are in large fissures or spatter cones. Lava
tubes are present in good numbers on San Cris-
tóbal, Santa Cruz, Santiago, Isabela, and Fernan-
dina, as well as Floreana. In future attempts to
describe the natural fauna of the Galápagos,
these islands will provide rich opportunities for
prospecting. The first four islands either are or
have been inhabited by man, and thus have their
fair share of introduced plants and animals. As
was the case on Floreana, a fossil record from
these islands would be expected to yield remains
of animals that have become extinct within the
past 200 years. For example, fossils from San
Cristóbal could provide information on the pres-
ently uncertain status of *Geospiza nebulosa*, *G.
magnirostris*, and *G. psittacula* on that island. On
Santa Cruz, I have excavated several sites (briefly
summarized in Steadman, 1981), a preliminary
analysis of which reveals three species of extinct
rodents and all 10 species of Darwin's finches
that are known historically from Santa Cruz, but
in different relative abundances than exist today.
On Pinzón, one should keep an eye out for fossils
of rodents, mockingbirds, and *Geospiza scandens*.
Santiago is yet unexplored paleontologically, but
has much potential for important discoveries,
especially of rodents. Isabela, for which there is
a limited fossil record, already has yielded new
rodents (Steadman, 1981). Fernandina has never
been inhabited by humans, and does not harbor
any introduced mammals. The high levels of
historic volcanic activity (Simkin and Howard,
1970) may be why the status of many vertebrates
on Fernandina is poorly known. Natural extinc-
tions are entirely possible. Fossils from Fernan-
dina could shed light on the former status of
tortoises, rodents, *Geospiza magnirostris*, *G. scan-
dens*, and *G. pallida*, among others.

The vertebrate fossil record of the Galápagos
has not gone with certainty beyond the Holo-
cene. Older lava flows should be checked care-
fully for lava tubes, for Pleistocene fossils may be
the key to many intriguing evolutionary ques-
tions. Within the next decade we can expect the
emergence of a much more complete picture of
the natural vertebrate fauna of the Galápagos.

Summary and Conclusions

Isla Floreana (Charles Island) is a relatively
large, diverse island in the south-central part of
the Galápagos Archipelago. I have collected and
identified over 20,000 late Holocene vertebrate
fossils from Floreana, representing more than
1100 individual animals of 24 native species. This
study is the first faunal survey of fossil verte-
brates from the Galápagos Islands. The fossils
were collected from both surface and sub-surface
levels of sediments from four lava tubes in the
arid Post Office Bay region. None of the fossil
sites is more than 1 km from the ocean, or more
than 60 m in elevation. The lava tubes are in
flows of Brunhes normal magnetic polarity, and
therefore less than 0.79 million years old. The
oldest of six radiocarbon age determinations
from surface remains in three of the caves was
2400 years B.P. Although fossils in the underly-
ing sediment must be older than the surface
material, the sub-surface levels yielded no or-
ganic material suitable for radiocarbon dating,
and thus their age is not known precisely. There
is no reason to believe, however, that any of the
fossils are pre-Holocene in age.

Except for non-hatchling tortoises, nearly all
of the fossils probably were deposited in the caves
as pellets regurgitated by the Galápagos Barn
Owl (*Tyto punctatissima*). A detailed analysis of
the fossil fauna elucidates the past feeding habits
of barn owls on Floreana. Because Floreana
lacked native rodents, the barn owls there fed
mainly on reptiles and small birds. The fossil
fauna includes six indigenous species of verte-
brates that are now extinct on Floreana: the
Galápagos tortoise (*Geochelone elephantopus*), Flo-
reana snake (*Alsophis biserialis*), Galápagos Barn

Owl (*Tyto punctatissima*), Floreana Mockingbird (*Mimus trifasciatus*), Sharp-beaked Ground Finch (*Geospiza nebulosa*), and Large Ground Finch (*Geospiza magnirostris*). Based on calculated minimum numbers of individuals, these extinct species are, respectively, 1st, 7th, 16th, 6th 15th, and 2nd in abundance among the 24 species recorded as fossils. Together the extinct species make up 57.2% of the individuals in the entire fossil assemblage. Furthermore, the 3rd and 4th most numerous fossil taxa, the lava lizard (*Tropidurus grayii*) and Galápagos Dove (*Zenaida galapagoensis*), are exceedingly rare on Floreana today. Of the 7 most common fossil taxa, only a small gecko (*Phyllodactylus baurii*) survives in what may approach natural numbers. If percent of occurrence in the fossil record approximates relative population size, then historic extinction has changed the composition of Floreana's vertebrate fauna even more than might be suggested by the number of extinct species alone. The fossil record shows that the fauna we see today on Floreana is drastically different from that of pristine times.

While details of the process are unknown and the evidence is largely circumstantial, I believe that all extinction on Floreana may be related to human impact, including direct predation, habitat alteration, and the introduction of alien mammals. Floreana's first large human settlement began in 1832, accompanied immediately or very shortly thereafter by alien mammals such as black rats, house mice, cats, dogs, pigs, goats, cattle, horses, and donkeys. Direct human predation may have been involved in all extinctions to some extent, but it probably was the main cause only for the tortoise and the Galápagos Hawk (*Buteo galapagoensis*), the latter not recorded as a fossil. Predation by feral mammals, particularly rats, cats, dogs, and pigs, may also have been involved to some extent in all extinctions except perhaps the hawk. Extinction of the Galápagos Barn Owl was probably due to predation in combination with reduction or loss of preferred prey species, such as snakes, lava lizards, doves, mockingbirds, and certain finches, especially the Large Ground Finch. Extinction on Floreana of the Floreana

Mockingbird and Large Ground Finch may have accompanied the depletion of prickly pear cactus (*Opuntia megasperma* var. *megasperma*) in the lowlands by feral goats and donkeys. Both the mockingbird and finch seem to have been dependent upon *Opuntia* for nesting and feeding, so the severe reduction in cactus was devastating to these specialized forms. The loss of the Sharp-beaked Ground Finch on Floreana may have been due to habitat change in the highlands, accompanied by a sudden burst of competition from other finches that moved into the highlands as man altered the vegetation. I believe that all extinction on Floreana occurred in historic times; whether or not this holds for other islands in the Galápagos awaits more digging for fossils.

Because of a paucity or lack of specimens with unequivocal locality data, scientists have questioned whether or not most of the extinct species discussed actually once occurred on Floreana. The fossils demonstrate that they did. The absence of fossils of the Dark-billed Cuckoo (*Coccyzus melacoryphus*) and the Yellow Warbler (*Dendroica petechia*) is evidence that these species are very recent colonizers of the Galápagos. The cuckoo has not differentiated perceptibly from its mainland ancestors, and the warbler is only slightly differentiated from populations from coastal Ecuador and Peru, so the absence of these two species from fossil deposits even as young as late Holocene is not unexpected.

Fossils also allow us to compare the skeletal morphology of populations on Floreana to those from other islands, as well as from the Neotropical mainland. Based on plumage and osteology, I regard *Tyto punctatissima*, *Pyrocephalus nanus* (Galápagos Vermilion Flycatcher), *P. dubius* (San Cristóbal Vermilion Flycatcher), and *Mimus trifasciatus* as full species, the latter restricted to Floreana (formerly) and the nearby islets of Champion and Gardner-near-Floreana. *Geospiza nebulosa nebulosa*, a large race of Sharp-beaked Ground Finch, is recognized for Floreana only; it may have occurred also on San Cristóbal, but proper documentation is lacking. I regard *Geospiza magnirostris magnirostris* as having occurred only on Floreana and San Cristóbal. This largest

of all Darwin's finches was probably the most common bird in the lowlands of Floreana before human contact. The Red Bat, *Lasiurus borealis*, was the only indigenous mammal recorded from the fossil sites. Floreana apparently lacked native rodents, for had they been present, the barn owl would have preyed upon them and deposited their bones in the caves, as is the case elsewhere in the Galápagos, e.g., San Cristóbal, Santa Cruz, Rábida and Isabela. The absence of fossils of land iguanas (*Conolophus*) is evidence that this endemic Galápagos lizard also never occurred on Floreana.

The fossils from Floreana allow us to reconstruct the natural, unperturbed (= pre-human) vertebrate fauna of this island much more completely than previously possible. This exposes a major limitation in the popular "equilibrium theory of island biogeography," namely that quantitative inter-island comparisons of faunas usually are made with no historical basis. Without a fossil record, one cannot determine with confidence the extent of man-related extinction on an island. As a result, biogeographers generally have little idea how natural their faunas are. Other theoretical and practical shortcomings show that quantitative biogeographical models oversimplify natural phenomena to the point where little or no meaningful information is generated. MacArthur and Wilson have initiated a great

amount of interest in islands, but much of this interest has been channeled into the testing of generalized models with poorly controlled data rather than the gathering of new data. By putting the theoretical cart before the empirical horse, biogeographers of the past two decades seem to be overlooking the complexities of insular biotas. Such concepts as turnover and biotic equilibrium may eventually be demonstrated or refuted through long-term field studies, whether paleontological or neontological. A sufficiently rich and well-dated Holocene fossil record, for example, might disclose natural turnover. To date, none is evident, and instead we find unnatural extinction without replacement.

Availability of fossil sites limits the extent to which paleontology can reveal the natural fauna of the Galápagos or any other islands. The Galápagos lack the aeolianites, fine-grained alluvium, calcareous mucks, phosphate deposits, and the limestone caves, crevices, and sinkholes that have produced rich fossil sites on other oceanic islands. Lava tubes are the primary source of vertebrate fossils in the Galápagos, although other volcanic features may serve as natural traps or as owl roosts, such as earthquake crevices and steep-walled spatter cones. Expansion of the Galápagos fossil record to other islands may be limited somewhat by the occurrence of lava tubes.

Literature Cited

Abbott, Ian, and L.K. Abbott
  1978.   Multivariate Study of Morphological Variation in
            Galápagos and Ecuadorean Mockingbirds. *The
            Condor*, 80(3):302–308, 3 figures, 2 tables.
Abbott, Ian, L.K. Abbott, and Peter R. Grant
  1977.   Comparative Ecology of Galápagos Ground
            Finches (*Geospiza* Gould): Evaluation of the Im-
            portance of Floristic Diversity and Interspecific
            Competition. *Ecological Monographs*, 47(2):151–
            184, 20 figures, 14 tables.
Abs, Michael, Eberhard Curio, Peter Kramer, and Jochen
    Niethammer
  1965.   Zur Ernährungsweise der Eulen auf Galapagos:
            Ergebnisse der deutschen Galapagos-Expedition
            1962/63, IX. *Journal für Ornithologie*, 106(1):49–
            57, 2 tables.
Agassiz, Alexander
  1892.   Reports on the Dredging Operations off the West
            Coast of Central America to the Galápagos, to the
            West Coast of Mexico, and in the Gulf of Califor-
            nia, in Charge of Alexander Agassiz, Carried on
            by the U.S. Fish Commission Steamer "Albatross,"
            Lieut. Commander Z.L. Tanner, U.S.N., com-
            manding, II: General Sketch of the Expedition of
            the "Albatross," from February to May, 1891.
            *Bulletin of the Museum of Comparative Zoology at
            Harvard College*, 23(1):1–89, 22 plates.
Alatalo, Rauno V.
  1982.   Bird Species Distributions in the Galápagos and
            Other Archipelagoes: Competition or Chance?
            Ecology, 63(4):881–887, 2 figures, 2 tables.
Allen, Joel Aseph
  1892.   On a Small Collection of Mammals from the Ga-
            lápagos Islands, Collected by Dr. G. Baur. *Bulletin
            of the American Museum of Natural History*, 4:47–
            50.
Alpert, Leo
  1963.   The Climate of the Galápagos Islands. *Occasional
            Papers of the California Academy of Sciences*, 44:21–
            44, 11 figures, 8 tables, appendix.
Ashmole, N.P.
  1963.   Sub-fossil Bird Remains on Ascension Island. *The
            Ibis*, 103b(3):382–389, plate 10.
Atkinson, I.A.E.
  1977.   A Reassessment of Factors, Particularly *Rattus
            rattus* L., That Influenced the Decline of Endemic
            Birds in the Hawaiian Islands. *Pacific Science*,
            31(2):109–133, 1 figure, 1 table.

Banning, George Hugh
  1933.   Hancock Expedition to the Galápagos Islands,
            1933: General Report. *Bulletin of the Zoological
            Society of San Diego*, 10:1–31, 25 figures.
Barber, Richard T., and Francisco P. Chavez
  1983.   Biological Consequences of El Niño. *Science*,
            222(4629):1203–1210, 7 figures, 1 table.
Barlow, Nora, editor
  1963.   Darwin's Ornithological Notes [with introduction,
            notes, and appendix]. *Bulletin of the British Museum
            (Natural History), Historical Series*, 2(7):201–278.
Barnett, Bruce D.
  1982.   Feral Dogs of the Galápagos Islands. *Informe An-
            ual 1981 Estacion Científica Charles Darwin*, pages
            205–216, 3 figures, 1 table.
Basilewsky, Pierre
  1968.   Les Calosomes de iles Galapagos (Coleoptera, Car-
            abidae). In *Mission Zoologique Belge aux iles Gala-
            pagos et en Ecuador (N. et J. Leleup, 1964–1965);
            Resultats Scientifiques*, pages 179–207. Bruxelles:
            Institut Royal des Sciences Naturelles de Belgique.
Baskin, Jonathan N., and Ernest E. Williams
  1966.   The Lesser Antillean *Ameiva* (Sauria, Teiidae):
            Re-Evaluation, Zoogeography, and the Effects of
            Predation. *Studies on the Fauna of Curacao and
            Other Caribbean Islands*, 23(89):144–176, figures
            42, 43, tables 12–20, 2 plates.
Baur, George
  1889.   The Gigantic Land Tortoises of the Galápagos
            Islands. *The American Naturalist*, 1889:1039–
            1057.
  1892.   Das Variiren der Eidechsen-gattung *Tropidurus*
            auf den Galapagos-Inseln. In *Festschrift zum Sieben-
            zigsten Geburtstage Rudolf Leuckarts*, pages 259–
            277, 3 figures. Leipzig.
  1895.   The Differentiation of Species on the Galápagos
            Islands and the Origin of the Group. In *Biological
            Lectures Delivered at the Marine Biological Labora-
            tory of Wood's Holl* [sic] *in the Summer Session of
            1894*, pages 67–78, 3 unnumbered tables.
Beebe, William
  1924.   *Galápagos: World's End*. 443 pages, frontispiece,
            82 figures, 8 color plates, 2 appendices. New York
            and London: G.P. Putnam's Sons.
Bell, Thomas
  1843.   Reptiles. In Charles Darwin, editor, *The Zoology of
            the Voyage of H.M.S. Beagle, under the Command of
            Captain Robert Fitzroy, R.N., during the Years 1832*

to 1836. part 5: 51 pages, 20 plates. London: Smith, Elder, and Co.

Boersma, P. Dee.
1978. Breeding Patterns of Galápagos Penguins as an Indicator of Oceanographic Conditions. *Science,* 200(4349):1481–1483, 2 figures.

Bonnott, Paul
1928. An Outlaw Barn Owl. *The Condor,* 30(5):320.

Boulenger, G.A.
1891. On the Galápagos Lizards of the Genus *Tropidurus. The Annals and Magazine of Natural History,* series 6, 7 (58):501–503.

Bowman, Robert I.
1961. Morphological Differentiation and Adaptation in the Galápagos Finches. *University of California Publication in Zoology,* 58:1–326, 74 figures, 63 tables, 22 plates.

Bowman, Robert I., and Anne Carter
1971. Egg-pecking Behavior in Galápagos Mockingbirds. *The Living Bird,* 10:243–270, 16 figures, 7 tables.

Brattstrom, Bayard H., and Thomas R. Howell
1956. The Birds of the Revilla Gigedo Islands, Mexico. *The Condor,* 58(2):107–120, 5 figures.

Brodkorb, Pierce
1963. Catalogue of Fossil birds, Part 1. *Bulletin of the Florida State Museum, Biological Sciences,* 7(4):179–293.

Broom, Robert
1929. On the Extinct Galápagos Tortoise That Inhabited Charles Island. *Zoologica,* 9(8):313–320, figures 306–309.

Brosset, A.
1963. Statut Actuel des mammiferes des Îles Galapagos. *Mammalia,* 27(3):324–338, plate 12.

Buden, Donald W.
1974. Prey Remains of Barn Owls in the Southern Bahamas Islands. *The Wilson Bulletin,* 86(4):336–343, 1 figure, 1 table.

Cane, Mark A.
1983. Oceanographic Events During El Niño. *Science,* 222(4629);1189–1195, 6 figures.

Carpenter, Charles C.
1966. Comparative Behavior of the Galápagos Lava Lizards (*Tropidurus*) *In* Robert I. Bowman, editor, *The Galápagos: Proceedings of the Galápagos International Scientific Project,* pages 269–273, 1 figure, 1 table. Berkeley: University of California Press.
1970. Miscellaneous Notes of Galápagos Lava Lizards (*Tropidurus*—Iguanidae). *Herpetologica,* 26(3):377–386, 2 figures, 1 table.

Chambers, Steven M., and David W. Steadman
In press. Holocene Terrestrial Gastropod Faunas from Isla Santa Cruz and Isla Floreana, Galápagos. *Transactions of the San Diego Society of Natural History,* volume 22.

Chesterman, Charles W.
1963. Contributions to the Petrography of the Galapagos, Cocos, Malpelo, Cedros, San Benito, Tres Marias, and White Friars Islands. *Proceedings of the California Academy of Sciences,* series 4, 32(11):339–362, 7 figures.

Chubb, Lawrence John
1933. Geology of the Galápagos, Cocos, and Easter Islands. *Bernice P. Bishop Museum Bulletin,* 110:1–44, 65–67, figures 1–8, tables 1–3, plates 1–5.

Clark, Deborah A.
1984. Native Land Mammals. *In* Roger Perry, editor, *Galápagos,* pages 225–231, 1 table. Oxford: Pergamon Press.

Coblentz, Bruce E.
1978. The Effects of Feral Goats (*Capra hircus*) on Island Ecosystems. *Biological Conservation,* 13(4):279–286, 2 figures.

Colinvaux, Paul A.
1968. Reconnaissance and Chemistry of the Lakes and Bogs of the Galápagos Islands. *Nature,* 219(5154):590–594, 7 figures, 3 tables.
1969. Paleolimnological Investigations in the Galápagos Archipelago. *Mitteilungen der Internationalen Vereinigung für Limnologie,* 17:126–130, plate 1.
1972. Climate and the Galápagos Islands. *Nature,* 240(5375):17–20, 3 figures.

Colinvaux, Paul A., and Eileen K. Schofield
1976a. Historical Ecology in the Galápagos Islands, I: A Holocene Pollen Record from El Junco Lake, Isla San Cristóbal. *Journal of Ecology,* 64(3)989–1012, 6 figures, 5 tables.
1976b. Historical Ecology in the Galápagos Islands, II: A Holocene Spore Record from El Junco Lake, Isla San Cristóbal. *Journal of Ecology,* 64(3):1013–1026, 3 figures, 1 table.

Connor, Edward F., and Earl D. McCoy
1979. The Statistics and Biology of the Species-area Relationship. *The American Naturalist,* 113(6):791–833, 5 figures, 7 tables, appendix with 3 tables.

Connor, Edward F., and Daniel Simberloff
1978. Species Number and Compositional Similarity of the Galápagos Flora and Avifauna. *Ecological Monographs,* 48(2):219–248, 3 figures, 10 tables.

Conway, Ainslie, and Frances Conway.
1947. *The Enchanted Islands.* 280 pages. New York, G.P. Putnam's Sons.

Cookson, W.E.
1876. [Letter from Commander W.E. Cookson to Dr. A. Gunther of May 29, 1876.] *Proceedings of the Zoological Society of London,* 1876:520–526.

Corbet, Gordon Barclay
1978. *The Mammals of the Palaearctic Region: A Taxonomic*

Review. 314 pages, 104 maps, 1 table. London: British Museum (Natural History).

Coulter, Malcolm C.
1982. The Dark-rumped Petrel, *Pterodroma phaeopygia*, on Isla Floreana, Galápagos. *Informe Anual 1981 Estacion Cientifica Charles Darwin*, pages 170–173, 1 table.

Cox, Allan
1983. Ages of the Galápagos Islands. *In* Robert I. Bowman, Margaret Berson, and Alan E. Leviton, editors, *Patterns of Evolution in Galápagos Organisms.* 568 pages. San Francisco: American Association for the Advancement of Science, Pacific Division.

Cox, Allan, and G. Brent Dalrymple
1966. Paleomagnetism and Potassium-argon Ages of Some Volcanic Rocks from the Galápagos Islands. *Nature*, 209:(5025):776, 777, 2 figures, 2 tables.

Crumly, Charles R.
1984. The Cranial Morphometry of Galápagos Tortoises. *Proceedings of the California Academy of Sciences*, 43(9):111–121, 5 figures, 8 tables.

Cruz, Felipe, and Tina Beach
1983. Weather Data on Floreana, 1982–83. *Noticias de Galapagos*, 38:28.

Darwin, Charles
1869. *Geological Observations on the Volcanic Islands and Parts of South America Visited during the Voyage of H.M.S.* Beagle. Third edition, 648 pages [pages 110–131, figures 11–14 on Galápagos]. New York: D. Appleton and Co.
1871. *Journal of Researches into the Natural History and Geology of the Countries Visited during the Voyage of H.M.S.* Beagle *Round the World, Under the Command of Capt. Fitz Roy, R.N.* Volume 2, 615 pages, unnumbered figures. New York: Harper and Bros.

Davis, D.H.S.
1959. The Barn Owl's Contribution to Ecology and Paleoecology. *The Ostrich*, supplement 3:144–153, 2 figures, 1 table.

Davis, John, and Alden H. Miller
1960. Family Mimidae. *In* Ernst Mayr and James C. Greenway, editors, *Check-list of Birds of the World*, 9:440–458. Cambridge, Massachusetts: Museum of Comparative Zoology, Harvard University.

Dawson, E. Yale
1962. Cacti of the Galápagos Islands and of Coastal Ecuador. *Cactus and Succulent Journal*, 34(3):67–74, figures 42–47; 34(4):99–105, figures 64–70.
1966. Cacti in the Galápagos Islands, with Special Reference to Their Relations with Tortoises. *In* Robert I. Bowman, editor, *The Galápagos: Proceedings of the Symposia of the Galápagos International Scientific Project*, pages 209–214. Berkeley: University of California Press.

DeBenedictis, Paul
1966. The Flight Song Display of Two Taxa of Vermilion Flycatchers, Genus *Pyrocephalus. The Condor*, 68(3):306, 307.

de Bruijn, O.
1979. Voedseloecologie van de kerkuil *Tyto alba* in Nederland. [Feeding Ecology of the Barn Owl *Tyto alba* in the Netherlands.] *Limosa*, 52(3–4):91–154, 4 figures, 14 tables.

Delano, Amasa
1817. *A Narrative of Voyages and Travels in the Northern and Southern Hemispheres Comprising Three Voyages around the World Together with a Voyage of Survey and Discovery in the Pacific Ocean and Oriental Islands.* 598 pages [pages 369–385 on Galápagos]. Boston: E.G. House. [Not seen by DWS.]

DeNiro, Michael J., and Samuel Epstein
1978. Carbon Isotopic Evidence for Different Feeding Patterns in Two Hyrax Species Occupying the Same Habitat. *Science*, 201:906–908.

De Paepe, Paul
1967. Cavity Filling in Rocks from Lava Tunnels on the Galápagos Islands. *Noticias de Galápagos*, 5/6:19, 20.

De Ridder, C.
1976. [Visit to Isla Champion, 21 January 1976]. [Unpublished field trip itinerary report, on file at the Charles Darwin Research Station Library, Santa Cruz, Galápagos.]

Duffy, David C.
1981. A Master Plan for Ornithology in the Galápagos Islands. *Noticias de Galápagos*, 34:10–16, 2 figures.

Durden, C.J.
1978. Fossil Cockroaches from a 1554 Spanish Shipwreck. *In* J.B. Arnold, III and R. Weddle, editors, *The Nautical Archeology of Padre Island: The Spanish Shipwrecks of 1554*, pages 407–416. New York: Academic Press. [Not seen by DWS.]

Eckhardt, Robert C.
1972. Introduced Plants and Animals in the Galápagos Islands. *BioScience*, 22(10):585–590, 3 figures, 1 table.

Fleming, Theodore H.
1982. Parallel Trends in the Species Diversity of West Indian Birds and Bats. *Oecologia*, 53(1):56–60, 3 figures, 2 tables.

Fosberg, F. Raymond, Marie-Helene Sachet, and D.R. Stoddart
1983. Henderson Island (Southeastern Polynesia): Summary of Current Knowledge. *Atoll Research Bulletin*, 272:47 pages, 2 figures, 12 plates.

Fritts, Thomas H., and Patricia R. Fritts, editors
1982. Race with Extinction: Herpetological Field Notes of J.R. Slevin's Journey to the Galápagos, 1905–1906. *Herpetological Monograph*, 1: 98 pages, 9

figures, 3 tables, 4 appendices.

Garman, Samuel
    1892. The Reptiles of the Galápagos Islands. *Bulletin of the Essex Institute*, 24:1–15.

Gifford, Edward Winslow
    1913. Expedition of the California Academy of Sciences to the Galápagos Islands, 1905–1906, VIII: The Birds of the Galápagos Islands, with Observations on the Birds of Cocos and Clipperton islands (Columbiformes to Pelecaniformes). *Proceedings of the California Academy of Science*, series 4, 2(1):1–132, plates 1–7.
    1919. Expedition of the California Academy of Sciences to the Galápagos Islands, 1905–1906, XIII: Field Notes on the Birds of the Galápagos Islands and of Cocos Island, Costa Rica. *Proceedings of the California Academy of Sciences*, series 4, 2(2):189–258.

Goodfriend, Glenn A., and Darden G. Hood
    1983. Carbon Isotope Analysis of Land Snail Shells: Implications for Carbon Sources and Radiocarbon Dating. *Radiocarbon*, 25(3):810–830, 4 figures, 3 tables.

Goodfriend, Glenn A., and Jerry J. Stipp
    1983. Limestone and the Problem of Radiocarbon Dating of Land-snail Shell Carbonate. *Geology*, 11(10):575–577, 2 tables.

Gould, John
    1837a. [Remarks on a series of "ground finches" from Mr. Darwin's collection, with descriptions of new species.] *Proceedings of the Zoological Society of London*, 5:4–7.
    1837b. [Two new species of the genus *Sterna*, a species of cormorant, and three species of the genus *Orpheus* from the Galápagos, in the collection of Mr. Darwin.] *Proceedings of the Zoological Society of London*, 5:26–27.
    1841. Birds. *In* Charles Darwin, editor, *The Zoology of the Voyage of H.M.S.* Beagle, *under the Command of Captain Robert Fitzroy, R.N., during the Years 1832 to 1836*, part 3: 156 pages, 50 plates. London: Smith, Elder, and Co.

Gramlich, John W., Virginia A. Lewis, and John J. Naughton
    1971. Potassium-argon Dating of Holocene Basalts of the Honolulu Volcanic Series. *Geological Society of America Bulletin*, 82(5):1399–1404, 1 figure, 1 table.

Grant, B. Rosemary
    1981. [Visit to Isla Champion, 5 January 1981.] [Unpublished field trip itinerary report, on file at the Charles Darwin Research Station Library, Santa Cruz, Galápagos.]

Grant, B. Rosemary, and Peter R. Grant
    1981. Exploitation of *Opuntia* Cactus by Birds on the Galápagos. *Oecologia*, 49 (2):179–187, 2 figures, 6 tables.

    1982. Niche Shifts and Competition in Darwin's finches: *Geospiza conirostris* and Congerers. *Evolution*, 36(4):637–657, 5 figures, 8 tables.

Grant, Peter R.
    1975. Four Galápagos Islands. *Geographical Journal*, 141(1):76–87. 2 figures, 2 tables, 4 plates.
    1980. [Visit to Isla Champion, 6–23 August 1980.] [Unpublished field trip itinerary report, on file at the Charles Darwin Research Station, Santa Cruz, Galápagos.]
    1981. Speciation and the Adaptive Radiation of Darwin's Finches. *American Scientist*, 69(6):653–663, 8 figures, 1 table.

Grant, Peter R., and B. Rosemary Grant
    1980. The Breeding and Feeding Characteristics of Darwin's Finches on Isla Genovesa, Galápagos. *Ecological Monographs*, 50(3):381–410, 16 figures, 19 tables.

Grant, Peter R., and K. Thalia Grant
    1979. Breeding and Feeding Ecology of the Galápagos Dove. *The Condor*, 81(4):397–403, 1 figure, 4 tables.

Grant, Peter R., and Nicola Grant
    1979. Breeding and Feeding of Galápagos Mockingbirds, *Nesomimus parvulus*. *The Auk*, 96(4):723–736, 1 figure, 5 tables.

Gregg, D.R.
    1972. Holocene Stratigraphy and Moas at Pyramid Valley, North Canterbury, New Zealand. *Records of the Canterbury Museum*, 9(2):151–158, 3 figures.

Groot, R.S. de
    1983. Origin, Status and Ecology of the Owls in Galápagos. *Ardea*, 71(2):167–182, 3 figures, 6 tables, 3 appendices.

Guilday, John E., Paul W. Parmalee, and Harold W. Hamilton
    1977. The Clark's Cave Bone Deposit and the Late Pleistocene Paleoecology of the Central Appalachian Mountains of Virginia. *Bulletin of the Carnegie Museum of Natural History*, 2: 87 pages, 21 figures, 23 tables.

Gunther, Albert
    1860. On a New Snake from the Galápagos Islands. *Annals and Magazine of Natural History*, series 3, 6:78, 79.
    1875. Description of the Living and Extinct Races of Gigantic Tortoises, Part I: Introduction; Part II: The Tortoises of the Galápagos Islands. *Philosophical Transactions of the Royal Society of London*, 165(1)7:251–284, plates 33–45, unnumbered tables.
    1877a. Account of the Zoological Collection Made during the Visit of H.M.S. "Peterel" to the Galápagos Islands. *Proceedings of the Zoological Society of London*, 1877:64–91, plates 11–13.
    1877b. *The Gigantic Land-Tortoises Living and Extinct in*

the Collection of the British Museum. 96 pages, 54 plates. London: British Museum.

1896. *Testudo ephippium. Novitates Zoologicae*, 3(4):329–334, plates 20–22.

1902. Testudo galapagoensis [sic]. *Novitates Zoologicae*, 9:184–192, plates 16–21.

Haas, Peter H.
1975. Some Comments on Use of the Species-area Curve. *The American Naturalist*, 109(967):371–373, 1 figure.

Hamann, Ole
1975. Vegetational Changes in the Galápagos Islands during the Period 1966–1973. *Biological Conservation*, 7(1):37–59, 7 figures, 13 tables.

1979. On Climatic Conditions, Vegetation Types, and Leaf Size in the Galápagos Islands. *Biotropica*, 11(2):101–122, 19 figures, 6 tables, appendix.

1981. Plant Communities of the Galápagos Islands. *Dansk Botanisk Arkiv*, 34(2):1–163, 54 figures, 20 tables.

Hamilton, Terrell H., and Ira Rubinoff
1963. Isolation, Endemism, and Multiplication of Species in the Darwin's Finches. *Evolution*, 17(6):388–403, 6 figures, 4 tables.

1964. On Models Predicting Abundance of Species and Endemics for the Darwin's Finches in the Galápagos Archipelago. *Evolution*, 18(2):339–342, 1 figure, 2 tables.

1967. On Predicting Insular Variation in Endemism and Sympatry for the Darwin's Finches in the Galápagos Archipelago. *The American Naturalist*, 101(918):161–171, 2 figures, 2 tables.

Harcourt, Sylvia
1982. [Visit to Isla Champion, 4 January 1982.] [Unpublished field trip itinerary report, on file at the Charles Darwin Research Station, Santa Cruz, Galápagos.]

Harlan, Richard
1827. Description of a Land Tortoise, from the Gallápagos [sic] Islands, Commonly Known as the "Elephant Tortoise." *Journal of the Academy of Natural Sciences of Philadelphia*, 5(2):284–292, plate 11.

Harris, Michael P.
1968. Egg-eating Behavior in Galápagos Mockingbirds. *The Condor*, 70(3):269, 270, 1 figure.

1973. The Galápagos Avifauna. *The Condor*, 75(3):265–278, 2 figures, 3 tables.

1974. *A Field Guide to the Birds of Galápagos.* First edition, 160 pages, 68 figures, 12 plates. New York: Taplinger Publishing Co., Inc.

1982. *A Field Guide to the Birds of Galápagos.* Second edition. 160 pages, 68 figures, 12 plates. London: William Collins Sons & Co., Ltd.

Hatch, Jeremy J.
1965. Only One Species of Galápagos Mockingbird Feeds on Eggs. *The Condor*, 67(3):354, 355.

Heller, Edmund
1903. Papers from the Hopkins Stanford Galápagos Expedition, 1898–1899, XIV: Reptiles. *Proceedings of the Washington Academy of Sciences*, 5:39–98, unnumbered tables.

1904. Mammals of the Galápagos Archipelago, Exclusive of the Cetacea. *In* Papers from the Hopkins Stanford Galápagos Expedition, 1898–1899. *Proceedings of the California Academy of Sciences*, third series (Zoology), 3(7)233–250, plates 23, tables.

Hellmayr, Charles E.
1934. Catalogue of Birds of the Americas, part VII. *Field Museum of Natural History, Zoological Series*, 8(330):1–531.

1935. Catalogue of Birds of the Americas, part VIII. *Field Museum of Natural History, Zoological Series*, 8(347):1–541.

Hendrickson, John D.
1966. The Galápagos Tortoises, *Geochelone* Fitzinger, 1835 (*Testudo* Linnaeus, 1758, in part). *In* Robert I. Bowman, editor, *The Galápagos: Proceedings of the Symposia of the Galápagos International Scientific Project*, pages 252–257, 1 table. Berkeley: University of California Press.

Herrera, Carlos M., and Fabian M. Jaksić
1980. Feeding Ecology of the Barn Owl in Central Chile and Southern Spain: A Comparative Study. *The Auk*, 97(4):760–767, 1 figure, 3 tables.

Hertlein, Leo G.
1972. Pliocene Fossils from Baltra (South Seymour) Island, Galápagos Islands. *Proceedings of the California Academy of Sciences*, series 4, 39(3):25–46, 39 figures.

Hey, Richard, G., Leonard Johnson, and Allen Lowrie
1977. Recent Plate Motions in the Galápagos Area. *Geological Society of America Bulletin*, 88(10):1385–1403, 15 figures, 3 tables.

Heyerdahl, Thor
1963. Archaeology in the Galápagos Islands. *Occasional Papers of the California Academy of Sciences*, 44:45–51.

Heyerdahl, Thor, and Arne Skjolsvold
1956. Archaeological Evidence of Pre-Spanish Visits to the Galápagos Islands. *Memoirs of the Society for American Archaeology*, 12:1–71, 48 figures, 2 tables, appendix.

Hickman, Carole S., and Jere H. Lipps
1985. Geologic Youth of Galápagos Islands Confirmed by Marine Stratigraphy and Paleontology. *Science*, 227:1578–1580, 2 figures.

Hooker, Joseph Dalton
1847. Enumeration of the Plants of the Galápagos Islands, with Descriptions of Those Which are New. *The Transactions of the Linnean Society of London*, 20(2)9:163–233.

Houvenaghel, Guy T.
1974. Equatorial Undercurrent and Climate in the Galápagos Islands. *Nature*, 250(5467):565, 566, 2 figures.

Howell, John Thomas
1933. The Cactaceae of the Galápagos Islands. *Proceedings of the California Academy of Sciences*, series 4, 21(5):41–54, plates 2, 3.
1934. Cacti in the Galápagos Islands. *Cactus and Succulent Journal*, 5(8):515–518, 6 figures.
1941. Hugh Cuming's Visit to the Galápagos Islands. *Lloydia*, 4(4):291–292.

Howmiller, Richard, and Keith Dahnke
1969. Chemical Analysis of Salt from Tagus Crater lake, Isabela, Galápagos. *Limnology and Oceanography*, 14(4):602–604, 1 figure, 2 tables.

Jaksić, Fabian M., Robert L. Seib, and Carlos M. Herrera
1982. Predation by the Barn Owl (Tyto alba) [sic] in Mediterranean Habitats of Chile, Spain and California: A Comparative Approach. *The American Midland Naturalist*, 107(1):151–162, 1 figure, 3 tables, appendix.

Jaksić, Fabian M., and Jose L. Yáñez
1980. Differential Utilization of Prey Resources by Great Horned Owls and Barn Owls in Central Chile. *The Auk*, 97(4):895, 896, 1 table.

Janzen, Daniel H.
1976. The Depression of Reptile Biomass by Large Herbivores. *The American Naturalist*, 110(973):371–400, 1 table.

Johnson, Ned K.
1983. The California Islands: Proceedings of a Multidisciplinary Symposium [Review]. *The Auk*, 100(3):782–784.

Johnson, R.G.
1982. Brunhes-Matuyama Magnetic Reversal Dated at 790,000 yr B.P. by Marine-astronomical Correlations. *Quaternary Research*, 17(2):135–147, 11 figures, 2 tables.

Johnston, David W.
1972 [1974]. Food of the Barn Owl on Grand Cayman, B.W.I. *Quarterly Journal of the Florida Academy of Sciences*, 35(4):171, 172.
1975. Ecological Analysis of the Cayman Island Avifauna. *Bulletin of the Florida State Museum, Biological Sciences*, 19(5):235–300, 19 figures, 18 tables, 3 appendices.

Juvik, J.D., and A.P. Austring
1979. The Hawaiian Avifauna: Biogeographic Theory in Evolutionary Time. *Journal of Biogeography*, 6:205–224, 2 figures, 6 tables, appendix.

Koford, Carl B.
1966. Economic Resources of the Galápagos Islands. *In* Robert I. Bowman, editor, *The Galápagos: Proceedings of the Symposia of the Galápagos International Scientific Project*, pages 286–290. Berkeley: University of California Press.

Lack, David
1945. The Galápagos Finches (Geospizinae): A Study in Variation. *Occasional Papers of the California Academy of Sciences*, 21: 159 pages, 4 plates, 16 text-tables, 10 main tables.
1946. The Names of the Geospizinae (Darwin's Finches). *Bulletin of the British Ornithologicists' Club*, 67(469):15–22, 1 table.
1947. *Darwin's Finches.* 204 pages, 27 figures, 3 plates, 32 tables, 4 supplementary tables. Cambridge, England: Cambridge Univ. Press.
1969. Subspecies and Sympatry in Darwin's Finches. *Evolution*, 23(2):252–263, 2 tables, 3 appendices.

Lanyon, Wesley E.
1978. Revision of the *Myiarchus* Flycatchers of South America. *Bulletin of the American Museum of Natural History*, 161(4):427–628, 89 figures, 48 tables.

Laruelle, Jacques
1966. Study of a Soil Sequence on Indefatigable Island. *In* Robert I. Bowman, editor, *The Galápagos: Proceedings of the Symposia of the Galápagos International Scientific Project*, pages 87–92, 8 tables. Berkeley: University of California Press.

Lévêque, Raymond
1963. Le Statut actuel des vertebres rares et menaces de l'archipel des Galápagos. *La Terre et la Vie*, 4:397–430, 12 figures, 9 maps, 4 tables.

Levinson, M.
1982. Taphonomy of Microvertebrates—from Owl Pellets to Cave Breccia. *Annals of the Transvaal Museum*, 33(6):115–121, 5 figures.

Lewin, Roger
1983. Finches Show Competition in Ecology. *Science*, 219(4591):1411, 1412, 1 figure.

Linsley, E.G.
1977. Insects of the Galápagos (Supplement). *Occasional Papers of the California Academy of Sciences*, 125:50 pages.

Linsley, E.G., and R.L. Usinger
1966. Insects of the Galápagos Islands. *Proceedings of the California Academy of Sciences*, series 4, 33(7):113–196, 1 table.

Loomis, Leverett Mills
1918. Expedition of the California Academy of Sciences to the Galápagos Islands, 1905–1906, XII: A Review of the Albatrosses, Petrels, and Diving Petrels. *Proceedings of the California Academy of Sciences*, series 4, 2(2):1–187, plates 1–17, unnumbered tables.

MacArthur, Robert H., and Edward O. Wilson
1963. An Equilibrium Theory of Insular Biogeography.

Evolution, 17(4):373–387, 5 figures, 3 tables, appendices.

1967. *The Theory of Island Biogeography*. 203 pages, 60 figures, 13 tables. Princeton, New Jersey: Princeton University Press.

MacFarland, Craig G., José Villa, and Basilio Toro

1974a. The Galápagos Giant Tortoise (*Geochelone elephantopus*), Part 1: Status of the Surviving Populations. *Biological Conservation*, 6(2):118–133, 7 figures, 8 tables.

1974. The Galápagos Giant Tortoise (*Geochelone elephantopus*), Part 11: Conservation Methods. *Biological Conservation*, 6(3):198–212, 5 figures, 10 tables.

Maglio, Vincent J.

1970. West Indian Xenodontine Colubrid Snakes: Their Probable Origin, Phylogeny, and Zoogeography. *Bulletin of the Museum of Comparative Zoology at Harvard University*, 141(1):1–54, 37 figures, 2 tables, appendix.

Marchant, Stephen

1958. The Birds of the Santa Elena Peninsula, S.W. Ecuador. *The Ibis*, 100(3):349–387, 1 figure.

1959. The Breeding Season in S.W. Ecuador. *The Ibis* 101(2):137–152, 1 figure, 1 table.

Markham, A.H.

1880. A Visit to the Galápagos Islands in 1880. *Proceedings of the Royal Geographical Society and Monthly Record of Geography*, new series, 2(12):742–755.

Marlow, Ronald W., and James L. Patton

1981. Biochemical Relationships of the Galápagos Giant Tortoises (*Geochelone elephantopus*). *Journal of Zoology, London*, 195(3):413–422, 1 figure, 4 tables.

McBirney, Alexander R., and Ken-ichiro Aoki

1966. Petrology of the Galápagos Islands. *In* Robert I. Bowman, editor, *The Galápagos: Proceedings of the Symposia of the Galápagos International Scientific Project*, pages 71–77, 4 figures, 2 tables. Berkeley: University of California Press.

McBirney, Alexander R., and Howel Williams

1969. Geology and Petrology of the Galápagos Islands. *Geological Society of America Memoir*, 118:197 pages, 48 figures, 21 plates, 21 tables.

McCulloch, Beverly, and Michael M. Trotter

1979. Some Radiocarbon Dates for Moa Remains from Natural Deposits. *New Zealand Journal of Geology and Geophysics*, 22(2):277–279.

Mearns, Edgar A.

1903. Feathers Beside the Styx. *The Condor*, 5(2):36–38.

Mertens, Robert

1960. Uber die Schlangen der Galapagos. *Senckenbergiana Biologica*, 41(3/4):133–141.

Montoriol-Pous, Joaquín, and Oleguer Escolá

1975. Contribución al conocimiento vulcano-espeleoló-gico de la isla Floreana (Galápagos, Ecuador). *In* V Symposium de Espeleología. *Speleon*, 1: 57–67.

Morton, S.R., and A.A. Martin

1979. Feeding Ecology of the Barn Owl, *Tyto alba*, in Arid Southern Australia. *Australian Wildlife Research*, 6(2):191–204, 4 figures, 4 tables.

Murphy, Robert Cushman

1936. *Oceanic Birds of South America*. Volume 1, 640 pages, frontispiece, 61 figures, 5 unnumbered color plates, 38 numbered black-and-white plates. New York: American Museum of Natural History.

Newell, Reginald E.

1973. Climate and the Galápagos Islands. *Nature*, 245(5420):91, 92, 1 table.

Niethammer, Jochen

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(4):593–606, 4 figures, 4 tables.

Norman, F.I.

1970. Food Preferences of an Insular Population of *Rattus rattus*. *Journal of Zoology, London*, 162 (4):493–503, 2 figures, 3 tables.

1975. The Murine Rodents *Rattus rattus*, *exulans*, and *norvegicus* as Avian Predators. *Atoll Research Bulletin*, 182:1–13.

Olson, Storrs L.

1975. Paleornithology of St. Helena Island, South Atlantic Ocean. *Smithsonian Contributions to Paleobiology*, 23: 49 pages, 10 figures, 6 plates, 8 tables.

1977. Additional Notes on Subfossil Bird Remains from Ascension Island. *The Ibis*, 119(1)37–43, 2 figures.

1978. A Paleontological Perspective of West Indian Birds and Mammals. *In* Frank B. Gill, editor, Zoogeography in the Caribbean: The 1975 Leidy Medal Symposium. *Academy of Natural Sciences of Philadelphia Special Publication*, 13:99–117, 1 figure.

1979. Multiple Origins of the Ciconiiformes. *Proceedings 1978 Conference of the Colonial Waterbird Group*, pages 165–170.

1981. Natural History of Vertebrates on the Brazilian islands of the Mid South Atlantic. *National Geographic Society Research Reports*, 13:481–492.

Olson, Storrs L., and William B. Hilgartner

1982. Fossil and Subfossil Birds from the Bahamas. *In* Storrs L. Olson, editor, Fossil Vertebrates from the Bahamas. *Smithsonian Contributions to Paleobiology*, 48:22–56, figures 2–12, tables 5–12.

Olson, Storrs L., and Helen F. James

1982a. Fossil Birds from the Hawaiian Islands: Evidence for Wholesale Extinction by Man before Western

Contact. *Science*, 217 (4560):633–635, 1 figure, 1 table.

1982b. Prodromus of the Fossil Avifauna of the Hawaiian Islands. *Smithsonian Contributions to Zoology*, 365: 59 pages, 12 figures, 5 tables.

1984. The Role of Polynesians in the Extinction of the Avifauna of the Hawaiian Islands. *In* Paul S. Martin and Richard G. Klein, editors, *Quaternary Extinctions*, pages 768–780, 3 figures, 2 tables. Tucson: University of Arizona Press.

Orr, Robert T.
1966. Evolutionary Aspects of the Mammalian Fauna of the Galápagos. *In* Robert I. Bowman, editor, *The Galápagos: Proceedings of the Symposia of the Galápagos International Scientific Project*, pages 276–281, 4 figures. Berkeley: University of California Press.

Otteni, Lee C., Eric G. Bolen, and Clarence Cottam
1972. Predator-prey Relationships and Reproduction of the Barn Owl in Southern Texas. *The Wilson Bulletin*, 84(4):434–448, 1 figure, 11 tables.

Palmer, Clarence E., and Robert L. Pyle
1966. The Climatological Setting of the Galápagos. *In* Robert I. Bowman, editor, *The Galápagos: Proceedings of the Symposia of the Galápagos International Scientific Project*, pages 93–99, 4 figures. Berkeley: University of California Press.

Patton, James L., Suh Y. Yang, and Philip Myers
1975. Genetic and Morphologic Divergence among Introduced Rat Populations (*Rattus rattus*) of the Galápagos Archipelago, Ecuador. *Systematic Zoology*, 24(3):296–310, 2 figures, 7 tables.

Paynter, Raymond A., Jr.
1970. Subfamily Emberizinae, Buntings and American Sparrows. *In* Raymond A. Paynter, Jr., and Robert W. Storer, editors, *Check-list of Birds of the World*, 13:3–214. Cambridge, Massachusetts: Museum of Comparative Zoology, Harvard University.

Pitt, William D., and Matt J. James
1983. Late Cenozoic Marine Invertebrate Paleontology of the Galápagos Islands [Abstract]. In *Western Society of Malacologists Annual Report*, 15:14, 15.

Porter, David
1822. *Journal of a Cruise Made to the Pacific Ocean by Captain David Porter in the United States Frigate Essex in the Years 1812, 1813, 1814*. Second edition, 2 volumes. New York.

Power, Dennis M.
1975. Similarity among Avifaunas of the Galápagos Islands. *Ecology*, 56(3):616–626, 8 figures, 1 table.

Pregill, Gregory K.
1981. Late Pleistocene Herpetofaunas from Puerto Rico. *University of Kansas Museum of Natural History Miscellaneous Publications*, 71: 72 pages, 26 figures, 5 tables.

1982. Fossil Amphibians and Reptiles from New Providence Island, Bahamas. *In* Storrs L. Olson, editor, Fossil Vertebrates from the Bahamas. *Smithsonian Contributions to Paleobiology*, 48:8–21, tables 1–4.

Preston, Frank W.
1962a. The Canonical Distribution of Commonness and Rarity, Part 1. *Ecology*, 43(2):185–215, figures 1–31, tables 1–13.

1962b. The Canonical Distribution of Commonness and Rarity, Part II. *Ecology*, 43(3):410–432, figures 32–37, tables 14–24.

Pritchard, Peter Charles Howard
1967. *Living Turtles of the World*. 288 pages, color and black-and-white figures and plates, appendix. Jersey City, New Jersey: T.F.H. Publications, Inc.

Quinn, William H., and Wayne V. Burt
1970. Prediction of Abnormally Heavy Precipitation over the Equatorial Pacific Dry Zone. *Journal of Applied Meteorology*, 9(1):20–28, 3 figures, 1 table.

Racine, Charles H., and Jerry F. Downhower
1974. Vegetation and Reproductive Strategies of *Opuntia* (Cactaceae) in the Galápagos Islands. *Biotropica*, 6(3):175–186, 5 figures, 4 tables.

Ramage, C.S.
1975. Preliminary Discussion of the Meteorology of the 1972–73 El Niño. *Bulletin of the American Meteorological Society*, 56(2):234–242, 13 figures, 2 tables.

Rasmusson, Eugene M., and John M. Wallace
1983. Meteorological Aspects of the El Niño/Southern Oscillation. *Science*, 222(4629):1195–1202, 6 figures.

Ray, Clayton E., and Frank C. Whitmore, Jr.
1973. Paleontology. *In* Tom Simkin, William G. Reeder, and Craig G. MacFarland, editors, *Galápagos Science: 1972 Conference*, pages 67, 68. Washington, D.C. [Printed for the Smithsonian Institution; sponsored by the National Science Foundation and the University of Wisconsin.]

Reynolds, T.N.
1835. *Voyage of the United States Frigate* Potomac *under the Command of Commodore John Downes, During the Circumnavigation of the Globe, in the Years 1831, 1832, 1833, and 1834*. 560 pages. New York. [Not seen by DWS.]

Richardson, Constance
1933. Petrology of the Galápagos Islands. *Bernice P. Bishop Museum Bulletin*, 110:45–67, figure 9, tables 4–7.

Ridgway, Robert
1889 [1890]. Scientific Results of Explorations by the U.S. Fish Commission Steamer *Albatross*, 1: Birds

Collected on the Galápagos Islands in 1888. *Proceedings of the United States National Museum*, 12(767):101–128, 6 figures.

1893. Remarks on the Avian Genus Myiarchus [sic], with Special Reference to M. yucatanensis [sic] Lawrence. *Proceedings of the United States National Museum*, 16(955):605–608.

1894. Descriptions of Twenty-two New Species of Birds from the Galápagos Islands. *Proceedings of the United States National Museum*, 17(1007):357–370.

1897. Birds of the Galápagos Archipelago. *Proceedings of the United States National Museum*, 19(1116):459–670, 7 figures, plates 56, 57, unnumbered maps and tables.

1901. The Birds of North and Middle America: Family Fringillidae—The finches. *Bulletin of the United States National Museum*, 50 (I): 715 pages, 20 plates, unnumbered tables.

1907. The Birds of North and Middle America: Family Turdidae—Thrushes [through] Family Cotingidae—Chatterers. *Bulletin of the United States National Museum*, 50(4): 973 pages, 34 plates, unnumbered tables.

Robinson, B.L.
1902. Flora of the Galápagos Islands. *Proceedings of the American Academy of Arts and Sciences*, 38(4):77–269, 3 plates, 4 tables.

Robinson, William Albert
1936. *Voyage to the Galápagos.* 279 pages, illustrations, plates, maps. New York: Harcourt, Brace and Co.

Rose, Ruth
1924. Man and the Galápagos. *In* William Beebe, *Galápagos: World's End*, pages 332–417, figures 78, 79. New York and London: G.P. Putnam's Sons.

Roth, Louis M.
1982. Introduction. *In* W.J. Bell and K.G. Adiyodi, editors, *The American Cockroach*, pages 1–14. London: Chapman and Hall. [Not seen by DWS.]

Rothschild, Walter
1902. Note Regarding *Testudo elephantopus. Novitates Zoologicae*, 9:448.

1907. *Extinct Birds.* xii + 244 pages, 42 plates. London: Hutchinson & Co.

Rothschild, Walter, and Ernest Hartert
1899. A Review of the Ornithology of the Galápagos Islands, with Notes on the Webster-Harris Expedition. *Novitates Zoologicae*, 6(2):85–205, plates 5, 6, unnumbered figures and tables.

1902. Further Notes on the Fauna of the Galápagos Islands: Notes on the Birds. *Novitates Zoologicae*, 9:381–418, plate 10, 2 figures.

Ruprecht, Andrej L.
1979. Food of the Barn Owl, *Tyto alba guttata* (C. L. Br.)

from Kujawy. *Acta Ornithologica*, 16(19):493–511, 2 figures, 1 table.

Salvin, Osbert
1876. On the Avifauna of the Galápagos Archipelago. *Transactions of the Zoological Society of London*, 9(9):447–510, plates 84–89, 1 map, unnumbered figures.

1883. A List of the Birds Collected by Captain A.H. Markham on the West Coast of America. *Proceeding of the Zoological Society of London*, 1883:419–432.

Sauer, Jonathan D.
1969. Oceanic Islands and Biogeographic Theory: A Review. *The Geographical Review*, 59(4):582–593.

1982. Cayman Islands Seashore Vegetation: A Study in Comparative Biogeography. *University of California Publications in Geography*, 25: xii + 161 pages, 1 map, 25 profiles, 39 plates, 13 tables.

Schluter, D., and Peter R. Grant
1982. The Distribution of *Geospiza difficilis* in Relation to *G. fuliginosa* in the Galápagos Islands: Tests of Three Hypotheses. *Evolution*, 36(6):1213–1226, 6 figures, 5 tables.

Seebohm, Henry
1881. Catalogue of the Passeriformes, or Perching Birds, in the Collection of the British Museum: Cichlomorphae, Part II: Containing the Family Turdidae (Warblers and Thrushes). In *Catalogue of the Birds in the British Museum*, 5:426 pages, 18 color plates. London: British Museum.

Seemann, Berthold Carl
1853. *Narrative of the Voyage of H.M.S.* Herald *during the Years 1845–1851 under the Command of Captain Henry Kellett, R.N., Being a Circumnavigation of the Globe and Three Cruises to the Arctic Region in Search of Sir John Franklin.* 2 volumes in 1, frontispiece, map. London.

Sharpe, R. Bowdler
1888. Catalogue of the Passeriformes, or Perching Birds, in the Collection of the British Museum: Fringilliformes, Part III: Containing the Family Fringillidae. In *Catalogue of the Birds in the British Museum*, 12: 871 pages, 16 color plates. London: British Museum.

Shurcliff, Sidney Nichols
1930. *Jungle Islands: The "Illyria" in the South Seas.* 298 pages, 90 illustrations, 2 maps, unnumbered drawings and color plates, appendix. New York: G.P. Putnam's Sons.

Simkin, Tom
1984. Geology of the Galápagos. *In* Roger Perry, editor, *Galápagos*, pages 15–41, 10 figures. Oxford: Pergamon Press.

Simkin, Tom, and Keith A. Howard
1970. Caldera Collapse in the Galápagos Islands, 1968. *Science*, 169(3944):429–437, 6 figures.

Simkin, Tom, Lee Siebert, Lindsay McClelland, David Bridge, Christopher Newhall, and John H. Latter
1982. *Volcanoes of the World*. 232 pages, 6 figures, 2 tables. Stroudsburg, Pennsylvania: Hutchinson Ross Pub. Co.

Simpson, Beryl B.
1975. Glacial Climates in the Eastern Tropical Pacific. *Nature*, 253(5486):34–36, 1 figure.

Slevin, Joseph R.
1931. Log of the Schooner "Academy" on a Voyage of Scientific Research to the Galápagos Islands, 1905–1906. *Occasional Papers of the California Academy of Sciences*, 17: 162 pages, 16 plates, 1 map.

1935. An Account of the Reptiles Inhabiting the Galápagos Islands. *Bulletin of the New York Zoological Society*, 38(1):3–24, 25 figures.

1955. Charting the "Enchanted Isles." In *Essays in the Natural Sciences in Honor Captain Allan Hancock on the Occasion of His Birthday, July 26, 1955*, pages 99–110, 4 maps. Los Angeles: University of Southern California Press.

1959. The Galápagos Islands: A History of Their Exploration. *Occasional Papers of the California Academy of Sciences*, 25: x + 150 pages, 31 figures.

Snodgrass, Robert E., and Edmund Heller
1904. Papers from the Hopkins-Stanford Galápagos Expedition, 1898–1899, XVI: Birds. *Proceedings of the Washington Academy of Sciences*, 5:231–372, unnumbered tables.

Steadman, David W.
1981. Vertebrate Fossils in Lava Tubes in the Galápagos Islands. In Barry F. Beck, editor, *Proceedings of the Eighth International Congress of Speleology*, 2:549, 550. Americus: Georgia Southwestern College.

1982. The Origin of Darwin's Finches. *Transactions of the San Diego Society of Natural History*, 19(19):279–296, 3 figures.

1984. The Status of *Geospiza magnirostris* on Isla Floreana, Galápagos. *Bulletin of the British Ornithologists' Club*, 104(3):99–102, 1 table.

1985. Fossil Birds from Mangaia, Southern Cook Islands. *Bulletin of the British Ornithologists' Club*, 105(2):58–66, 1 table.

Steadman, David W., and Storrs L. Olson
1985. Bird Remains from an Archaeological Site on Henderson Island, South Pacific: Man-caused Extinction on an "Uninhabited" Island. *Proceedings of the National Academy of Sciences, USA*, 82(18):6191–6195, 2 figures, 1 table.

Steadman, David W., Gregory K. Pregill, and Storrs L. Olson
1984. Fossil Vertebrates from Antigua, Lesser Antilles: Evidence for Late Holocene Human-caused Extinctions in the West Indies. *Proceedings of the National Academy of Sciences, USA*, 81:4448–4451, 2 figures, 2 tables.

Steadman, David W., and Clayton E. Ray
1982. The Relationships of *Megaoryzomys curioi*, an Extinct Cricetine Rodent (Muroidea, Muridae) from the Galápagos Islands, Ecuador. *Smithsonian Contributions to Paleobiology*, 51: 23 pages, 11 figures, 1 table.

Steindachner, Franz
1876. Die Schlangen und Eidechsen der Galapagos-Inseln. *Festschrift Deutsch Kaiserlich-koniglichen Zoologische-Botanische Gesellschaft in Wien*, 1876:301–330, plates 1–7.

Stewart, A.
1911. A Botanical Survey of the Galápagos Islands. *Proceedings of the California Academy of Sciences*, series 4, 1(1):7–288.

Strauch, Dore
1936. *Satan Came to Eden*. xii + 274 pages, 15 photographs, 2 drawings, 2 maps. New York: Harper and Bros.

Stuiver, M., and H.A. Polach
1977. Reporting ^{14}C Data. *Radiocarbon*, 19(3):355–363, 1 figure, 1 table.

Sulloway, Frank J.
1982a. Darwin and His Finches: The Evolution of a Legend. *Journal of the History of Biology*, 15(1):1–53, 8 figures.

1982b. The *Beagle* Collections of Darwin's Finches (Geospizinae). *Bulletin of the British Museum (Natural History)*, *Zoology Series*, 43(2):49–94, 6 figures.

Sundevall, Carl J.
1871. On Birds from the Galápagos Islands. *Proceedings of the Zoological Society of London*, 1871:124–130.

Svenson, Henry K.
1935. Plants of the Astor Expedition, 1930 (Galápagos and Cocos Islands). *American Journal of Botany*, 22:208–277.

Swarth, Harry S.
1931. The Avifauna of the Galápagos Islands. *Occasional Papers of the California Academy of Sciences*, 18: 299 pages, 57 figures, 1 map, unnumbered tables.

Tanner, Z.L.
1888. [Report on the Galápagos Islands.] [Unpublished Manuscript in the Library of the Museum of Comparative Zoology, Harvard University.] 16 pages.

Thomas, Richard, and Kim R. Thomas.
1977. A Small-vertebrate Thanatocenosis from Northern Peru. *Biotropica*, 9(2):131, 132, 1 table.

Thornton, Ian
1971. *Darwin's Islands: A Natural History of the Galápagos*. xiv + 322 pages, 36 photographs, 28 figures. Garden City, New York: Natural History Press.

Townsend, Charles Haskins

1925a. The Galápagos Tortoises in Their Relation to the Whaling Industry. *Zoologica*, 4(3):55–135, figures 20–32.

1925b. The Whaler and the Tortoise. *The Scientific Monthly*, 21(8):166–172.

1928. The Galápagos Islands Revisited. *Bulletin of the New York Zoological Society*, 31(5):148–169, 32 figures.

1930. Astor Expedition to the Galápagos Islands. *Bulletin of the New York Zoological Society*, 33(4):135–155, 30 figures.

Treherne, J.

1983. *The Galápagos Affair.* xv + 223 pages, 33 photographs, 6 figures. New York: Random House, Inc.

Trost, Charles H., and J. Howard Hutchison

1963 [1964]. Food of the Barn Owl in Florida. *Quarterly Journal of the Florida Academy of Sciences*, 26(4)382–384, 1 table.

Vanalek, George J.

1982. *Nycteris cinerea* (*Lasiurus cinereus*) of the Galápagos. *Informe Anual 1981 Estacion Cientifica Charles Darwin*, pages 189–191, 1 figure, 1 table.

Van Denburgh, John

1912a. Expedition of the California Academy of Sciences to the Galápagos Islands, 1905–1906, IV: The Snakes of the Galápagos Islands. *Proceedings of the California Academy of Sciences*, series 4, 1:323–374, plates 22–30, unnumbered tables.

1912b. Expedition of the California Academy of Sciences to the Galápagos Islands, 1905–1906, VI: The Geckos of the Galápagos Archipelago. *Proceedings of the California Academy of Sciences*, series 4, 1:405–430, unnumbered tables.

1914. Expedition of the California Academy of Sciences to the Galápagos Islands, 1905–1906, X: The Gigantic Land Tortoises of the Galápagos Archipelago. *Proceedings of the California Academy of Sciences*, series 4, 2(1):203–374, plates 12–124, unnumbered tables.

Van Denburgh, J., and J.R. Slevin

1913. Expedition of the California Academy of Sciences to the Galápagos Islands, 1905–1906, IX: The Galápagos Lizards of the Genus *Tropidurus*; with Notes on the Iguanas of the Genera *Conolophus* and *Amblyrhynchus*. *Proceedings of the California Academy of Sciences*, series 4, 2(1):133–202, plates 8–11, unnumbered tables.

Vernon, C.J.

1972. An Analysis of Owl Pellets Collected in Southern Africa. *The Ostrich*, 43(2):109–124, 11 tables, appendix.

Voigt, Birgit

1977a. [Visit to Isla Champion, 1–11 May 1977]. Unpublished field trip itinerary report, on file at the Charles Darwin Research Station Library, Santa Cruz, Galápagos.

1977b. [Visit to Isla Champion, 19 September to 6 October 1977.] Unpublished field trip itinerary report, on file at the Charles Darwin Research Station Library, Santa Cruz, Galápagos.

Voigt, Birgit, and Aksel Voigt

1977. [Visit to Isla Champion, 27 February to 6 March 1977.] Unpublished field trip itinerary report, on file at the Charles Darwin Research Station Library, Santa Cruz, Galápagos.

Vries, Tjitte de

1975. The Breeding Biology of the Galápagos Hawk, *Buteo galapagoensis*. *Le Gerfaut*, 65(1–4):29–57, 13 figures, 2 tables.

1976. Prey Selection and Hunting Methods of the Galápagos Hawk, *Buteo galapagoensis*. *Le Gerfaut*, 66(1–2):3–42, 6 figures, 9 tables.

Wallace, George J.

1948. The Barn Owl in Michigan: Its Distribution, Natural History and Food Habits. *Michigan State College Agricultural Experimental Station Technical Bulletin*, 208: 61 pages, 2 figures, 7 tables.

Wetmore, Alexander, and Bradshaw H. Swales

1931. The Birds of Haiti and the Dominican Republic. *United States National Museum Bulletin*, 155: iv + 483 pages, 26 plates.

Wiggins, Ira L., and Duncan M. Porter

1971. *Flora of the Galápagos Islands.* xx + 998 pages, 268 figures, 96 color plates, 2 tables. Stanford, California: Stanford University Press.

Williams, Howel

1966. Geology of the Galápagos Islands. *In* Robert I. Bowman, editor, *The Galápagos: Proceedings of the Symposia of the Galápagos International Scientific Project*, pages 65–70. Berkeley: University of California Press.

Williamson, Mark

1981. *Island Populations.* 286 pages, many tables and figures. Oxford: Oxford University Press.

Wittmer, Margret

1961. *Floreana Adventure.* 239 pages, 22 photographs, 2 maps. New York: E.P. Dutton and Co., Inc. [Translated from the German by Oliver Coburn.]

Wooster, Warren S., and Oscar Guillen

1974. Characteristics of El Niño in 1972. *Journal of Marine Research*, 32(3):387–404, 11 figures.

Plates

PLATE 1.—Coracoids of *Tyto*: A, modern specimen of *T. alba* from Maryland, USNM 500619, female; B, modern specimen of *T. punctatissima* from Santa Cruz, UCMVZ 140963, female; C, fossil of *T. punctatissima* from Barn Owl Cave, USNM 331288; all specimens × 1.8.
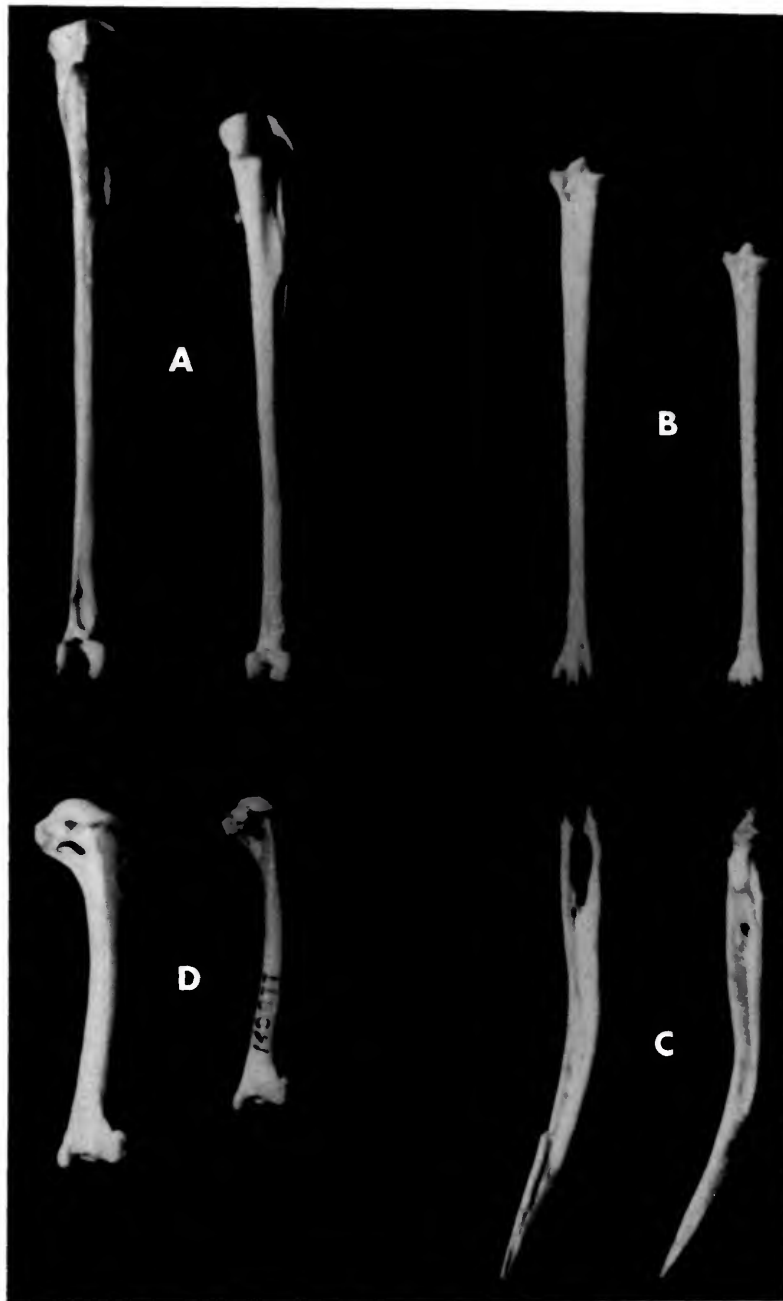
PLATE 2.—Fossils of *Mimus trifasciatus* compared to modern specimens of *M. parvulus* from Santa Cruz, UCMVZ 140977, on the right: A, tibiotarsus, USNM 284371, CPOS; B, tarsometatarsus, USNM 284361, CPOI; C, mandible, USNM 284371, CPOS; D, humerus, USNM 284371, CPS. (Note larger size of *M. trifasciatus* in each element; all specimens × 1.9.)
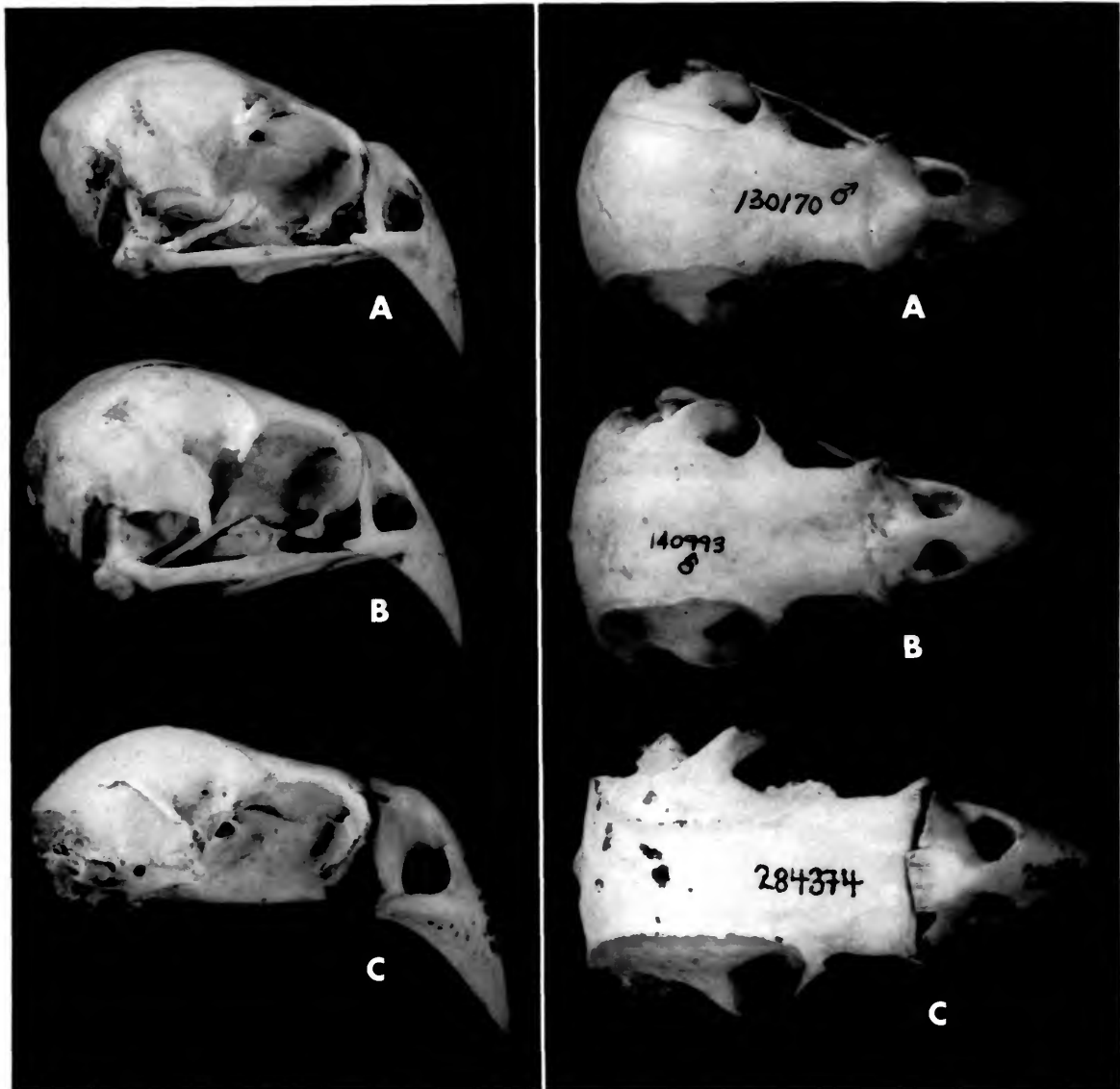
PLATE 3.—Skulls of *Geospiza magnirostris*, in lateral and dorsal aspect: A, *G. m. strenua*, UCMVZ 130170, Santa Cruz, male; B, *G. m. strenua*, UCMVZ 140993, Genovesa, male; C, *G. m. magnirostris* fossil, USNM 284374 (cranium), 28435 (rostrum), Cueva de Post Office (Superior), Floreana. (Note that fossil cranium lacks quadrates, jugals, pterygoids, and palatines, thus giving false appearance of being shallower than modern specimens; also note large size of fossil rostrum; note in fossil cranium the large, strong origin for *M. adductor mandibularis externus superficialis* on each side of temporal region, as well as wide interorbital area just behind rostrum; all specimens approximately × 1.5)
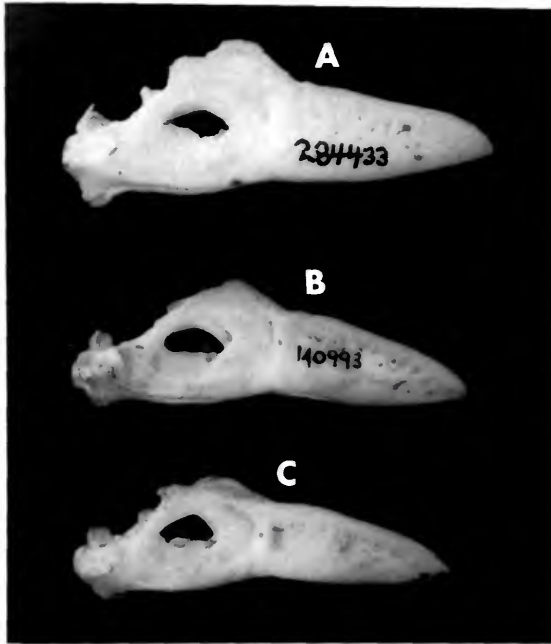
PLATE 4.—Mandibles of *Geospiza magnirostris*, in lateral and dorsal aspect: A, *G. m. magnirostris* fossil, USNM 284433, Cueva de Post Office (Superior), Floreana; B, *G. m. strenua*, UCMVZ 140993, Genovesa,male; C, *G. m. strenua*, UCMVZ 130170, Santa Cruz, male. (Note overall larger size of fossil, especially in elevated surangular region; also note more powerful nature of fossil, especially in large internal process (mandibular articulation); all specimens × 1.5.)