References and Notes

1. A 50,000-man army, of the Persian general Cambyses, is reported by Herodotus [H. Carter, *The Histories of Herodotus* (Heritage, 1958), book 3, chapter 26] to have perished in a sand storm in 525 B.C. while trying to reach and destroy the temple of Jupiter Amun by crossing the Sand Sea presumably from Dakhla Oasis. In more recent times a camel caravan route from Kufra Oasis in Libya to Abu Mungar Well in Egypt crossed the southern end by winding its way through gaps in the longitudinal (seif) dunes.
2. G. Rohlfs, *Drei Monate in der Libyschen Wüste* (Theodor Fischer, Cassel, 1875).
3. P. A. Clayton and L. J. Spencer, *Mineral. Mag.* **23**, 501 (1934); R. A. Bagnold, *Libyan Sands* (Hodder and Staughton, London, 1935), chap. 7; L. de Almasy, *Publications Speciale de la Societe Royale de Geographie d'Egypte* (Schindler, Cairo, 1936), p. 43.
4. R. A. Bagnold, *The Physics of Blown Sand and Desert Dunes* (Methuen, London, 1941).
5. The concept of a fluvial origin for the sand grains of the Western Desert has been stated by C. Squyres (personal communication); R. Said in (*6*), p. 281; C. S. Breed, J. F. McCauley, M. J. Grolier, *J. Geophys. Res.*, in press; B. Issawi, *Geol. Soc. Am. Abstr. Programs*, in press.
6. F. Wendorf and R. Schild, Eds., *Prehistory of the Eastern Sahara* (Academic Press, New York, 1980).
7. C. Squyres and S. E. Whitten, personal communication.
8. Originally called Libyan Desert silica glass, the chunks of clear pale greenish glass have eluded unequivocal explanation [L. J. Spencer, *Mineral. Mag.* **25**, 425 (1939)]. My investigation of the Sand Sea began with a preliminary trip to the area 80 km west of the remote well of Ain Dalla (Fig. 1) in 1978 in an effort to find playa deposits within the Sand Sea while en route to the LDG area (C. V. Haynes, Jr., *Natl. Geogr. Soc. Res. Rep., 1978 Proj.*, in press). Although one playa deposit was believed to have been seen at a distance, it was not visited because of mechanical difficulties. It was with great pleasure, therefore, that I accepted an invitation to visit the southwestern edge of the Sand Sea in March 1981. The expedition, organized by B. Issawi, Geological Survey of Egypt, and R. E. Giegengack, University of Pennsylvania, consisted of specialists in aeolian processes, stratigraphy, physics, archeology, and Quaternary geochronology (R. F. Giegengack *et al.*, in preparation). My function was to attempt to date the linear dunes by studying the stratigraphic relations of the playa deposits and artifacts described to me by R. F. Giegengack on the basis of a trip to the area in 1980 [R. F. Giegengack and J. R. Underwood, Jr., *NASA Tech. Memo. 82385* (1980), pp. 314–316].
9. The streets between the linear dunes were given letter designations during the pioneering study of the LDG by P. A. Clayton and L. J. Spencer [*Mineral. Mag.* **23**, 501 (1934)]. Dune ridge B-C is therefore between streets B and C.
10. Radiocarbon date A-2517 is on shell carbonate, as are dates of 6290 ± 150 (A-2518) and 6270 ± 50 (A-2515) years ago, but the latter sample was large enough to allow analysis of the organic carbon to provide A-2516 after pyrolysis and hydrolysis. Because carbonates are subject to exchange with atmospheric CO_2, A-2516 is considered to be the most accurate of the three values closest to it in apparent age.
11. F. Wendorf, R. Schild, R. Said, C. V. Haynes, A. Gautier, M. Kobuseiwicz, *Science* **193**, 103 (1976); B. Issawi, *Ann. Geol. Surv. Egypt* **8**, 295 (1978); F. Wendorf and R. Schild, (*6*); C. V. Haynes, Jr., in *ibid.*, p. 353. The term pluvial is used here in the general sense of a period of greater effective moisture for vegetation, soil development, and ground water recharge whether due to increased precipitation, decreased evaporation, or both.
12. J. W. Olsen, unpublished manuscript.
13. D. A. Roe, J. W. Olsen, J. R. Underwood, Jr., R. F. Giegengack, *Antiquity*, in press.
14. Absolute dates pertaining to the end of the Early Paleolithic are few and unknown for Egypt; 300,000 ± 100,000 years is a minimum estimate based on potassium-argon dates for the Middle Paleolithic in Ethiopia. See F. Wendorf, R. L. Laury, C. C. Albritton, R. Schild, C. V. Haynes, P. E. Damon, M. Shafiqullah, R. Scarborough, *Science* **187**, 740 (1975); C. E. Stearns, *ibid.* **190**, 809 (1975); R. G. Klein, *ibid.* **197**, 115 (1977).
15. C. V. Haynes, Jr., in preparation; G. E. Wickens, *Boissiera* **24**, 43 (1975); H.-J. Pachur and G. Braun, in *Palaeoecology of Africa and the Surrounding Islands*, E. M. Van Zinderen Bakker, Sr., and J. A. Coetzee, Eds. (Balkema, Rotterdam, 1980), p. 351.
16. C. V. Haynes, Jr., in (*6*), p. 353.
17. ———, *Geogr. J.* **146**, 59 (1980).
18. Soil colors are indexed according to the Munsell system. Where specified, the first value/chroma ratio is for dry soil, the second for moist soil.
19. R. Said, in (*6*), p. 281.
20. The Qoz is an area of ancient dunes and red soils, between 10° and 16°N, stabilized by vegetation [A. Warren, *Z. Geomorphol. Suppl.* **10**, 154 (1970)].
21. The recurrence interval is not known, but R. A. Bagnold [in *Biology of Deserts*, J. L. Cloudsley-Thompson, Ed. (Institute of Biology, London, 1954), p. 7] estimates 30 to 50 years. We are probably still a long way from learning the actual value because, as he points out, "it is against human nature to look conscientiously at an empty rain gauge for several years on end. By the time rain does come the gauge has probably been put to some other use, or the observer is elsewhere."
22. P. J. Mehringer, Jr., *Natl. Geogr. Soc. Res. Rep., 1976 Proj.*, in press; C. V. Haynes, P. J. Mehringer, Jr., El S. A. Zaghloul, *Geogr. J.* **145**, 437 (1979). Mehringer is currently analyzing fossil pollen samples from a Holocene sequence of laminated, organic lake beds at Selima Oasis, Sudan, and from lake sediment cores from Birqet Qarun, Faiyum depression, Egypt.
23. N. Wade, *Science* **185**, 234 (1974); S. W. Matthews, *Natl. Geogr. Mag.* **150**, 576 (1976).
24. Investigations supported by grants from the Smithsonian Foreign Currency Program (grant FC-10215300), the National Science Foundation (grant EAR-7926362), and the National Geographic Society (grant 2258) in cooperation with the Geological Survey of Egypt, and the Geological and Mineral Resources Department, Ministry of Energy and Mining, Sudan. Radiocarbon samples were pretreated by J. Quade and analyzed under the auspices of A. Long. Participation in the Libyan Desert Glass expedition was made possible by R. F. Giegengack and B. Issawi. Participation of P. J. Mehringer, Jr., is appreciated. Reading of preliminary versions of the manuscript by C. C. Albritton, Jr., R. F. Giegengack, and M. Grolier is appreciated.

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Fossil Birds from the Hawaiian Islands: Evidence for Wholesale Extinction by Man Before Western Contact

Abstract. *Thousands of fossil bird bones from the Hawaiian Islands collected since 1971 include remains of at least 39 species of land birds that are not known to have survived into the historic period; this more than doubles the number of endemic species of land birds previously known from the main islands. Bones were found in deposits of late Quaternary age; most are Holocene and many are contemporaneous with Polynesian culture. The loss of species of birds appears to be due to predation and destruction of lowland habitats by humans before the arrival of Europeans. Because the historically known fauna and flora of the Hawaiian Islands represent only a fraction of natural species diversity, biogeographical inferences about natural processes based only on historically known taxa may be misleading or incorrect.*

Since 1971, tens of thousands of fossil bird bones have been found in various geological settings on five of the main Hawaiian islands (*1*). At least 39 endemic species of land birds and one species of seabird are now known only from fossil remains (*2*); only three of these have been named previously (*3*). We have completed a general overview of the fossil deposits and their faunas (*1*), but systematic revisions and descriptions of new taxa are not completed (*4*). We now report on the role of Polynesians, who colonized the Hawaiian Islands by A.D. 600, and perhaps as early as A.D. 400 (*5*), in the disappearance of native birds.

The largest collections of fossil birds were found on the islands of Molokai, Oahu, and Kauai (*6*) (Fig. 1), and a few remains were found in lava tubes on Maui and Hawaii. Bones of prehistorically extinct birds (that is, extinct before Europeans arrived to keep written records, beginning in 1778) have also been recovered from archeological midden sites on Hawaii, Molokai, and Oahu.

The endemic species of land birds (*7*) that survived into the historic period on the main Hawaiian Islands include a goose, a hawk, a flightless rail, a crow, two thrushes, a flycatcher, five honeyeaters, and 27 Hawaiian finches (Drepanidini, previously called "Hawaiian honeycreepers"). To these, the fossil record now contributes the following additional endemic taxa: at least seven species of geese (many of them flightless), two species of flightless ibises, a sea eagle (*Haliaeetus*), a small hawk (*Accipiter*), seven flightless rails (Rallidae), three species of owls belonging to an extinct genus, two large crows (*Corvus*), one honeyeater (*Chaetoptila*), and at least 15 Hawaiian finches (Drepanidini). Thus, the number of species of endemic land birds known for the main islands has been more than doubled by the fossil taxa. The number of colonizations by birds that are known to have produced endemic species in the main islands has likewise now been doubled (*1*).

In addition to providing evidence of the extinction of many species, the fossil record shows that numerous taxa with restricted ranges in the historic period were formerly more widely distributed. For instance, certain species that are known historically only from the Hawaiian Leeward Islands (*Pterodroma hypo-*

leuca, *Psittirostra cantans*, and *Psittirostra ultima*) or only from the island of Hawaii (*Branta sandvicensis*, *Buteo solitarius*, *Chaetoptila angustipluma*, *Psittirostra bailleui*, *Psittirostra kona*, *Psittirostra flaviceps*, and *Ciridops anna*) are represented in fossil deposits from other islands by the same or closely allied species.

As an indication of the extent of extinction, a combined total of only 33 island populations of endemic land birds were recorded from Molokai, Oahu, and Kauai during the historic period, whereas 74 populations are known from the same islands as fossils (Table 1). Only 22 (30 percent) of these fossil populations survived long enough to be recorded by ornithologists. In addition, at least five species of marine birds became extinct or were reduced in range prehistorically (*1*).

Extinction took varying proportions of different elements of the avifauna. Of the 24 endemic species of nonpasserine land birds now known from the main Hawaiian Islands, only three (12.5 percent) are definitely known to have survived into the historic period, whereas 62 percent of the species of passerines discovered so far survived. Of the 13 to 17 species of flightless birds that occur as fossils, only one small rail is known historically. Only one endemic species of raptorial bird (*Buteo solitarius*) now exists in the archipelago, whereas at least five species in three genera became extinct prehistorically, a situation that must alter assumptions concerning the role of predation in the evolution of the Hawaiian avifauna. Because the fossil record is incomplete, the figures on the extent of survivorship may actually be exaggerated.

Although at least one of the Hawaiian fossil deposits is of late Pleistocene age (*1*, *8*), most of the important sites appear to be late Holocene. The major deposits on Molokai and Kauai have yielded maximum radiometric ages ranging from 5145 ± 60 to 6740 ± 80 years before present (B.P.) (*9*), an indication that the extinct species in these deposits survived any Pleistocene climatic perturbations that may have affected the Hawaiian Islands.

At least 12 species that are either extinct, or that were extirpated on the island where their bones were found, have been collected in prehistoric archeological sites; these provide evidence that prehistorically extinct species of birds persisted until Polynesians colonized the islands. Charcoal from a hearth in a large sinkhole at Barber's Point, Oahu, was associated with charred bones of extinct birds and yielded a radiocarbon age of 770 ± 70 years B.P. (*1*). Noncultural deposits at Barber's Point also provide evidence of the contemporaneity of prehistoric man and extinct birds. In these sites, the Pacific rat *Rattus exulans* and the adventive land snail *Lamellaxis* (*10*), both introduced by Polynesian colonists, are ubiquitous in the same stratigraphic levels that contain the greatest concentrations of bones of extinct birds. This evidence suggests that all of the 23 extinct populations of land birds from the Barber's Point deposits were present on Oahu when Polynesians first arrived.

Table 1. Island areas and numbers of species of endemic land birds in the historic and fossil avifaunas of Oahu, Kauai, and Molokai. For comparison, the large island of Hawaii (10,464 km²) has only 23 historically known endemic species of land birds.

Island	Area (km²)	Endemic species of land birds	
		Historic	Fossil
Oahu	1536	11	32
Kauai	1422	13	21
Molokai	676	9	21

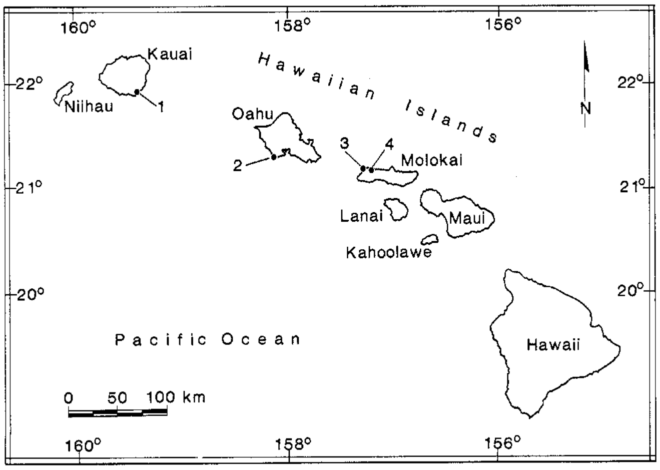

Fig. 1. The main Hawaiian Islands, showing the more important collecting localities for fossil birds: 1, Makawehi dunes, Kauai; 2, Barber's Point, Oahu; 3, Ilio Point, Molokai; and 4, Moomomi dunes, Molokai.

The Polynesian residents may have been responsible for the disappearance of more than half the endemic avifauna of the Hawaiian Islands. We attribute the extinction that occurred to a combination of habitat destruction and predation. Flightless species, as well as ground-nesting land birds and burrowing seabirds, would have been particularly vulnerable to predation by humans and by the dogs, pigs, and rats that arrived with them. Predation, however, was probably not the principal factor in the prehistoric extinction of most Hawaiian birds. It is unlikely, for instance, that 29 extinct populations of small passerines succumbed to hunting pressure. A more plausible explanation for the disappearance of these and many other Hawaiian land birds is the clearing of lowland forest, primarily by fire, for agricultural purposes. Journals of early western voyagers to the islands, including those of James Cook, James King, and George Vancouver, record extensive deforestation and heavy cultivation of the lowlands, as well as the use of fire in clearing (*1*). Archeological research on prehistoric land use supports these early descriptions (*1*). Changes through time in the land snail fauna in the Barber's Point deposits on Oahu also reflect habitat alterations that took place in the prehistoric Polynesian period (*10*).

In the historic period, endemic Hawaiian forest birds have been reported mainly from the wet montane regions where native forest persisted. Yet evidence from the fossil deposits shows that many of these species once occurred, sometimes abundantly, in relatively dry regions near sea level. Early botanical surveys have shown that the drier lowland regions of the Hawaiian Islands once supported a distinctive forest vegetation with many endemic species of plants, although only scattered remnants of this flora were in existence when they were first described by botanists (*11*). Species of birds that were restricted entirely to such habitats would have become extinct. Wet montane forest was probably not the optimal habitat for many others, which perhaps accounts for the scarcity of certain species of Hawaiian birds throughout the historic period.

We should emphasize that the fossil record for the Hawaiian Islands is still incomplete. We have good fossil samples from only three of the main islands, and even these samples lack species that must have been present at the time of deposition (*1*). Fossil material from the two largest islands, Hawaii and Maui, is scant, and there is as yet no way to assess changes in the avifaunas of these islands caused by prehistoric man, although three species of birds are known to have become extinct prehistorically on each. There is no fossil record from the islands of Lanai, Kahoolawe, or Niihau. No endemic species of land birds were ever recorded from the last two, although the absence of endemic birds cannot be a reflection of natural conditions. It is probable that the historically known avifauna represents only a third, or less, of the total number of endemic species of birds that were present in the Hawaiian Islands when man first arrived there.

These findings have implications for studies of island biogeography. The equilibrium theory of island biogeography (*12*), for example, was applied to the historically known avifauna of the Hawaiian Islands, with the results being congruent with the theory (*13*); the fossil record shows these results to be spurious, however (*1*). The assumption that the historically known biota of a prehistorically inhabited island contains an intact complement of species in a natural state of equilibrium is invalid for the Hawaiian Islands, and is most likely invalid for other islands as well.

Note added in proof: Much more extensive deposits of bird bones have very recently been found in lava tubes on Maui. Two or three species of geese, including flightless forms, are represented, along with other birds.

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References and Notes

1. S. Olson and H. James, *Smithsonian Contrib. Zool.*, in press.
2. We use the term "fossil" to refer both to fossil and "subfossil" bones, including those from archeological midden sites.
3. The three previously described fossil species are *Geochen rhuax*, a goose known from fragmentary remains from the island of Hawaii [A. Wetmore, *Condor* **45**, 146 (1943)], *Thambetochen chauliodous*, a large flightless goose, and *Apteribis glenos*, a flightless ibis, both from Molokai [S. Olson and A. Wetmore, *Proc. Biol. Soc. Wash.* **89**, 247 (1976)].
4. S. L. Olson and H. F. James, in preparation.
5. P. Kirch, *Archaeol. Phys. Anthropol. Oceania* **9**, 110 (1974).
6. On Molokai and Kauai the major collecting localities are in calcareous dune sand. Those on Oahu are from a raised coral-algal reef replete with sinkholes and caverns containing abundant fossil birds.
7. We exclude taxa that are not endemic at the species level from the calculations; that is, five freshwater birds that are only subspecifically distinct from mainland species, as well as the short-eared owl *Asio flammeus*, which appears to have colonized the archipelago subsequent to the arrival of man (*1*).
8. H. Stearns, *Occas. Pap. Bernice Pauahi Bishop Mus.* **24**, 144 (1973).
9. Radiocarbon ages from dune deposits are based on three samples of land snail shells and one of crab claws (Smithsonian Radiation Biology Laboratory, Washington, D.C.).
10. P. Kirch and C. Christensen, "Nonmarine molluscs and paleoecology at Barber's Point, Oahu (unpublished report prepared for the U.S. Corps of Engineers; manuscript No. ARCH 14-115; copy deposited in Smithsonian Institution Libraries) (1981), pp. 242–286; C. Christensen and P. Kirch, *Bull. Am. Malacol. Union* **1981**, 31 (1981).
11. J. Rock, *The Indigenous Trees of the Hawaiian Islands* ("Published under patronage," Honolulu, 1913).
12. R. H. MacArthur and E. O. Wilson, *The Theory of Island Biogeography* (Princeton Univ. Press, Princeton, N.J., 1967).
13. J. Juvik and A. Austring, *J. Biogeogr.* **6**, 205 (1979).
14. We thank the many persons who aided our research and who are acknowledged in detail in (*1*); we also thank A. Kaeppler and D. W. Steadman for reading the manuscript.

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Androgens Alter the Tuning of Electroreceptors

Abstract. *Weakly electric fish possess electroreceptors that are tuned to their individual electric organ discharge frequencies. One genus,* Sternopygus, *displays both ontogenetic and seasonal shifts in these frequencies, possibly because of endocrine influences. Systemic treatment with androgens lowers the discharge frequencies in these animals. Concomitant with these changes in electric organ discharge frequencies are decreases in electroreceptor best frequencies; hence the close match between discharge frequency and receptor tuning is maintained. These findings indicate that the tuning of electroreceptors is dynamic and that it parallels natural shifts in electric organ discharge frequency.*

In communicatory and active sensory systems, motor outputs and sensory inputs are often matched so that sensory receptors are most sensitive to the frequency components that predominate in the output. For example, in different species of weakly electric fish, tuberous electroreceptors, which are modified hair cells, are most sensitive to the peak power of the species-specific electric organ discharge (EOD) used in electrolocation and communication (*1, 2*). Among the "wave" species, so called because their EOD is nearly sinusoidal, each animal discharges within a species-specific frequency band, with each individual typically discharging at its own characteristic frequency within that band. These individual differences in discharge frequency are reflected in individual variations in electroreceptor tuning: the receptors of a given fish are closely tuned to its EOD frequency (*1*).

Despite the high stability of discharge frequencies in these fish (*3*), there may be changes over the lifetime of an individual. In the South American gymnotoid *Sternopygus* there is a sexual dimorphism in discharge frequencies whereby mature males discharge at lower frequencies than mature females (*4*). This difference apparently results from (i) the gradual divergence of male and female discharge frequencies from the intermediate discharge frequencies found in juveniles (*4, 5*) and (ii) a seasonal enhancement of the difference between male and female discharge frequencies (*5*). These shifts in EOD frequency may be under hormonal control, since treatment of fish

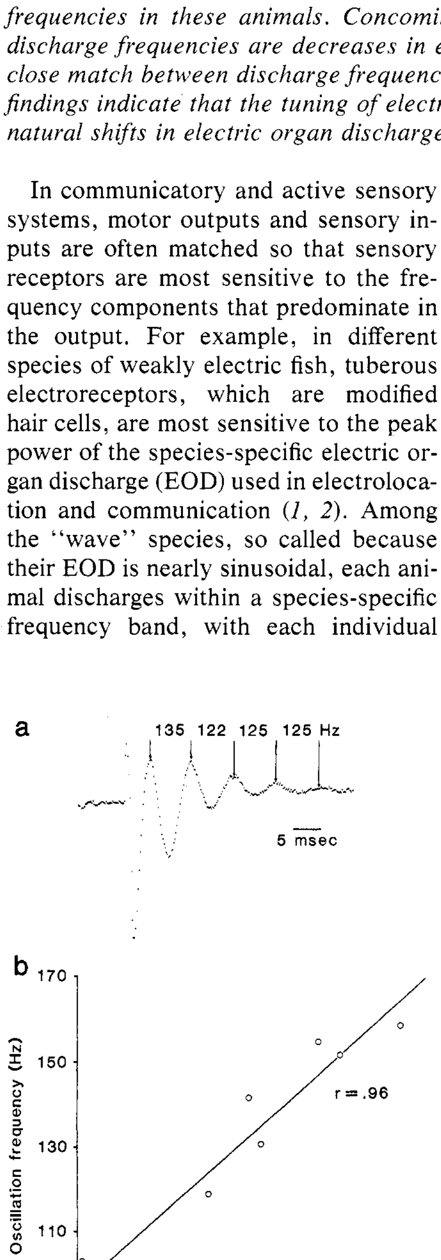

Fig. 1. Receptor oscillation characteristics in *Sternopygus*. (a) Average oscillation from a fish whose EOD frequency was 122 Hz, showing the initial stimulus artifact followed by five peaks. The signal was analog-to-digital converted at a sampling rate of 5 kHz: each point represents a bin width of 200 μsec. We used 512 stimulus presentations in obtaining this response. The number of bins between each peak was used to calculate the period between peaks and then to calculate the frequency of the oscillation. The frequencies, as calculated from the four interpeak periods, are shown above the oscillation. (b) Illustration of the close correspondence between individual EOD frequencies and oscillation frequencies for the eight animals used in the study (day 0).

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