

ZOOGEOGRAPHY OF WEST INDIAN VERTEBRATES IN RELATION TO PLEISTOCENE CLIMATIC CYCLES

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Gregory K. Pregill and Storrs L. Olson

Department of Vertebrate Zoology, National Museum of Natural History,
Smithsonian Institution, Washington DC 20560

INTRODUCTION

In the course of our inquiries into the fossil record of late Pleistocene terrestrial vertebrates of the West Indies, we have become impressed by the number of extinctions of species characteristic of arid habitats, savannas, or grasslands. The fossils themselves come mostly from areas now too mesic to support an extensive xerophilic fauna. This observation has led to the supposition that during the last glaciation, the West Indies were drier than they are now, and that those species presently restricted to xeric habitats are probably relicts of this period of aridity. The available data on late Pleistocene climates and sea levels are concordant with the hypothesis that the extinction of a considerable number of vertebrate species was a result of climatic changes since the end of the Pleistocene, 10-12,000 years ago. We find the application of this concept to be of great use in interpreting puzzling patterns of distribution.

Because there is a compelling need for a better historical perspective in many ecological models of island biogeography, we have attempted to synthesize the literature on the late Pleistocene fossil record and to relate this to the influence of Pleistocene climatic and sea level changes on vertebrate distributions in the West Indies. In this regard the remarks of Ernest Williams (129) seem especially cogent: "Until proper account is taken of the Pleistocene and its consequences, all discussions of island diversity, extinction, and related phenomena in this latest period of geologic time will lack in realism." Evidence that Pleistocene glacial climates significantly altered

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continental environments to the north and south of the Caribbean has led to the concept of refugia, particularly in neotropical biogeography (23, 33, 45, 104, 105). For the West Indies, the presence of a fairly extensive fossil record permits a more direct test of similar hypotheses.

We have limited our examples to land vertebrates, particularly amphibians, reptiles, and birds, because we are familiar with their fossil record, and because many of the taxa are sensitive indicators of environmental changes. Limits on space make it impossible to treat each vertebrate species or each island, so we have selected examples and patterns that have some didactic application to the overall problem.

We review the available data on Pleistocene sea level and climate in the Antilles, survey the fossil record of terrestrial vertebrates, and attempt to relate this to past climatic conditions and present distributional patterns. We then apply the results to certain ecological corollaries of island biogeography. The MacArthur & Wilson (63) paradigm has been subjected to repeated experimental and statistical tests in the hope of isolating the relative contributions made by land area, competition, habitat diversity, and chance in determining species composition on islands. The results are often equivocal, and historical considerations are usually ignored in attempts to apply the theory. Up to the present, paleontology has been the least-utilized resource in studies of island biogeography.

PLEISTOCENE CLIMATE AND SEA LEVEL

It is well known that Pleistocene climates affected biomes world-wide. Most of the limited data on the Antilles come from piston core samples taken from the mid-Caribbean sea floor and analyzed for oxygen isotope ratios and sediment composition (34, 35). Paleocological conditions have also been inferred from fossil foraminifera gathered in the Tongue of the Ocean, a cul-de-sac oceanic trench extending into the middle of the Great Bahama Bank (61, 62). These studies indicate that sea-surface temperatures probably dropped by at least 3° or 4°C during glacial stages of the late Pleistocene. On land, arid conditions prevailed owing to a reduction of rainfall and humidity (18). These estimates for the Caribbean are compatible with palynological studies on the adjacent continents. In South America, Andean glaciation produced an increasingly arid climate and consequent contraction of lowland wet forest and its associated fauna. The importance of these refugia in the process of speciation and in interpretations of biogeography has received considerable emphasis (23, 33, 45, 105). Studies of fossil pollen from central and northern Florida also indicate a cooler and drier regime during the Wisconsinan glacial advance 24,000–17,000 years ago (115–117). As far as we have been able to determine, no palynological

studies conducted in the West Indies have addressed this issue directly. However, some interesting indirect support is available from an examination of Pleistocene cave-floor sediments in Las Villas, Cuba (101, 113). Charcoal layers present in several stratigraphic profiles were postulated to represent the washed-in remnants of huge range fires that occurred during periods of severe drought. The charcoal layers were found at several levels, suggesting alternate wet and dry periods during the Pleistocene.

We should emphasize at this point that it may be misleading simply to declare that the West Indies were drier only during the late Pleistocene. Lowland thornscrub still characterizes nearly all small Antillean islands of low relief, as well as the rainshadows of the larger, mountainous ones. However, the Wisconsinan and previous glaciations would have brought on a more extensive development of xeric habitats, both in the lowlands and at higher elevations.

Oxygen isotope composition of benthic foraminifera has been used to measure eustatic changes in sea level (62), as have studies of fossil reef terraces and other submerged forms of karst topography (43). A number of estimates have been proposed for Pleistocene sea level stands, and while no two fully agree (29), a 120 m depression appears to be a reasonable maximum figure for 17,000 years ago (43). At that time, many adjacent islands were coalesced, and the distance between large banks was greatly reduced, a fact readily demonstrated by any map with adequate bathymetric data. The Great Bahama Bank, for example, was a single emergent land mass an order of magnitude greater in area than the sum of the areas of the individual islands today. By contrast, toward the end of the last interglacial, 65,000 years ago, sea level was evidently about 8–10 m *above* the present level (5). Except for isolated hills and ridges, practically all of the Bahamas would have been submerged. Thus, the reduction or total loss of land would have caused numerous extinctions, and dispersal between islands would have been much more difficult for certain organisms during interglacial periods.

THE FOSSIL RECORD

The fossil record of West Indian terrestrial vertebrates has been derived to a large extent from owl pellets deposited in limestone caves and sinkholes. The earliest efforts at recovering this material for study began about 70 years ago during H. E. Anthony's (6–10) explorations in the Greater Antilles. These studies were augmented by those of W. D. Matthew (64, 65), Gerrit Miller (68–73), and Glover Allen (1–4). Their discoveries received considerable attention because of the extinct mammals that were found, notably sloths, insectivores, and rodents. Alexander Wetmore (119–125)

brought attention to some of the fossil birds from the same deposits. The remains of amphibians and reptiles were largely ignored. These pioneering studies in West Indian paleontology were mostly descriptive, with emphasis on naming new taxa. They demonstrated, however, that the West Indies previously harbored a greater diversity of vertebrates than at present, although a general explanation for the pervasive extinction observed in the fossil record received only cursory treatment. Vertebrate paleontology in the West Indies languished for a period after the novelty of new taxa had passed, but the 1950s and 1960s brought renewed interest in the subject by way of taxonomic studies of fossil lizards (36–40, 47), tortoises (12, 126, 127), birds [see papers by Brodkorb and by Arredondo cited in (79)], bats (53–58), and rodents (11). Recent investigations have emphasized analysis of more comprehensive late Pleistocene vertebrate faunas and the conditions under which they lived (74, 80, 83, 85).

Hundreds of living and extinct species of West Indian vertebrates are now represented as fossils, practically all of them coming from the Greater Antilles. The Lesser Antilles remain relatively unknown paleontologically. Most studies of West Indian fossils must deal with certain limitations, particularly the imprecise information on ages of the deposits; but despite this, a consistent picture of late Pleistocene history is beginning to emerge. In the only published attempt at dating West Indian vertebrate deposits radiometrically (83), carbon-14 ages were derived from shells of land snails, but landsnails are unfortunately subject to contamination by extrinsic carbonate sources in the limestone environment of the caves and thus often yield ambiguous results. Cave deposits usually lack any meaningful stratigraphy, but chronological inferences can often be made between cave faunas according to variation in relative abundance of different taxa. When used with caution, the color of the bones themselves and their degree of permineralization are rough gauges of relative age. Certain cave deposits are clearly Holocene, whereas the oldest faunas known probably date from the late Wisconsinan, about 20,000 years ago (81, 83). Even deposits in closely adjacent caves may vary greatly in age, and the assumption common in the early literature that all such deposits are coetaneous "latest Pleistocene" or "sub-Recent" is invalid (83).

Cave deposits may occasionally be dominated by one or two species of mammal or lizard. "Nesophontes Cave" in Puerto Rico (83), for example, is named for the predominance of fossils of that extinct insectivore. Usually, however, the predatory barn owls (*Tyto* spp.) that were responsible for the deposition of smaller vertebrates were opportunistic feeders (24, 49, 74, 83, 85). Consequently, the use of fine-mesh screening techniques can produce remarkably diverse fossil assemblages, and at times may provide a fairly complete sampling of a local fauna at the time of deposition. Nevertheless,

there are still researchers who destroy such valuable information by using crude techniques in their quest for specimens of larger animals.

Exclusive of bats, about 75% of the species of Greater Antillean land mammals are known only from fossils (90, 111, 112). Meager remains of primates are known from Jamaica and Hispaniola, but two subfamilies of megalonychid sloths are amply represented by fossil species from Cuba, Hispaniola, and Puerto Rico. In the Insectivora, only two species of *Solenodon* survive today, one each on Cuba and Hispaniola, but at least one other genus, *Nesophontes*, and ten other named species of insectivores were present on Cuba, Hispaniola, and Puerto Rico in the late Pleistocene (76, 111). A giant form was recently reported from Cuba, based on a fossil femur some 27% larger than in any previously known taxa in the Antilles (76). The most diverse members of the non-Chiropteran mammalian fauna are the caviomorph rodents, of which at least 16 genera and more than 50 species have been described to date (111, 112); many of these taxa have not been evaluated critically. Approximately 70% of these species occur only as fossils. Perhaps the most spectacular was the almost bear-size rodent *Amblyrhiza inundata* described by Cope (27, 28) from Anguilla and St. Martin in the Lesser Antilles. Bats commonly occur in fossil assemblages, as would be expected because of the cave roosting habits of many species. Several extinct species are known, and fossils of living forms have repeatedly been found outside their present ranges in the West Indies (14, 26, 101, 102).

Fossils have been recovered and described for many of the 20 orders and 64 families of birds with resident species in the Antilles (79). Extinct forms are common in fossil avifaunas, and several of these are especially useful indicators of past arid habitats, as discussed below.

Six families of lizards inhabit the West Indies. The Iguanidae and Gekkonidae have the greatest number of species because of the great diversity of *Anolis* and *Sphaerodactylus*, respectively. These two genera in combination with the dominant genus of anuran, *Eleutherodactylus*, account for over 60% of the approximately 450 species of amphibians and reptiles in the Antilles. The remainder of the herpetofauna is scattered among 55 other genera. Because of the difficulty in recovering the remains of very small individuals (e.g. of *Sphaerodactylus*) the fossil record often does not reflect the composition of the herpetofauna entirely accurately, even though *Anolis* usually does predominate, as would be expected. Fossil herpetofaunas often contain forms that are useful as paleoenvironmental indicators, examples being the lizards *Leiocephalus*, *Cyclura*, and *Aristelliger*, certain species of *Anolis*, and the endemic West Indian toads, *Peltophryne*.

Fossil reptiles that were not deposited in owl pellets include specimens of crocodiles from Grand Cayman (75) and from New Providence (85),

where neither of the two extant Antillean species of *Crocodylus* occur today. As well, fossils of giant tortoises (*Geochelone*), which are perhaps the least understood of extinct West Indian vertebrates, have been recovered from Sombrero, Mona, Cuba, and the Bahamas (12, 126, 127). These are regarded as derivatives from South American stock (13), but none of the fossil taxa are known from sufficient material for a critical taxonomic appraisal.

PATTERNS OF RELICT DISTRIBUTION

The best evidence for aridity in the late Pleistocene comes from organisms that are obligate xerophiles with restricted, relict distributions, but for which fossils are known outside the present range of the species. Xerophiles with restricted or disjunct distributions, but no fossil record, provide additional, if somewhat less convincing, supportive evidence. Naturally, there is little to infer about past habitats from species whose natural history is poorly known, or from the many taxa that are known only as fossils, such as the majority of rodents and insectivores, and all of the edentates of the West Indies. There is, however, the Bahaman hutia *Geocapromys ingrahami*, now restricted to tiny East Plana Cay, which is very arid and scrubby. This rodent once had a much wider distribution in the Bahamas, where it must have survived until fairly recent times, as it is known from Amerindian middens (81). To what extent the present distribution of this species was a result of habitat changes or was caused by human predation is unknown.

The habitat requirements of West Indian bats are poorly understood except for their usual roosting sites. A number of species of bats in the West Indies have become extinct or have experienced range contractions [see tables in (14)]. Environmental changes have been postulated as a possible cause: "Why the species *Brachyphylla pumila* became extinct on Jamaica while other members of the genus have been so successful elsewhere in the Caribbean is an unanswered question. However, it does point up the fact that past environmental or other conditions may have caused elimination of some species even in these relatively depauperate faunas" (14). The history of species such as *Brachyphylla pumila* can be explained by an hypothesis of climatic changes since the late Pleistocene, but these species do not in themselves provide evidence for it. A more corroborative example, pointed out elsewhere (81), is that of the modern and fossil distribution of the endemic Bahaman bat *Natalus tumidifrons*, which closely parallels that of the Bahaman races of the West Indian Red-bellied Woodpecker, *Melanerpes superciliaris*. These taxa exhibit the same relict distribution and the woodpecker at least appears to have suffered from a degradation of broad-leaf forest or scrub habitat (80).

Among birds there are several excellent examples of extinctions or reductions in ranges of species that are characteristic of xeric environments. The best documented of these (80) is the Burrowing Owl, *Athene cucularia* (Figure 1), a species that is characteristic of open, arid prairie or scrubland and that requires soft, sandy soil for burrowing. Historically, the Burrowing Owl has been known in the Greater Antilles only from the Bahamas and Hispaniola, and in the Lesser Antilles from Nevis, Antigua, and Marie Galante. The Lesser Antillean populations, divisible into two endemic subspecies, are now extinct, presumably having been extirpated by introduced predators. Four disjunct populations were found recently in Cuba, three of which are known to be breeding populations (44). At least one of these represents a distinct, undescribed subspecies. Thus, the Burrowing Owl is not a recent colonizer to Cuba. This was further confirmed by fossils collected from a cave near Daiquirí in southeastern Cuba (80).

Elsewhere in the West Indies, fossils of burrowing owls have been found in Jamaica, Cayman Brac, Mona Island, Puerto Rico, Barbuda, Antigua, and two islands of the Bahamas (74, 80, 82). Those from Puerto Rico are

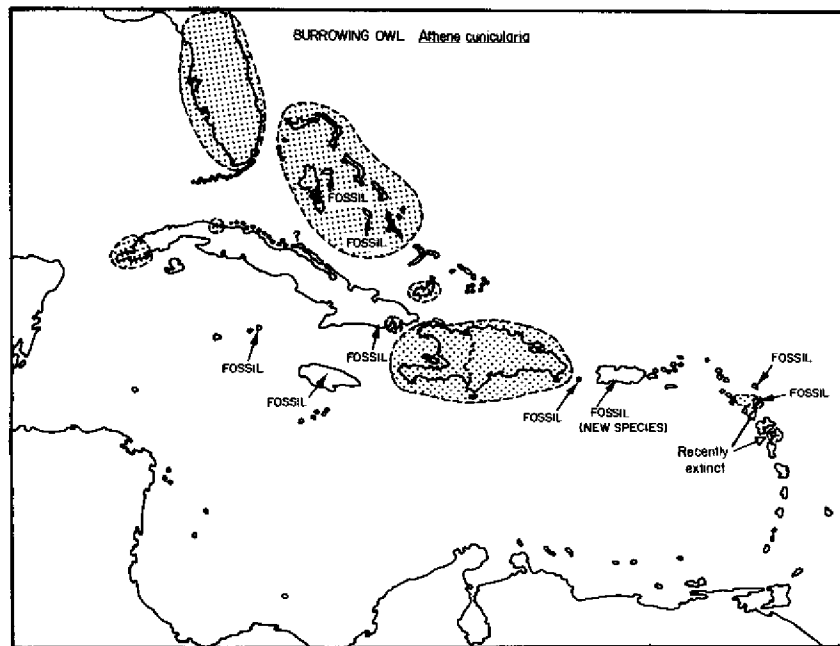


Figure 1 Recent (stippled) and fossil distributions of the Burrowing Owl (*Athene cucularia*) in the West Indies and Florida. The species, which also occurs in the western United States and much of Central and South America, is an obligate xerophile; its distribution in the West Indies, and even within Cuba, is obviously relictual and is the result of the loss of dry habitats since the end of the Pleistocene.

quite distinct from any of the other populations and may represent a different species. The living Bahaman form is consubspecific with the modern Florida population and is possibly a recent invader to the islands, having arrived after a smaller Pleistocene form became extinct (80). The fossil evidence and the modern distribution of the Burrowing Owl show how widespread this bird once was in the West Indies. Its distinctly relictual modern distribution is best explained by the loss or decrease of dry, prairie-like habitat since the late Pleistocene.

Another xeric-adapted species with a relict distribution is the Bahaman Mockingbird, *Mimus gundlachi*. Currently, the species lives only in the Bahamas, on two cays off the northern coast of Cuba (42), and in a small area of the driest part of Jamaica (59). It is now known as a fossil from Puerto Rico (80). In the Bahamas, the species is decidedly more abundant in the drier southern islands than it is in the wetter islands of the Little Bahama Bank, where it is rare on Grand Bahama and absent altogether from Great Abaco (80). Like the Burrowing Owl, the Bahaman Mockingbird was once more widely distributed but has apparently retreated with the loss of xeric habitat.

The thick-knees, *Burhinus*, are charadriiform birds restricted in the New World almost entirely to dry, scrubby or rocky plains. Their importance as paleoecological indicators of arid, open habitat was emphasized by Feduccia (41). The only living population of *Burhinus* in the West Indies is the endemic subspecies *B. bistriatus dominicensis* of Hispaniola. A smaller form, *B. bistriatus nanus*, is known as a fossil from New Providence Island, Bahamas (22, 80), and fossils of *Burhinus* have been examined from deposits in Havana Province, Cuba (80). Thus, the living *Burhinus* of Hispaniola is obviously a relict.

Caracaras (*Polyborus*, *Milvago*) are scavenging falcons that are likewise characteristic of open prairies and savannas. The only caracara in the Recent Antillean fauna is the Cuban population of *Polyborus plancus*, which is inseparable taxonomically from the patently relictual population in the prairies of southern Florida. Elsewhere, the species ranges from the southwestern United States to Tierra del Fuego. An extinct species, *Polyborus creightoni*, is known from the Pleistocene of the Bahamas (22, 80), and another more problematical form was found in the Pleistocene of Puerto Rico (78, 80, 119). Caracaras of the genus *Milvago* exist in savannas through most of South America, but at present do not occur north of Costa Rica. However, a fossil species, *M. alexandri*, is known from Hispaniola (78), and an allied species, *M. readei*, was present in the late Pleistocene (Rancholabrean) of Florida (25). The significance of the Florida occurrences of *Milvago* and *Polyborus plancus* should be emphasized, as they bring to mind several other taxa that currently exist as relicts in the scrub forest

or prairies of south-central Florida. Among them are the Scrub Jay, *Aphelocoma coerulescens*, the Burrowing Owl, *Athene cunicularia*, the tortoise, *Gopherus polyphemus*, and the fence lizard, *Sceloporus woodi*. Because the closest relatives of these species live much farther west, a xeric corridor must have extended along the gulf coast region into northern Mexico in the Pleistocene. Fossil mammals from Florida provide further evidence of this corridor (118). Movement of species into or out of the Caribbean through Florida may have been facilitated by this pathway, and it is thus not unreasonable to expect that the closest relatives of certain arid-adapted Caribbean species might be found living in the southwestern United States or northern Mexico.

Relictual distributions in arid habitats are also evident for many members of the Antillean herpetofauna. The curly-tailed lizards of the iguanid genus *Leiocephalus* are one of the best examples. Endemic to the West Indies, the genus includes 21 species found mostly in dry areas of Cuba, the Cayman Islands, the Bahamas, and Hispaniola. The few specimens of the apparently now extinct *L. herminieri* on Martinique, and fossils of extinct species from Barbuda, Hispaniola, Puerto Rico and Jamaica document a much wider occurrence of these lizards, particularly in the Pleistocene (37-39, 83).

Rock iguanas of the genus *Cyclura* are endemic to the West Indies; the eight recognized species are obligate xerophiles and obvious relicts (98). Although there has been considerable extermination of these lizards by humans in modern times, there are fossils of *Cyclura* from Puerto Rico (83) and the Bahamas (40, 85) from outside the historically known range of extant species, demonstrating that this genus also had a wider distribution during the late Pleistocene.

The xerophilic gekko *Phyllodactylus wirshingi* is known from three widely scattered subspecies, each inhabiting dry, lowland scrub. This lizard is of special interest because it is one of the few species of reptiles in the Greater Antilles to inhabit more than one island. *Phyllodactylus w. wirshingi* occurs in the dry southwestern part of Puerto Rico, *P. w. hispaniolae* borders the arid Valle de Neiba in the Dominican Republic, and *P. w. sommeri* dwells in a small region of the Department de l'Artibonite, Haiti (95). Although no fossils of the species are known, its distribution is obviously relictual and could only have been more continuous in a dry period.

COMBINED EFFECTS OF CLIMATIC CHANGE AND SEA LEVEL FLUCTUATIONS

We have seen that the fossil record and relict distributions of xerophilic vertebrates provide strong evidence that conditions of climate and habitat were appreciably different during the last glaciation. We then need to

consider what the combined effect would have been on the composition and distribution of West Indian faunas if these climatic changes acted in combination with those brought about by eustatic fluctuations in sea level. For example, the Puerto Rican Bank became fragmented by rising sea level about 7,000 years ago, at which time the Virgin Islands were separated from each other and from the Puerto Rican mainland (46). During the late Pleistocene, xeric environments extended throughout the lowlands of Puerto Rico eastward through the rest of the emergent bank. The lowland herpetofauna included such xerophilic species as *Cyclura pinguis*, now restricted to Anegada Island at the eastern extreme of the bank, two species of *Leiocephalus* now extinct, and the endemic toad, *Peltophryne lemur*, confined today to isolated xeric areas on Puerto Rico and possibly Virgin Gorda (83, 84). Also, several upland forest species of *Anolis* occurred at lower elevations than they do at present, perhaps in response to cooler montane temperatures.

Among the late Pleistocene avifauna of Puerto Rico that included the Burrowing Owl, the Bahaman Mockingbird, and the extinct caracara already mentioned, there was also an extinct palm swift of the genus *Tachornis* (S. L. Olson, manuscript). Swifts of this genus now occur only on Hispaniola, Cuba and Jamaica, and they nest and roost in large palm trees in open savanna, a habitat now absent from Puerto Rico.

The Bahamas were probably affected by Pleistocene events more than any other islands in the Antilles. This vast archipelago of low, flat limestone islands and cays was united as five major island complexes during the lowered sea level of the Wisconsinan glaciation: the Little Bahama Bank, Great Bahama Bank, Crooked-Aklins Bank, Turks-Caicos Bank, and Great Inagua [see Figure 1 in (81)]. To the south of these were the now-submerged islands of the Mouchoir, Silver, and Navidad Banks. The Great Bahama Bank, the largest of these complexes, stretched for over 300 km from north to south as an enormous savanna and scrub woodland (81). With the rise in sea level at the end of the Pleistocene, most of this habitat was lost, along with many of the species that lived there. We have already mentioned several examples of vertebrates from the fossil record of New Providence Island that were characteristic of dry, open country. At least 20% of the fossil herpetofauna from New Providence no longer exists on the island (85): the rock iguana, *Cyclura*; a large xerophilic gekko, *Aristelliger*; and the giant tortoises, *Geochelone*. This is but a fraction, however, of the loss among birds. Fully 50% of the species in the fossil avifauna no longer occur on New Providence, and 40% of them are gone from the Bahamas altogether (80). The xerophilic caracaras and thick-knees have already been noted. Meadowlarks (*Sturnella*), obligate inhabitants of grasslands, were also present, but are known in the West Indies today only on Cuba.

In the Bahamas, the post-Pleistocene rise in sea level was accompanied by more pluvial conditions moving from the north southward, producing a latitudinal rainfall gradient. The southern Bahamas (Crooked-Aklins Bank, Turks-Caicos Bank, Inagua, and Mayaguana) receive about half the annual precipitation of Grand Bahama and Great Abaco, the most northern islands (48). Interestingly, the southern Bahamas have, collectively, a much richer herpetofauna (26 species; 19 endemics) than the Little Bahama Bank islands of Grand Bahama and Great Abaco (7 species; 1 endemic), although the two regions have approximately the same land area. The disparity in their respective herpetofaunas may be at least in part attributable to the persistence of dry thornscrub on the southern islands, whereas that habitat on the Little Bahama Bank was predominantly replaced by a monoculture of pine forest (48, 81, 85).

As individual islands, Cuba and Hispaniola are difficult to deal with zoogeographically because of their large size and physiographic complexity. In southwestern Cuba, three genera of birds confined to the Zapata Swamp were discovered as late as 1926 (15, 17): a nearly flightless rail, *Cyanolimnas cerverai*; a wren, *Ferminia cerverai*; and a sparrow, *Torreornis inexpectata*. Barbour (16) believed that these species had evolved in response to special conditions met with only in the Zapata Swamp, but in 1958 a distinct new subspecies of *Torreornis inexpectata* was discovered in southeastern Oriente Province (106) in the very driest part of the island, where the habitat is desert scrub. Subsequently, another isolated population was discovered on Cayo Coco off northern Camagüey (79). Fossils of *Cyanolimnas* have been found on the Isle of Pines and in Pinar del Rio (77), and fossils of *Torreornis* are known from caves in Oriente and Havana Provinces outside the present range of the species (S. L. Olson, in preparation). Because the Zapata Swamp practically dries up at certain times of the year, the habitat of *Torreornis* there is actually more like that of scrub grassland. It thus seems that the original habitat of the species was arid scrub, and that this habitat must have been continuous across most of Cuba in the late Pleistocene.

On Hispaniola, the herpetofauna of over 175 species is fairly well known, largely through the prodigious efforts of Albert Schwartz and Richard Thomas [(100) and other works]. The lizard *Anolis whitemani* is but one example of a xeric-adapted species showing a striking pattern of relictualness in its distribution. It exists as three disjunct subspecies in the very xeric regions of the Valle de Neiba plain, the southeastern base of the Haitian Presqu'île du Nord-Ouest, and in the northwestern tip of this same peninsula (96). A fourth, as yet undescribed population may exist in northwestern Dominican Republic near Monti Cristi. This clearly relictual distribution of *Anolis whitemani* is broken by a series of mesic and semi-mesic valleys. Apparently the species occupied a more continuous range during an arid

period. Similar patterns are evident for species of the ground lizards *Ameiva* (99), the leaf-litter gekkos *Sphaerodactylus* (93), and at least one of the two species of toad, *Peltophryne* (84).

The east-west trending Cul de Sac-Valle de Neiba has long been recognized as an obstacle to the exchange of species between the northern and southwestern portions of Hispaniola. This vast dry plain, below sea level in some places, extends northwest from Barahona in the Dominican Republic to near Port-au-Prince, Haiti. The Neiba plain was inundated by high sea level stands during the Pliocene, and probably during the Pleistocene. Thus, Hispaniola was divided into north and south islands on at least one occasion in the Quaternary (67, 94, 99, 128). A number of faunal distributions reflect this division. There are several species pairs of Hispaniolan birds whose differentiation is best explained by their having originated separately on the two islands (50): the todies, *Todus subulatus* and *T. angustirostris*; the palm tanagers, *Phaenicophilus palmarum* and *P. poliocephalus*; and the ground warblers, *Microligea palustris* and *M. (Xenoligea) montana*. The chat-tanagers, *Calyptophilus*, should be included also. The south island form, *C. tertius*, of Haiti is distinct from *C. frugivorus* of the north island, and probably is best considered a separate species, as it was originally described (123), rather than a subspecies of *C. frugivorus*, as is the current practice (19, 21).

The division of the Hispaniolan herpetofauna into north and south island components was extensively documented by Schwartz (97), who tallied the number of species restricted to each of the two islands, the number that apparently are recent invaders from one island to the other, and the number whose origins are obscured by wide distributions. The results were puzzling: The south island was found to have decidedly more species than the north island, although the latter is about seven times larger. There is no apparent reason for this, but a reexamination of the distributions of the more restricted taxa might provide some answers in light of Pleistocene events.

Because the Wisconsinan glaciation obviously had a profound effect on West Indian vertebrate distributions, it is logical that glacial/interglacial cycles earlier in the Pleistocene may have produced similar drastic changes in the environment, thus casting a bewildering complexity on aspects of Antillean zoogeography. The alternate exposure and submergence of land, and the correlated alternation of xeric and mesic environments, would have resulted in repeated events of faunal isolation, speciation, and extinction, such that relict distributions would be superimposed on one another as a mosaic through time.

The effects of the Wisconsinan glaciation are naturally the most evident because this was the most recent and severe of the Pleistocene climatic events. Also, no terrestrial vertebrate fossil faunas are yet known in the

West Indies that are older than this period. Nonetheless, it is important to attempt to identify those vertebrates with distributions suggesting the effects of earlier glacial or interglacial periods. The Mimidae (mockingbirds and thrashers) of the Lesser Antilles may represent such taxa. The mimids are a North American group with their greatest diversity in Mexico and the deserts of the southwestern United States. The few species that occur in South America are not closely related to those in the Lesser Antilles, and it is probably safe to assume that the ancestors of the Lesser Antillean genera *Ramphocinclus*, *Cinlocerthia*, and *Margarops* (including *Allenia*) arrived by way of the Greater Antilles. However, none of these genera has been found in any Greater Antillean cave deposits, which suggests that their ancestors arrived in the Lesser Antilles prior to the Wisconsinan glaciation. *Ramphocinclus* is a xeric-adapted genus restricted to portions of Martinique and St. Vincent, whereas *Cinlocerthia* is widely distributed in the Lesser Antilles and forages mainly in epiphytic bromelads in humid forests (133). *Margarops fuscatus* has apparently spread to Puerto Rico and the Bahamas from the Lesser Antilles quite recently, as it does not occur as a fossil in either place (80). Thus, the distributional history and habitat requirements of these taxa seem to indicate that they are products of climatic conditions that prevailed in pre-Wisconsinan times.

That repeated climatic cycles were responsible for complex specific differentiation is also evident in frogs of the genus *Eleutherodactylus*. On the south island of Hispaniola, which consists of three major mountain ranges and countless valleys, *Eleutherodactylus* is represented by more than 30 species, 26 of which are endemic. These are found from sea level to over 2400 meters (92) in an intricate pattern of distributions not matched anywhere else in the Antilles. Species are unevenly distributed here, and closely related forms often occur in widely disjunct areas. There is a near absence of frogs in some places where habitat seems quite suitable, whereas adjacent areas may abound in species (92). A probable explanation for the complex radiation of *Eleutherodactylus* on the south island is that habitats fluctuated along altitudinal gradients with changing climatic cycles, resulting in repeated isolation and fragmentation of populations.

The preceding examples indicate that cyclic changes in climate and sea level in the Pleistocene have influenced the distribution of species and the composition of faunas in the West Indies. By extending our perspective even farther back in time, we find that the complex tectonic history of the Antilles (86) adds yet another intricacy to these distributional patterns. Thus, any attempt to interpret the zoogeography of individual organisms or the species composition of islands without accounting for their history is bound to have limited success. We discuss a few such unsatisfactory studies in the following section.

SOME APPLICATIONS TO ECOLOGICAL BIOGEOGRAPHY

Since its publication, MacArthur & Wilson's (63) *Theory of Island Biogeography* has generated many attempts to explain the composition of insular faunas, particularly of birds, by the application of statistical probability theory to various physical and ecological constraints such as island height and area, habitat diversity, and distance from the presumed source of colonization. Authors have addressed such factors as interspecific competition, niche-space, species packing, trophic counterparts, and other "assembly rules" that are believed to determine the "saturation of a community." Some researchers consider these ecological models of biogeography to be mutually exclusive of the systematic and paleontological approaches employed by historical biogeographers (91), although "historical ecology" in the study of insular faunas is not impossible, as Williams (129, 130) has shown.

Terborgh and his associates (107-110) studied the avifauna of the northern Lesser Antilles to assess patterns of colonization and "saturation" of communities. In one study (110) they found it "astonishing" and "paradoxical" that the avifauna of the northern Lesser Antilles was practically homogeneous throughout the islands and that great differences in habitat between islands seemed to have a relatively minor influence in species composition. They cited the fact that 20 of the 24 species known to inhabit the low, dry island of Antigua also occur on the high, wet island of Montserrat. Terborgh et al (110) invoked an ecological solution to the paradox: Because most of the species in the northern Lesser Antilles are found in scrub habitats on the larger island of Guadeloupe, that island was the source of colonization for those to the north. They further suggested that scrub-adapted birds are superior colonizers capable of expanding their foraging zones vertically on such high, forested islands as Montserrat, where most of the forest-adapted birds of Guadeloupe are absent.

An historical rather than ecological perspective probably offers a more satisfying explanation for the composition of the avifauna of the northern Lesser Antilles. There is certainly no a priori reason for regarding Guadeloupe as the source island for the species in question simply because of its size and the affinities of its avifauna. During the lowered sea levels of the late Pleistocene, most of the islands of the northern Lesser Antilles were united to form three much larger islands: Antigua-Barbuda; Anguilla-St. Martin-St. Barthelemy; and St. Kitts-Nevis-St. Eustaius. In area, the first two of these islands were equal to or greater than Guadeloupe, and in combination the three islands would have been as diverse topographically. Because dry scrub and savanna were the predominant vegetation types in

the West Indies at this time, and species adapted to mesic forests would have been confined to reduced windward upland habitats on the higher islands, we find nothing astonishing or paradoxical in the fact that the Lesser Antillean avifauna consists mainly of scrub-adapted species. This is merely a reflection of the conditions that prevailed during the last glaciation. Nor is it surprising that the avifauna is relatively homogeneous, because most of the present day small islands were once part of larger islands that were closer to one another and that probably had a nearly uniform habitat of scrub. The studies by Terborgh and his associates are perhaps most useful in demonstrating that scrub-adapted species have evidently expanded their niches as certain islands became more mesic, but we cannot support their assumptions concerning sources of colonization.

The historical perspective has also made us skeptical of a particular ecological model that attempts to explain the distributional patterns of West Indian birds in terms of a so-called "taxon cycle;" the model postulates that species go through progressive "stages" of expansion in range, differentiation, contraction, and extinction. The concept is credited to Wilson (132), who based his studies on Melanesian ants. We are not prepared to assess Wilson's data, but as applied to West Indian birds (87-89), the hypothesis of a taxon cycle can be shown to be seriously flawed.

Ricklefs & Cox (88) recognized four stages in the taxon cycle, as follows:

Stage I: "Species with widespread or continuous distribution through the islands with little or no subspeciation."

Stage II: "Species generally widespread throughout the islands, but that show considerable differentiation of populations into subspecies."

Stage III: "Species with fragmented and reduced distributions and well-differentiated populations."

State IV: "Species endemic to single islands."

These are not really stages, of course, but simply criteria that define a set of distributional patterns; almost any species in any archipelago would fall into one of these categories. Nevertheless, the hypothesis of the taxon cycle in West Indian birds proceeds entirely from these definitions. Hence, the evidence for the taxon cycle is completely tautological in origin, as actually stated by Ricklefs & Cox (88): "The reality of the cycle, that is the inference that stages I-IV occur in succession, is supported by data on the level of endemism and degree of subspecific differentiation of species in different stages." The data merely show, however, that the distributions of the species under consideration fit the criteria established for the four "stages." The fact that different species of birds in the West Indies have different patterns of distribution does not in itself indicate that each species will exhibit each of these patterns during its history. Indeed, proof of the taxon cycle must come from data showing that a single species actually went through such

a cycle. Given the time involved, the fossil record would presumably be required to demonstrate the existence of such a "cycle."

The taxon cycle does not account for the fact that very different evolutionary histories can yield similar distributional patterns, i.e. "stages." For example, the Smooth-billed Ani, *Crotophaga ani*, is absent from fossil deposits in the West Indies, as is the Cave Swallow, *Hirundo fulva*, on Puerto Rico (S. L. Olson, in preparation). Both can be considered recent arrivals to the West Indies, where they are widespread "Stage I" species today. Their history is obviously different from that of the White-crowned Pigeon, *Columba leucocephala*, a species that is practically endemic to the West Indies, but which has a "Stage I" distribution, and occurs commonly in Pleistocene deposits. Ricklefs & Cox (88, 89) noted that certain species with good dispersal ability, particularly doves and pigeons, seem to delay "their progress through the taxon cycle," which could as easily be interpreted as their not going through the cycle at all.

There are at least three ways by which a species may become endemic to a single island (Stage IV), two of which do not fit the constraints of the taxon cycle in requiring that all endemic species be relicts. Certainly many species are relicts, as the fossil record demonstrates. But a species with a Stage II or III distribution could also have some or all of its populations differentiate into new species, each thus becoming a Stage IV endemic without being a relict in the sense that *Burhinus* is on Hispaniola. A possible example of such a pattern is seen in the warblers, *Dendroica angelae* of Puerto Rico, *D. pharetra* of Jamaica, *D. plumbea* of Guadeloupe and Dominica, and *D. bishopi* of St. Vincent; these mainly "Stage IV" species are probably members of a single radiation (52) and not relicts each of which once had a wider distribution.

Not all endemic species in the West Indies belong to groups that were once widespread. A number of endemics appear to have colonized an island from the mainland and differentiated at the specific level without having dispersed to other islands. Thus, they are autochthons rather than relicts. For example, the vertebrate fauna of Jamaica is quite distinct from that of the rest of the Greater Antilles, perhaps because it was the only one of these islands colonized by taxa originating farther south in Central America, near Nicaragua and Honduras. Jamaica lacked sloths and insectivores, and the rodent fauna is for the most part different from that known elsewhere in the Greater Antilles. No toads of the endemic Greater Antillean genus *Peltophryne* occur there, and there is a dominance of "beta" anoles as opposed to those belonging to the "alpha" radiation that exploded elsewhere in the West Indies (36, 131). The Jamaican Becard, *Platyptaris niger*, is the only member of the Cotingidae found in the West Indies, and there

is neither evidence nor expectation of its ever having occurred on other Antillean islands. Other endemic species of Jamaican birds that probably had a similar autochthonous history are the owl, *Pseudoscops grammicus*; the hummingbird, *Trochilus polytmus*; the flycatchers, *Myiopagis cotta*, *Myiarchus validus*, and *M. barbirostris*; the thrushes, *Turdus aurantius* and *T. jamaicensis*; the vireo, *Vireo osburni*; the tanager, *Euphonia jamaica*; and the emberizines, *Loxipasser anoxantha* and *Euneornis campestris*. The failure to distinguish between relicts and autochthons may account for the inconsistencies in relative abundance that Ricklefs & Cox (89) noted between "Stage IV" endemics on Jamaica and those on St. Lucia.

In attempting to explain the cause of the taxon cycle, Ricklefs & Cox (88) mentioned the possibility that "progress through the cycle may be an 'internal' process of the population uninfluenced by external factors, but if so, the mechanism involved is obscure." There is an unstated assumption here, as in much other literature on island biogeography dealing with faunal turnover, that some intrinsic factor may ultimately cause species on islands to become extinct. Ricklefs & Cox went on to hypothesize, however, that "for a particular species the cycle results from progressively reduced competitive ability caused by the counterevolution of the island biota toward that species. The cycle is driven by competition from newly arriving colonists that are initially free of a counteradapted load." Ecological doctrine and good sense revolt at the idea that a species with a long history of adaptation to a particular environment would be at a competitive disadvantage with newly arriving colonists. If the taxon cycle is in fact driven by "competitive pressure from new immigrants" then on a given island there should be a newly arrived species for nearly every resident that had progressed past Stage I. However, this does not agree with the fact that the great majority of West Indian birds would have to be categorized as belonging to Stages II to IV. In other words, if Ricklefs & Cox were correct, competitive replacement would have to be a very common, ongoing phenomenon; but with the possible exception of the flycatchers, *Elaenia flavogaster* and *E. martinica* (30), there are no examples of an established "counteradapted" insular species being replaced by a newcomer.

The concept of "counteradaptation" is an artificial construct needed to explain a nonexistent phenomenon—the taxon cycle. The patterns of distribution that constitute the "stages" of the taxon cycle are more reasonably interpreted in terms of the effects that the cycling of habitats had on species during the alternate wet and dry periods of the Pleistocene, in combination with the varying dispersal abilities of the individual species.

The idea of faunal "turnover" is pervasive in island biogeographic theory, and many attempts have been made to document its existence by comparing

rates of extinction and immigration on test islands over relatively short periods of time (31, 32, 103, 108). The results are often equivocal, owing to either an unreliable earlier census or a failure to account for human-induced alterations in habitats (60). In most analyses, environmental stability is an unstated premise, yet as we have seen, this assumption is not valid for the West Indies. Probably most cases of "turnover" observed under natural conditions will ultimately be linked to habitat changes, and are independent of the rate of colonization of islands by new species. This is implicit in Mayr's (66) statement that "the more stable the environment, apparently, the slower the turnover, other things being equal." We see no reason why a species adapted to a particular set of conditions on an island would not persist indefinitely, provided that its environment did not change.

Another consideration is that if different habitats support different numbers of species, the replacement of one habitat by another might either augment or diminish species diversity on an island. Bond (20), who has traveled widely throughout the West Indies, commented that "Of all habitats that I have visited in the Antilles, that in the vicinity of Pointe-à-Raquette on the southern coast of Gonâve Island was the richest both in respect to variety of indigenous land birds and in population densities. . . . The vegetation is semi-arid scrub forest." This subjective impression of the richness of arid habitat in the West Indies was confirmed by Kepler & Kepler (51), who found that the relictual xeric scrubland in southwestern Puerto Rico harbors twice as many species of birds and nearly three times as many individuals as are found in montane rainforest. There is also nearly twice the insect density in the dry forest (50). Whatever the cause may be for the higher species diversity in dry scrub forest, it seems quite clear that if such habitats in the West Indies suffered degradation and contraction after the Pleistocene and were replaced by more mesic habitats, then extinction and a corresponding decrease in species diversity would follow. This, of course, is exactly what the fossil record indicates.

CONCLUSIONS

Through the vertebrate fossil record and related lines of evidence, we have shown that environmental conditions in the West Indies during the last Pleistocene glaciation differed from those at present by the predominance of arid savanna, grassland, and xeric scrub forest. The subsequent change to more mesic habitats had a profound effect on the distribution of organisms in the archipelago. Presumably the previous glacial and interglacial periods of the Pleistocene would likewise have exerted a powerful influence

on zoogeographic patterns. We have as yet made no attempt to distinguish between the effects on distributional patterns of island area, per se, and those attributable strictly to changes in climate and habitat. In the Pleistocene, these factors probably influenced most vertebrate populations in a synergetic manner.

We have attempted to show that the historical perspective offered by fossils may be used to provide alternative solutions to problems in island biogeography that hitherto have been in the realm of theoretical ecology. Recently, Vuilleumier & Simberloff (114) questioned the basic premise that interspecific competition is of paramount importance in determining the distribution of insular organisms, on the grounds that it is largely unproven. They recognized the probable importance of historical factors in zoogeography and attempted through elaborate faunal and statistical analyses to distinguish between the ecological and historical influences on high Andean birds that show patchy, insular patterns of distribution. Their results were ambiguous, however, and they were unable to determine unequivocally what caused the patterns they observed.

As systematists and morphologists, when we set out to study fossil vertebrates in the West Indies it was not with the idea of examining what seemed to us to be purely ecological problems. Nevertheless, we found fossils to provide concrete evidence that bears directly on ecological theory in showing the importance of historical events in shaping the distributions and adaptations of organisms. A single fossil of a species from outside its present range provides evidence of a kind that simply cannot be obtained in studies that consider only information based on the present. Although we personally harbor doubts about the utility of modern ecological theories of island biogeography, we entertain no illusions that the fossil record will tell us everything we want to know. Still, it is an underestimated resource and one that provides crucial clues not available elsewhere. In our work we are more or less obliged to adopt an historical perspective. We hope to have emphasized that it would be wise for ecologists to do so as well.

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