SMITHSONIAN CONTRIBUTIONS TO PALEOBIOLOGY • NUMBER 48

Fossil Vertebrates from the Bahamas

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EDITOR

SMITHSONIAN INSTITUTION PRESS

City of Washington

1982

Family Thraupidae or Emberizidae

Spindalis zena (Linnaeus) or *Loxigilla violacea* (Linnaeus)

Material Examined.—New Providence: 1 complete, 1 proximal and 1 distal ends of humeri; 1 distal end of ulna (USNM 283339-283341, 283392); minimum number of individuals, 2.

Remarks.—The humeri of the tanager *Spindalis zena zena* and the finch *Loxigilla violacea violacea* are identical in size and we were unable to detect any qualitative features that would separate them. Both of these birds are found on New Providence today and neither would be unexpected in the Banana Hole deposits.

Family Icteridae

Sturnella sp.

Margarops fuscatus.—Wetmore, 1937b:441 [Pleistocene, "Great Exuma" = Little Exuma].

Material Examined.—Little Exuma: 2 complete humeri (MCZ 2269); minimum number of individuals, 2. New Providence: 1 premaxilla, 1 proximal end of scapula, 1 proximal end of humerus (USNM 283336, 283353, 283364); minimum number of individuals, 1.

Remarks.—A distinctive premaxilla from Banana Hole (Figure 12) definitely establishes meadowlarks as former inhabitants of the Bahamas. The straight, very flat culmen, combined with size, distinguishes this specimen from any other icterids likely to occur in the Bahamas. The two humeri from Little Exuma, identified by Wetmore (1937b) as *Margarops fuscatus*, definitely do not belong with the Mimidae, as the medial bar separating the tricipital fossae is reduced and does not extend to the shaft, as in that family. Furthermore, the fossils are too small for *Margarops fuscatus*. The characters of these specimens place them with the New World nine-primaried oscines, within which they are too large for anything other than icterids, or for any Icteridae now found in the Bahamas. They fall within the range of variation of *Sturnella magna*, the only other Antillean icterid of comparable size being *Dives atroviolaceus* of Cuba, for which we had insufficient comparative material. In view of the certain presence of *Sturnella* on New Providence, it seems likely that the Little Exuma specimens are also referable to that genus.

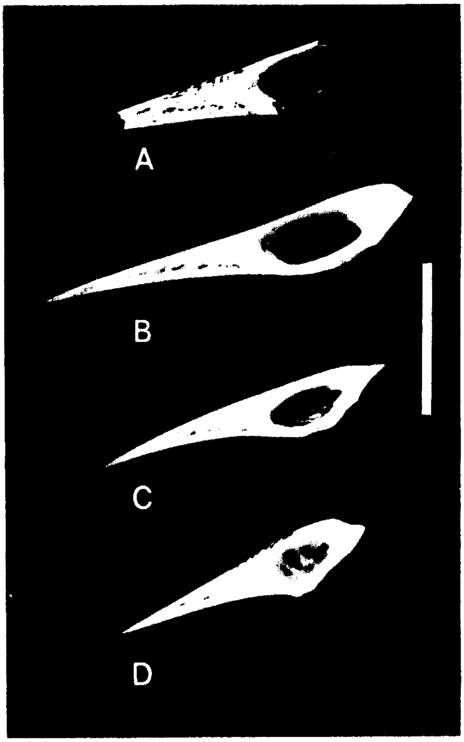

Figure 12.—Premaxillae of Icteridae in lateral view: a, fossil *Sturnella* sp. from New Providence (USNM 283364); b, *Sturnella magna*; c, *Icterus dominicensis portoricensis*; d, *Agelaius phoeniceus bryanti*. (Scale = 1 cm.)

This is one of the more interesting discoveries among the recently collected fossils from Banana Hole. The Eastern Meadowlark, *S. magna*, ranges through much of North, Middle, and South America, but occurs in the West Indies only on Cuba, where there is an endemic subspecies, *S. m. hippocrepis*. The species is quite characteristic of open, short-grass pastures and meadows and would doubtless have occupied a similar niche in the Bahamas. *Sturnella magna* is partially migratory, but does not migrate to any localities where there are not resident populations also. Regardless of whether the Bahaman birds were migrants or residents, their habitat requirements would have been the same.

Discussion

Our re-examination of the supposedly extinct fossil species of birds from the Bahamas considerably alters previous ideas about the nature of the Pleistocene avifauna. We have proposed the following synonymies or changes in nomenclature: *Calohierax quadratus* = *Buteo* sp., *Burhinus nanus* = *Burhinus bistriatus nanus*, *Glaucidium dickinsoni* = *Athene cunicularia*, *Otus providentiae* = *Athene cunicularia*, *Bathoceleus hyphalus* = *Melanerpes superciliaris*, and *Corvus wetmorei* = *Corvus nasicus*. Thus, of the nine new species described by Wetmore (1937b) and Brodkorb (1959), only three represent taxa that are certainly extinct at the species level: the giant hawk *Titanohierax gloveralleni*, the giant barn owl *Tyto pollens*, and the poorly known caracara *Polyborus creightoni*. Other possible extinctions of taxa at either the specific or subspecific levels involve an enigmatic large snipe *Capella* sp., a small subspecies of thick-knee *Burhinus bistriatus nanus*, and the Pleistocene burrowing owl of the Bahamas, which, if a valid taxon, would be known as *Athene cuncicularia providentiae*. Of equal or greater importance, however, are the numerous extant species that are represented as fossils but which either no longer occur in the Bahamas or are now absent from the islands where they were found as fossils.

The archeological remains from Crooked Island are of interest in connection with the distribution of two seabirds, *Pterodroma cahow* and *P. hasitata*, and also for the presence of *Eudocimus albus*, *Amazona leucocephala*, and *Corvus nasicus*, which no longer are found on the island.

The fossils from Little Exuma are so few in number that generalizations about them cannot be made with confidence. It is significant that all 13 species were also found in the New Providence deposits. This faunal similarity might be attributable to approximate contemporaneity of the two deposits and also to the fact that both Little Exuma and New Providence are on the Great Bahama Bank and would have been part of a single continuous land mass when sea levels were lower during the last glaciation. Of the 13 species found as fossils on Little Exuma, only one, *Athene cunicularia*, is known from the Exumas today. If, as we have suggested, the burrowing owl in the Pleistocene of the Bahamas was different from the extant form, then all of the Exuma fossils would represent taxa that are now extinct on the island. Of the twelve certainly extinct species, only four presently exist elsewhere in the Bahamas: *Geotrygon chrysia*, *Melanerpes superciliaris* (ab-

TABLE 11.—Current status of avian taxa occurring as fossils in Banana Hole, New Providence Island, Bahamas (asterisk denotes taxa also found as fossils on Little Exuma Island, where all except possibly *Athene* are now extinct; *Accipiter striatus* and *Corvus nasicus* are regarded as extinctions for the Bahamas, and perhaps *Athene cunicularia* should be as well; see p. 40)

EXTINCT	EXTANT
THROUGHOUT RANGE	NEW PROVIDENCE
**Titanohierax gloveralleni*	*Nyctanassa violacea*
Polyborus creightoni	*Falco sparverius*
**Tyto pollens*	*Porzana carolina*
	Columba leucocephala
BAHAMAS	*Zenaida aurita*
**Accipiter striatus*	**Geotrygon chrysia*
**Buteo* sp.	*Saurothera merlini*
**Capella* sp.	*Tyto alba*
Burhinus bistriatus	**Athene cunicularia*
**Columba squamosa*	*Chordeiles* sp.
Trochilidae genus and species indeterminate	*Myiarchus sagrae*
	Mimus gundlachii
**Colaptes* sp.	**Turdus plumbeus*
**Corvus nasicus*	*Dendroica* spp.
Corvus palmarum	*Coereba flaveola*
**Sturnella* sp.	*Spindalis* or *Loxigilla*
NEW PROVIDENCE	
Amazona leucocephala	
Chlorostilbon ricordii	
**Melanerpes superciliaris*	

sent from the Great Bahama Bank), *Turdus plumbeus*, and *Corvus nasicus* (restricted to Caicos). Eight species (62%) in the Exuma fossil fauna no longer occur in the Bahamas (Table 11). Even given the probable bias towards larger species induced by the collecting methods, the extinction rate for this fauna seems high.

The taxa occurring in the Banana Hole deposits are listed according to their current status on New Providence in Table 11. The results of this tabulation are rather striking. Of the 32 species in the fossil fauna, 16 (50%), and possibly 17 or 18 counting *Athene cuncicularia* and *Falco sparverius*, are extinct on New Providence and 13 (40%) no longer occur in the Bahamas (excepting *Corvus nasicus* in Caicos). Only 3 species (9%) are totally extinct and all of these are large raptors. Birds of prey account for 8 of the species in the fauna (25%) and of these, 5 (possibly 6, counting *Athene cunicularia* ssp.) are extinct in the Bahamas.

In terms of actual numbers of specimens (354), the Banana Hole sample is rather small; it is certainly not comprehensive enough to enable speculation on which species not represented were actually absent from the island at the time of deposition. Nevertheless, sampling bias cannot account for peculiarities in the ratio of extinct to extant taxa, as the species represented range in size from giant hawks and owls to hummingbirds and warblers. Although additional specimens of smaller species might raise the proportion of extant species, they could as easily augment the number of extinct taxa.

Our reassessment of the species composition of Brodkorb's much smaller original sample from Banana Hole (65 specimens) is contrasted with his original identifications in Table 12. Coincidentally, there are 15 species in each instance. Although by our analysis there is a lower percentage of extinct species than by Brodkorb's, the percentages (60% extinct on New Providence; 47% extinct in the Bahamas) are actually quite similar (50% and 40%, respectively) to those obtained when the sample was increased to 354 specimens and the number of species was more than doubled. In the smaller sample of 15 species,

TABLE 12.—Analysis of the sample of fossils from Banana Hole, New Providence, that was studied by Brodkorb (1959), and our re-evaluation of the same sample (*Corvus nasicus* is here regarded as extinct in the Bahamas)

Brodkorb (1959)	This study
Calohierax quadratus	*Buteo* sp.
Caracara creightoni	*Polyborus creightoni*
Burhinus nanus	*Burhinus bistriatus nanus*
Columba squamosa	*Columba squamosa*
Columba leucocephala	*Columba leucocephala*
Zenaida aurita	{*Zenaida aurita* {*Geotrygon chrysia*
Amazona leucocephala	*Amazona leucocephala*
Tyto pollens	*Tyto pollens*
Tyto alba	*Tyto alba*
Glaucidium dickinsoni *Otus providentiae* }	*Athene cunicularia*
Melanerpes superciliaris *Bathoceleus hyphalus* }	*Melanerpes superciliaris*
Corvus wetmorei	*Corvus nasicus* *Corvus palmarum*
Mimus gundlachii	*Mimus gundlachii*
Total species: 15	15
Extinct on New Providence: 11 (73%)	9 (60%)
Extinct in Bahamas: 9 (60%)	7 (47%)

the substitution of a single extant species for an extinct one would result in percentages of extinct taxa nearly identical to those obtained with the larger sample containing 32 species. Thus, even if we were to obtain additional specimens from Banana Hole, the proportion of extinct taxa would be unlikely to change substantially, and we must still account for the extinction of roughly half of the avifauna of New Providence since the late Pleistocene.

One possible cause, of course, would be the great reduction and fragmentation in the land mass of the Bahamas with the postglacial rise in sea level following the Wisconsinan glacial stage. Brodkorb (1959:367) cited this as "the major factor in restricting the size of the avifauna." For whatever reasons, isolation and reduction in land area is usually correlated with a decrease in species diversity on islands, whether attributable to "area effects" alone or in combination with reduction in habitat diversity or other factors. Examples of this are the reduced numbers of species on the Isle of Pines versus western Cuba (Todd, 1916) and similarly on Tasmania versus southeastern Australia (Ridpath and Moreau, 1966), both of these islands having been joined to the mainland 12,000 years ago or less. This "island effect" no doubt played a part in the extinction of some species on New Providence, but probably cannot account for the disappearance of 40% of the Banana Hole fauna from all or most of the Bahaman archipelago.

It is quite obvious from the fossil record that habitats must have changed rather drastically in the Bahamas since the Pleistocene. Some of the species represented are certain indicators of open grassland or prairie environments that no longer exist in the Bahamas. Included here are the caracara *Polyborus creightoni*, the thick-knee *Burhinus bistriatus nanus*, and the meadowlark *Sturnella* sp. In southern Florida and elsewhere, burrowing owls (*Athene cunicularia*) are found in association with caracaras and are characteristic of prairies. If the fossil burrowing owl is in fact taxonomically distinct from the one inhabiting the Bahamas now, its extinction could be attributed to the same degradation of prairie-type habitat that caused the disappearance of caracaras, thick-knees, and meadowlarks. The large snipe (*Capella* sp.) found in the fossil deposits likewise fits well with the picture of more open habitats in the Pleistocene, although it is a less certain indicator, inasmuch as the modern species *Capella gallinago* occurs in the Bahamas under present environmental conditions. On the other hand, some of the species in the fossil fauna that are absent in the Bahamas today indicate the former presence of broadleaf forest of some sort. These include *Corvus nasicus* and *Columba squamosa*. The presence of a flicker (*Colaptes*) would be in accordance either with open habitats, broadleaf forest, or both. The relictual distribution of *Melanerpes superciliaris*, and its extinction on some islands, appears to be linked to the disappearance or reduction of broadleaf woodland.

At least one of the species now absent from the Bahamas, *Corvus palmarum*, seems to thrive best in arid, scrubby areas, often in association with pines, but also with palms. It is not clear to what extent the extinction of the rodent *Geocapromys* from all of the Bahamas except East Plana Cay is due to habitat change, but the only remaining population is now well adapted to a particularly arid, scrubby habitat. The fates of the giant predators *Titanohierax gloverallem* and *Tyto pollens* were almost surely linked to the well-being of *Geocapromys*; if habitat changes were largely responsible for the disappearance of the rodent from much of its former range, then they were equally responsible for the extinction of its predators.

If the late Pleistocene environment of the Bahamas was more arid and increased precipitation was actually a major cause of extinction, then the marked rainfall gradient observed from north to south in the Bahamas today (p. 1) should have a marked effect on the fauna. We can then postulate that there would have been a greater number of extinctions on the wetter islands of the Little Bahama Bank, whereas more species would have persisted on the drier southern islands. Unfortunately, we do not as yet have any fossil faunas from the Little Bahama Bank. Nevertheless, the pattern of distribution of the Recent reptilian fauna of the Bahamas fits the above hypothesis remarkably well (p. 19), as, to a lesser extent, do the bats. The only Recent bird that clearly fits this pattern is *Corvus nasicus*, which is restricted in the Bahamas to the Caicos, whereas it is known as a fossil from islands of the Great Bahama Bank and from subfossils on the Crooked-Acklins Bank. *Mimus gundlachii* also fits this pattern, as it is most abundant in the southern islands, but is apparently absent from Abaco and has only recently been reported from Grand Bahama, where it is decidedly uncommon (Emlen, 1977:122).

The avifauna of the Little Bahama Bank is not proportionately as depauperate as the herpetofauna. Birds, being more vagile, compensate more rapidly for extinctions by subsequent colonization. Examples are *Dendrocopos villosus piger*, *Sitta pusilla insularis*, and *Dendroica dominica flavescens*, which are endemic to the pine forests of the Little Bahama Bank (the nuthatch is restricted to Grand Bahama alone). All of these are derived from the North American mainland but are markedly distinct from their parental stock, particularly the nuthatch and the warbler. This differentiation has presumably taken place since the end of the Pleistocene, when pine forest presumably invaded the Little Bahama Bank. The woodpecker has spread to Andros and New Providence, where it has differentiated further (*Dendrocopos villosus maynardi*). *Dendroica pinus achrustera*, a pine-inhabiting warbler derived from the mainland, is also found on the islands of the Little Bahama Bank, as well as on New Providence and Andros. Another pine-inhabiting warbler, *Dendroica pityophila*, occurs only on the Little Bahama Bank but is evidently derived from Cuba, the only other place where the species occurs. The two populations of *D. pityophila* have not differentiated subspecifically, which, with the vegetational history outlined above, suggests that the Bahaman population is not relictual and that the species has colonized relatively recently. This in turn implies that the species passed over the islands of the Great Bahama Bank without colonizing them, presumably because of a lack of suitable habitat, at least at the time of dispersal.

It is our contention that drastic habitat changes caused the extinction of a significant proportion of the avifauna of the Bahamas in the late Pleistocene. These species were not replaced by similar taxa simply because there was no suitable habitat for them. There is no place left in the Bahamas in which thick-knees or meadowlarks, for example, could maintain viable populations.

Late Pleistocene extinctions, as a result of the loss of arid and savanna-type habitats, are not restricted to the Bahamas. Similar extinctions of reptiles, as well as birds, have also been documented for Puerto Rico (Pregill, 1981; Pregill and Olson, 1981), and it is probable that the relictual pattern of distribution of many species of West Indian vertebrates can be explained by changes in habitat caused by a postglacial pluvial period (Pregill and Olson, 1981).

Our findings have a direct bearing on several much-discussed modern ecological and biogeographical hypotheses, such as the equilibrium theory of island biogeography, which predicts that immigration balances extinction (MacArthur and Wilson, 1967). An outgrowth of this is the concept of "taxon cycles," which holds that a given species progresses through a series of stages in which it is first widespread but undifferentiated, later develops subspecies endemic to certain islands, followed by the extinction of some populations to leave discontinuous relict populations. Ultimately, the species is reduced to a form endemic to a single island and then the taxon eventually becomes extinct (Ricklefs and Cox, 1972, 1978). This "taxon cycle" was supposed to be powered by "counteradaptation" that renders island birds more susceptible to interspecific competition from new incoming colonizers that ultimately are responsible for the doom of established species (Ricklefs and Cox, 1972:217). In contrast with this counterintuitive theory is that of Lack (1976), which states that the habitats on an island determine the number of species, that populations of birds on islands are stable, and that once a population is established, its extinction and replacement by a new colonist is unlikely.

Although we do not subscribe to all of Lack's views on island biogeography, the fossil record of birds from the Bahamas would seem to come much closer to supporting the outline of his hypothesis, as presented above, than that of Ricklefs and Cox. Although half of the species occurring as fossils on New Providence are extinct there now, there is not the slightest evidence that these were displaced, or even replaced, by new colonists. Certainly there is nothing on New Providence today that occupies the niches of thick-knees, crows, meadowlarks, flickers, the large hummingbird, or any of the five extinct raptors. *Columba squamosa* was certainly not displaced by *C. leucocephala*, as both occurred together commonly as fossils and they co-exist everywhere else in the present range of *C. squamosa*. It is perhaps conceivable that *Philodice evelynae* has displaced *Chlorostilbon ricordii* on New Providence, but this seems highly unlikely because both species occur together on Andros, Abaco, and Grand Bahama, where *Chlorostilbon* predominates and where *Philodice* is much less abundant than on islands where it is the only resident hummingbird. It might also be argued that the Hairy Woodpecker (*Dendrocopos villosus*) is displacing *Melanerpes superciliaris*. The former, however, occurs almost entirely in pine forest, whereas the latter inhabits broadleaf coppice. Furthermore, *D. villosus* is present on two of the three islands on which *M. superciliaris* has been able to survive in the Bahamas.

The hypotheses of Lack (1976) and Ricklefs and Cox (1972, 1978) are both predicated on the unstated assumption that habitats are stable, which, as we have seen, was certainly not true for the late Pleistocene of the Bahamas. Changes in climate and habitat much more readily explain the relictual and disjunct distributions of most West Indian birds than the presupposition that a species is somehow "programmed" to effect its own extinction. There is no reason to assume that a species will not persist for an indefinite period of time provided that its environment does not change, whereas no evidence has been presented that shows extinction due to competition with newly arrived colonists to be a common event. Clearly it is habitats and environments that have been cycling in the West Indies and it is highly unlikely that taxa themselves are subject to any endogenous or exogenous "cycle" that cannot be linked directly to fluctuaticns in their environment (Pregill and Olson, 1981).

As far as faunal equilibrium is concerned, because the fossil sample from New Providence is not representative of the entire avifauna at the time of deposition, it is impossible by comparison with the Recent fauna to say whether extinctions have balanced immigrations. On New Providence we have observed 50% rate of extinction since the late Pleistocene, so it would seem reasonable that immigrations have not kept pace with extinctions. Although it appears that the northern islands of the Bahamas are being newly colonized by certain species of birds, the same is not true for reptiles, the difference probably being due to differential capabilities for dispersal. Different portions of a fauna might reach "equilibrium" at vastly different rates and thus the fauna as a whole might never be at "equilibrium." Furthermore, since different habitats in mainland areas support different numbers of species, there is no *a priori* reason why a certain number of species in a given habitat on an island would be replaced by the same number of species if the habitat were to change and cause the extinction of a large component of the original fauna.

We believe that when the faunal history of more islands is known, that Pleistocene fluctuations in climates and their subsequent effect on habitats will be seen to have had a greater influence on the composition of island faunas than any of the more easily quantifiable variables upon which MacArthur and Wilson's equations were based.

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