Fossil Vertebrates from the Bahamas

Storrs L. Olson

EDITOR
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 atrovioleucus 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.

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. hippocrates. 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 synonyms or changes in nomenclature: *Calophierax quadratus = Buteo sp.*, *Burhinus namus = Burhinus bistriatus namus*, *Glaucopterus dickinsoni = Athene cunicularia*, *Otus providentiae = Athene cunicularia*, *Bathoceles hyphalus = Melanerpes supercilii*, and *Corvus wetmorei = Corvus nasius*. 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 gloverallenii*, the giant barn owl *Tyto polenus*, and the poorly known caracara *Polyborus creightonii*. 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 namus*, and the Pleistocene burrowing owl of the Bahamas, which, if a valid taxon, would be known as *Athene cunicularia 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. havaiata*, and also for the presence of *Eudocimus albus*, *Amazona leucocephala*, and *Corvus nasius*, 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 chrysa*, *Melanerpes supercilii* (ab-

<table>
<thead>
<tr>
<th>Extinct Throughout Range</th>
<th>Extant New Providence</th>
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<tbody>
<tr>
<td><em>Titanohierax gloverallenii</em></td>
<td>Nyctanassa violacea</td>
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<tr>
<td><em>Polyborus creightonii</em></td>
<td>Falco sparverius</td>
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<tr>
<td><em>Tyto polenus</em></td>
<td>Porzana carolina</td>
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<tr>
<td><strong>Bahamas</strong></td>
<td><em>Geotrygon chryza</em></td>
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<tr>
<td><em>Acpecter stratus</em></td>
<td><em>Corvus merloni</em></td>
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<tr>
<td><em>Buteo sp.</em></td>
<td><em>Tyto alba</em></td>
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<tr>
<td><em>Capella sp.</em></td>
<td><em>Athene cunicularia</em></td>
</tr>
<tr>
<td><em>Burhinus bistriatus</em></td>
<td>Chordeiles sp.*</td>
</tr>
<tr>
<td><em>Colymbus squamosa</em></td>
<td>Myiarchus sagar*</td>
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<tr>
<td><em>Trochilidae genus and</em></td>
<td><em>Mimus gundlachi</em></td>
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<tr>
<td>species indeterminate*</td>
<td><em>Turdus plumbeus</em></td>
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<tr>
<td><em>Colaptes sp.</em></td>
<td><em>Dendroica spp.</em></td>
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<tr>
<td><em>Corvus nasius</em></td>
<td><em>Corvus flavifrons</em></td>
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<tr>
<td><em>Corvus palmanum</em></td>
<td><em>Spindalis or Lovigilla</em></td>
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<tr>
<td><em>Sturnella sp.</em></td>
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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 cunicularia* 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, 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. Ex-

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**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)**

<table>
<thead>
<tr>
<th>Brodkorb (1959)</th>
<th>This study</th>
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<tr>
<td>Calohierax quadratus</td>
<td>Buteo sp.</td>
</tr>
<tr>
<td>Caracara creightoni</td>
<td>Polyborus creightoni</td>
</tr>
<tr>
<td>Burhinus nanus</td>
<td>Burhinus bistriatus nanus</td>
</tr>
<tr>
<td>Columba squamosa</td>
<td>Columba squamosa</td>
</tr>
<tr>
<td>Columba leucocephala</td>
<td>Columba leucocephala</td>
</tr>
<tr>
<td>Zenaida aurita</td>
<td>Zenaida aurita</td>
</tr>
<tr>
<td>Geotrygon chrysa</td>
<td></td>
</tr>
<tr>
<td>Amazona leucocephala</td>
<td>Amazona leucocephala</td>
</tr>
<tr>
<td>Tyto pollens</td>
<td>Tyto pollens</td>
</tr>
<tr>
<td>Tyto alba</td>
<td>Tyto alba</td>
</tr>
<tr>
<td>Glaucescium dickinsoni</td>
<td>Athene cunicularia</td>
</tr>
<tr>
<td>Otus providentiae</td>
<td></td>
</tr>
<tr>
<td>Melanerpes superciliiars</td>
<td>Melanerpes superciliiars</td>
</tr>
<tr>
<td>Bathoeoleus hyphalbus</td>
<td>Corvus nasicus</td>
</tr>
<tr>
<td>Corvus uetemori</td>
<td>Corvus palmarum</td>
</tr>
<tr>
<td>Minus gundlachi</td>
<td>Minus gundlachi</td>
</tr>
</tbody>
</table>

| Total species: 15 | 15 |
| Extinct on |
| New Providence: 11 (73%) | 9 (60%) |
| Extinct in Bahamas: 9 (60%) | 7 (47%) |
amples 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 nasica 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 Gloveralleni and Tyto pellens 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 nasica, 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 agile, compensate more rapidly for extinctions by subsequent colonization. Examples are Dendrocopos villosus piper, 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 (*Dendroclus villosus maynardi*). *Dendroica pinnus 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 sub-specifically, which, with the vegetational history outlined above, suggests that the Bahaman population is not relicual 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 (Rickles 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 (Rickles 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 Rickles and Cox. Although half of the species occurring as fossils on New Providence are extinct there now, there is no 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 Phile-
dice is much less abundant than on islands where
it is the only resident hummingbird. It might also
be argued that the Hairy Woodpecker (Dendroco-
pos villosus) is displacing Melanerpes supercilios.
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. supercilios 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 fluctuations in their environ-
ment (Pregill and Olson, 1981).

As far as faunal equilibrium is concerned, be-
cause 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 differ-
ent rates and thus the fauna as a whole might
never be at “equilibrium.” Furthermore, since
different habitats in mainland areas support dif-
ferent 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 com-
ponent of the original fauna.

We believe that when the faunal history of
more islands is known, that Pleistocene fluctua-
tions in climates and their subsequent effect on
habitats will be seen to have had a greater influ-
ence 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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