

Crossbills were unlikely resident in the Bahamas; thus there was no population to be extirpated

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Steadman and Franklin (1) make the argument that the vast reduction in land surface area and shift in vegetation in the Bahamian Archipelago from ~15 to 9 ka coinciding with sea level rise caused declines and extirpation of resident populations. They focus on two bird species, the Eastern bluebird (*Sialia sialis*) and Hispaniolan crossbill (*Loxia megaplaga*), recovered as fossils from Sawmill Sink on the Bahamian island of Abaco. Land surface area of Abaco declined from ~17,000 km<sup>2</sup> to 1,214 km<sup>2</sup> and vegetation shifted from more open woodland to a more closed forest ~15–9 ka (1). The extensive loss of apparently suitable habitat could have caused the extirpation of the Eastern bluebird (*Sialia sialis*) from Abaco and perhaps from other islands in the Bahamas. A large reduction in suitable habitat could also prevent the long-term persistence of a resident crossbill (2). However, I question whether Steadman and Franklin (1) provide adequate evidence of a resident population of Hispaniolan crossbills to be extirpated, and even whether a more extensive forest of Caribbean pine (*P. caribaea*) would have been favorable for a resident crossbill population on Abaco or across the Bahama Archipelago.

Steadman and Franklin (1) reported on fossil bones from Sawmill Sink representing eight different crossbills from >9 ka. For one individual, they recovered a mandible. For two of three qualitative traits described for this mandible (Table 1 in 1), the match is better for *L. megaplaga*

than for either White-winged crossbills (*L. l. leucoptera*) or Red crossbills (*L. curvirostra*) from North America. *L. megaplaga* is a crossbill endemic to the upper elevation pine (*Pinus occidentalis*) forests in the mountains of Hispaniola (3–4) southeast of the Bahamas. However, examination of Steadman and Franklin’s (1) measurements of the post-cranial bones for some of their other specimens does not allow one to eliminate the possibility that they represent *L. curvirostra*, perhaps even multiple populations from the *L. curvirostra* complex.

Figure 1A illustrates this by showing the lengths of humeri and tibiotarsi from their Bahamian fossils (unidentified to sex), from fossil and recent specimens of *L. megaplaga*, and from a subspecies of North American Red crossbill *L. c. grinnelli* (data from Table S4 in 1). Their data for female *L. megaplaga* are not shown as only the measurement of one tibiotarsus is provided (27.26 mm, which is nearly identical to the mean for male *L. c. grinnelli* [27.20 mm]). Steadman and Franklin (1) also provided measurements for two other crossbill taxa, *L. c. stricklandi*, the largest North American subspecies, found nearly exclusively in the Sierra Madre Occidental in western Mexico, and *L. c. sitkensis* [*minor*], the smallest subspecies, normally found in the Pacific Northwest (5). I show only *L. c. grinnelli* in Figure 1, because this subspecies approximates the size of *L. curvirostra* associated with pine and is commonly found in the southern Appalachian Mountains in the southeastern United States (ecotype or “call type” 2; 5–6), and in proximity to the Bahamas. Figure 1A also shows data from (5) for the two *L. curvirostra* ecotypes (types 1 and 2) most common in the southern Appalachian Mountains (5–6). The lengths of humeri and tibiotarsi from Steadman and Franklin’s (1) Bahamian fossils overlap those for *L. c. grinnelli* and those for the two ecotypes (Fig. 1A). Thus, the fossil measurements do not allow one to exclude the possibility that these bones were from one or more populations of *L. curvirostra* dispersing from the southeastern United States.

Also shown are the ratios of the lengths of tibiotarsus to humerus (Fig. 1B). Steadman and Franklin (1) used this ratio and its similarity to fossils of *L. megaplaga* from Haiti (Fig. 1B) to further infer that the fossil specimens from the Bahamas represent *L. megaplaga*. One problem in using ratios with their specimens and comparing them to those from recent specimens is that the fossil bones represent different individuals of unknown sexes. For example, their relatively long tibiotarsus from the Bahamas could have been from a relatively large individual, whereas the relatively short humeri may have been from relatively small individuals (see Fig. 1A for the ranges in sizes of these bones for larger samples for types 1 and 2). Figure 1B shows the range of ratios for *L. c. grinnelli* when the shortest tibiotarsus is paired with the longest humerus and vice versa from the three *L. c. grinnelli* (both sexes included) in (1). The range of ratios for their *Loxia* fossils from the Bahamas overlap completely with those for fossil *L. megaplaga*, but they also overlap substantially with those for *L. c. grinnelli* (Fig. 1B). Such pairing of bones from types 1 and 2 (Fig. 1A) lead to an even wider range of variation (range of ratios for type 1: 1.35–1.63; type 2: 1.29–1.77) and to complete overlap with the Bahamian fossils. Although the mandible from one *Loxia* fossil might have been from *L. megaplaga*, measurements of the other fossil specimens do not support their inference that the fossils represent *L. megaplaga* rather than *L. curvirostra*.

An alternative hypothesis, which cannot be eliminated by the fossil evidence (Fig. 1), is that the individuals recovered as fossils represent individuals from one or more invasions of crossbills, rather than from a resident population. The types of conifer forests that *L. curvirostra* currently tend to occupy in the eastern United States (6–7) were farther south and closer to the Bahamas during the late Pleistocene (8). Furthermore, crossbills are well known for long distance movements (9–11). *L. curvirostra* in Eurasia are known to fly over 3,000 km between

natal and breeding locations, and between breeding locations, and are considered among the most dispersive of all bird species (10). Long movements (100s of km) occur for some if not most North American *L. curvirostra* subspecies (11–13). Steadman and Franklin (1), in contrast, stated that “modern populations of any species of *Sialia* or *Loxia* are either residents or short-distance diurnal migrants–wanderers.” However, most populations of *Loxia* are anything but “short-distance migrants–wanderers.” Consequently, we cannot rule out the possibility that the eight specimens represent non-resident individuals from multiple dispersal events to the Bahamas from even multiple continental populations during the last glacial.

Critical for distinguishing among the alternatives is assessing whether conditions were even suitable for a resident crossbill population in the Bahamas. Crossbills are highly specialized for feeding on seeds in conifer cones, and as mentioned above are generally nomadic, moving annually, often long distances, in search for developing seed crops (9). Although crossbills appear to become resident quite readily (within a generation; 13), this requires a stable year-round supply of conifer seeds. Such a resource is best exemplified by serotinous conifers that hold their seeds in cones for years and sometimes decades until the cones weather or are opened by high temperatures such as by fire (14). The only cone-bearing conifer in the Bahamas is Caribbean pine *P. caribaea*, and it does not produce serotinous cones (15) nor hold its seeds in its cones for extended periods (16). Steadman and Franklin (1) imply that crossbills could have been resident in the Bahamas when stating that “resident populations of *L. curvirostra* exist today in southern Mexico and northern Central America, including in lowland savannas and woodlands featuring Caribbean pine.” However, crossbills are “very scarce” in such habitat in Belize (17), Honduras (18), and Nicaragua (19). In the highland pine forests in Honduras, the Central American subspecies *L. c. mesamericana* is “fairly common” residing in areas of *P.*

*oocarpa* pine (18), which produces serotinous cones that hold seeds for extended periods (15). Without *P. oocarpa*, a resident Central American population of crossbills would be doubtful. Furthermore, *P. caribaea* has been planted extensively in the Dominican Republic, often near the lower elevational limits of *L. megaplaga*, but this crossbill has not been observed to feed on *P. caribaea* (14; S. Latta, personal communication).

In sum, the fossil crossbills in the Bahamas are unlikely to represent a resident population, contra (1). More likely, the crossbill fossils in the Bahamas >9 ka represent individuals, perhaps of both *L. megaplaga* and *L. curvirostra*, that dispersed to the Bahamas. This is when the coast of Florida was only ~75 km from the shore of Abaco (1), and when the conifer forests most commonly utilized by *L. curvirostra* in eastern North America (6–7) were shifted farther south into the southeastern United States (8). These crossbills however were unlikely to give rise to a resident population in the Bahamas, because elsewhere *P. caribaea* does not appear to support resident crossbill populations. Although the scenario that Steadman and Franklin (1) envision likely applies to some bird populations in the Bahamas ~15–9 ka, crossbills were unlikely one of them.

## References

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**Fig. 1.** Plots showing means and ranges of measurements of crossbill (*Loxia*) tibiotarsi and humeri (A), and the ratios of these measurements (B), from fossils from Sawmill Sink on the Bahamian island of Abaco and from Haiti (Hispaniola), and from recent specimens of *L. megaplaga* and *L. curvirostra*. The mean values in B are the ratios of the means in A. The ranges in B represent the range of ratios possible from values in A. Data for *L. curvirostra* ecotypes

(call types) in A are from (5), while the rest in A and B are from (1). The numbers above each datum in A represent number of individuals.

