The Role of Climate Change in the Evolution and Extinction of Birds in the Plio-Pleistocene of North America

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ABSTRACT

The fossil record in North America indicates that considerable turnover in avian species occurred during a series of Ice Ages that began at approximately 2.5 million years ago (Ma) and demonstrates the impact of climate change on speciation and extinction in birds. Prior to the onset of these Ice Ages, recent research on early Pliocene fossil birds from Kansas has shown that speciation also can be associated with long periods of climatic stasis, indicating that mechanisms other than climate change may lead to diversification in birds. Fossils of seven living songbirds from the early Pliocene Rexroad Formation evince that diversification in longspurs (Emberizidae: *Calcarius* spp.), pipits (*Anthus* spp.), and meadowlarks (*Sturnella* spp.) had occurred by this time, perhaps in relation to the concurrent formation of rich grassland habitats with high seasonal productivity in the mid-continental region. Continuous episodes of climate change during the Ice Ages caused further speciation, as well as many extinctions, in birds. This pattern is particularly evident in Florida, where the fossil record is relatively complete. Dozens of sites are known from this region that range in age from late Pliocene to late Pleistocene and Holocene. This record is comprised of 239 fossil and living taxa and previous analysis has shown that sea-level changes associated with climate change are correlated with originations and extinctions of birds in conjunction with loss or gain of land area. During interglacial periods, sea level rise affected coastal wetland habitats and caused extinctions of wetland birds, especially in south Florida, due to loss of habitat area. During glacial periods, falling sea levels increased exposure of the shallow continental shelf in the Gulf of Mexico and facilitated range expansions of Neotropical and western continental species into Florida. These range expansions probably caused competition and predation between native and immigrant species, resulting in additional extinctions and extirpations. Thus, climate change has caused a step-wise loss in avian diversity in Florida since the beginning of the Ice Ages, despite originations that also occurred during this time. Finally, the warming period at the late Pleistocene-Holocene transition caused further losses of avian diversity in North America, as modern communities developed by 6000 B. P. All these records indicate a steady loss of avian diversity in North America over the past 2.5 Ma and counter arguments that the Ice Ages had minimal impact on species extinctions. Current threats to avian diversity from rapid climate change are due to human-induced impacts, either direct or indirect, and portend a relatively greater loss to avian biodiversity than during any of the natural events that have occurred in the past.

Keywords: Fossil birds, Climate change, Evolution, Extinction

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INTRODUCTION

Climate change has long been considered an important mechanism in the natural selection of evolution of species. Numerous examples have been presented to support this contention among a wide variety of biological organisms including plants, insects, reptiles, birds and mammals [e.g., 1–2]. Here, I discuss the evolution of birds during the Plio-Pleistocene of North America, a dynamic period of climate change when a series of four major and as many as 21 minor glacial and interglacial events began at about 2.5 Ma and ended with the onset of the Holocene at 10,000 B. P. This record is extensive, but there are large gaps in many parts of North America where fossil preservation of birds is limited to non-existent (e.g., much of the northeastern U. S.). Other areas, such as Florida, have produced a large number of avian fossils spanning the entire Plio-Pleistocene [3]. Thus, this review will be limited to three regions of North America where the fossil record of birds has provided important information on their evolution and extinction during the Plio-Pleistocene: southeastern Kansas, Florida, and the southern Rocky Mountains in west-central Colorado. In addition, I include a description of one new site that promises to provide considerable information on tundra and subalpine Rocky Mountain communities during the late Pleistocene.

DISCUSSION

Early Pliocene climatic stasis

Prior to the onset of the Ice Ages at 2.5 Ma, there was a long period of climatic stasis in North America beginning at the onset of the Pliocene at 4.8 Ma. This relatively stable period was interrupted by one global cooling event at 3.5–3.0 Ma that caused sea levels to fall from glacial development, perhaps exposing the Panamanian land bridge in Central America for the first time [4]. However, in the mid-continental U. S., the early Pliocene began after woodland and savannah communities gave way to more open, grassland and prairie regions with rich seasonal productivity. Not only did species such as horses evolve from browsing to more grazing forms [5], we now have evidence for living species of songbirds appearing for the first time during this period.

The Fox Canyon locality of the Rexroad Formation, Meade Basin, southeastern Kansas, has provided a wealth of information on early Pliocene rodent communities in this changing environment. Originally excavated by C. W. Hibbard from 1947–1951, thousands of bones of reptiles and mammals, as well as dozens of birds, were recovered. More recent research in this region [6–7] has further elucidated the fossil rodent communities. Fossil birds recovered by Hibbard from Fox Canyon, however, were not analyzed until now [8], but have produced at least seven species of songbirds of which most represent living taxa. These specimens, primarily complete and partial premaxillary bones, compare well with the living species, especially in the shape and morphology of the bill, relative size and shape of the nasal openings, size and angle of the nasal bar, position and alignment of foramina on the lateral exterior surfaces of the premaxillae, position and depth of the ventral grooves, and other features. Thus, the identifications were based on a suite of characters that matched those of the living species allowing for confident and accurate identifications of Northern Mockingbird (*Mimus polyglottus*), Sprague's Pipit (*Anthus* cf. *A. spragueii*), Dark-eyed Junco (*Junco hyemalis*), McCown's (*Calcarius mccownii*), Lapland (*C. lapponicus*), and Chestnut-collared (*C. ornatus*) Longspurs, and Western Meadowlark (*Sturnella* cf. *S. neglecta*). Moreover, one possible living species of owl (*Otus* cf. *O. asio*) and the Northern Flicker (*Colaptes* cf. *C. auratus*) also have been identified from the Fox Canyon locality [9–10]. These identifications are notable as the general belief among avian paleontologists is that most living species of birds first appeared in the late Pliocene and early Pleistocene. The Fox Canyon records, however, push back the origin of these songbirds by at least another 2 Ma.

There are two other remarkable aspects of these identifications. Besides representing the oldest living species of songbirds now known from the fossil record of North America, these fossils indicate that diversification was occurring in four Families of Passeriformes during a long period of climatic stasis. If climate change did not drive speciation in this group, what factors would be most responsible for this? One possibility is that this diversification began with migratory behavior and the development of rich seasonal productivity of North American prairie and grassland communities that appeared by the early Pliocene. Once these communities were established, the rich food supplies may have facilitated niche specialization of many species. Smaller birds, especially songbirds, would likely have benefited most from this seasonal abundance as most of the food would have been of smaller prey-vast numbers of insects and seeds from grasses and other

plants. The second notable aspect of the living species identified from Fox Canyon is that most are migratory to this region today, either breeding in Kansas during the summer food abundance and migrating south for the winter (mockingbird, meadowlark), or breeding farther to the north and wintering in or transiting through Kansas (pipit, longspurs, junco). Could these species have been migratory in the early Pliocene as well? Did development of migratory behavior facilitate speciation events? Though we may never know the answer to these questions, it is intriguing to know that speciation of living taxa was occurring over 4 million years ago.

The Ice Ages in Florida: A dynamic history

The fossil record of birds in Florida has provided the longest and best record of evolution and extinction in avian communities during the Plio-Pleistocene than anywhere else in North America. This record is dominated by wetland species, but various fossil sites have also provided considerable information on terrestrial communities. This record also demonstrates the tremendous impact that sea-level and climate change has had on these communities, both in immigration of new species into Florida (primarily during low sea-level stands with the development of an extensive Gulf Coast corridor) and extinctions with loss of habitat associated with sea-level rise. In addition, the periods of low sea level facilitated the expansion of species not only with tropical affinities from the south, but also species associated with xeric habitats from the western U. S. While most of these species appear and disappear from the Florida fossil record with climate and sea-level change, there are some notable exceptions of species that still survive in this region today. One, the Burrowing Owl (*Speotyto cunicularia*) exists throughout the Florida peninsula [11] as a disjunct population from western U. S. populations while another, the Florida Scrub-jay (*Aphelocoma coerulescens*) is an endemic species now distinguished from western species of scrub-jays [12]. Many other western taxa, especially raptors and vultures, moved into Florida during periods of low sea-level via the Gulf Coast corridor, then became extinct. Certainly one of the most interesting species to arrive in Florida along this corridor from the tropics was the giant flightless ground predator, *Titanis walleri*, which actually first arrived in Texas in the early Pliocene and then Florida by the late Pliocene before disappearing from the fossil record [13].

Three types of fossil deposits in Florida have been responsible for the rich record of birds there: riverine deposits, limestone sinkholes (Fig. 1), and marine shell beds now above sea level located along the Gulf Coast (Fig. 2). Abundant fossil remains have been recovered from all these types of deposits that span the Plio-Pleistocene [14]. The marine shell beds in particular reflect the dynamic history of Florida and the effect of sea level changes. Terrestrial vertebrate remains are often found in these deposits, sandwiched between extensive shallow-marine shell beds, directly indicating the impact of sea level changes on terrestrial environments in Florida. Late Pliocene and early Pleistocene shell deposits at MacAsphalt (APAC), Richardson Road, and Leisey Shell Pits have been particularly important in providing a detailed record of birds that once existed along Florida's Gulf Coast [15–17]. These three sites also have provided information on wetland, coastal, and terrestrial habitats, respectively.

Further information on late Pliocene to late Pleistocene terrestrial bird communities has been provided by the rich records from the sinkhole deposits at Inglis 1A, Haile, Reddick, and the Cutler Site. These faunas were deposited during periods of lower sea level than today and have produced many species with subtropical and western affinities, including California Condor (*Gymnogyps californianus*), Black Hawk (*Buteogallus urubitinga*), Yellow-headed Caracara (*Milvago chimachima*), Northern Jacana (*Jacana spinosa*), Burrowing Owl, Black-billed Magpie (*Pica pica*), and Florida Scrub-jay [3, 18].

At least 239 taxa of birds have been identified from the Plio-Pleistocene of Florida of which 60 are extinct [3]. These extinctions can be contrasted with originations of species during five specific time periods in Florida when climate and sea-level changes were greatest (Fig. 3). While originations at 2.4–2.0 Ma are biased by lack of information prior to that time, these comparisons indicate that species originations far exceed extinctions during all but one of these periods from 1.6–1.0 Ma. In the late Pliocene (2.5–2.0 Ma), the majority of originations and extinctions (21 of 22 species) are of taxa associated with wetland and coastal environments. A marine transgression at 2.2–2.0 Ma probably accounts for most of the extinctions as approximately 60% land area of the Florida peninsula was submerged at that time. This period was followed by one of lower sea level that expanded the Gulf Coast corridor from 2.0–1.6 Ma. Here, originations and extinctions are not biased towards wetland species, but include numerous terrestrial taxa as well. Of 66 taxa that appear at this time, eight (12.1% of origi-

Fig. 1 Exposed limestone sinkholes at the Haile quarries, Alachua County, Florida. Each sinkhole can contain fossils ranging in age from thousands to millions of years old.

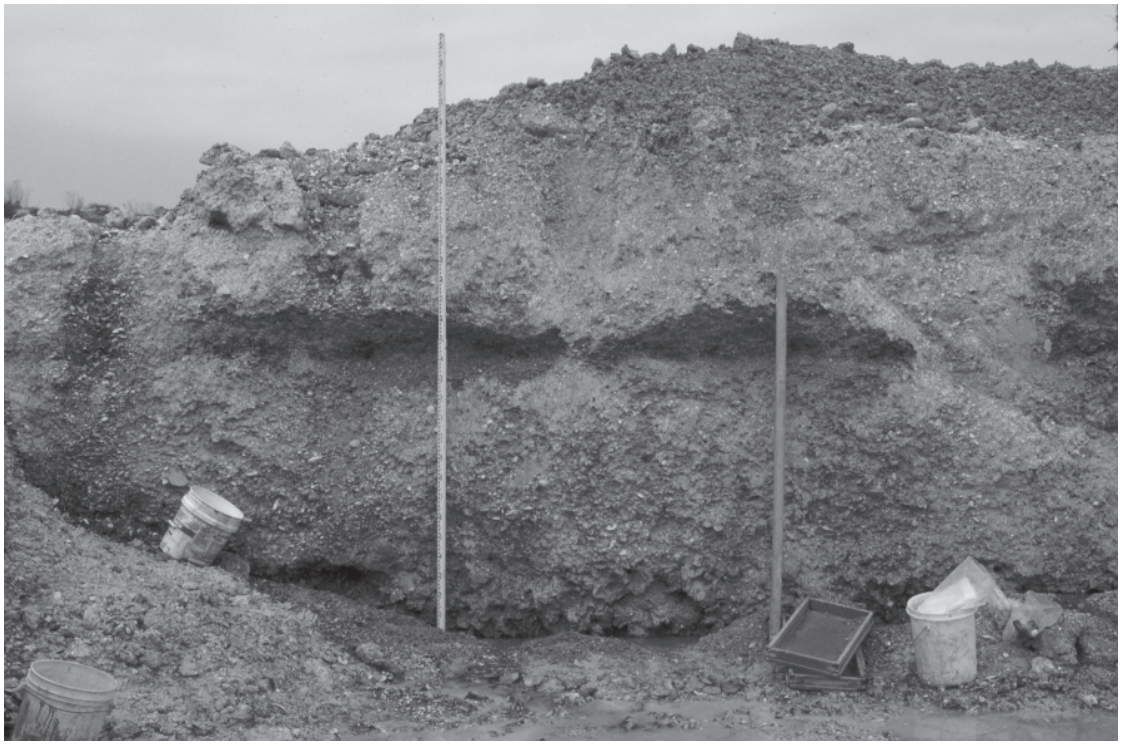

Fig. 2 Marine shell bed deposits on the central Gulf Coast of Florida provide direct evidence for the impact of sea level changes on terrestrial communities. Often, fossils of terrestrial mammals and birds are found sandwiched between layers of shallow-water marine shell faunas indicating wide fluctuations in sea level over the past 2.5 Ma.

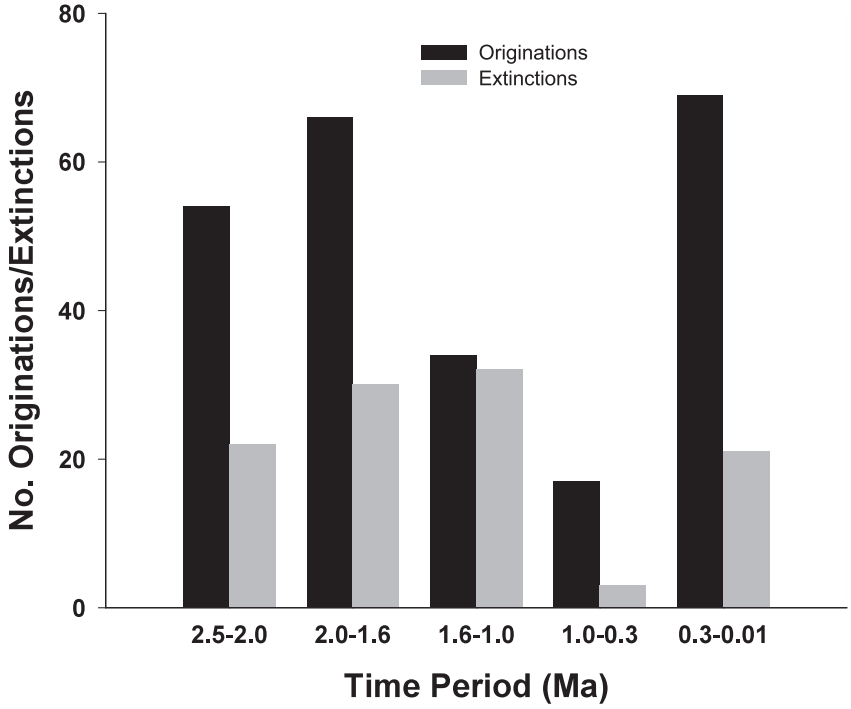

Fig. 3 Numbers of originations (first appearances) and extinctions (disappearance from fossil record in Florida) of avian taxa during five time periods spanning the Ice Ages in Florida.

nations) have tropical affinities (e.g., Least Grebe *Tachybaptus dominicus*, Ringed Kingfisher *Ceryle torquata*, Great Black-hawk *Buteogallus urubitinga*, and an extinct eagle *Amplibuteo concordatus*) while an additional 18 (27.3%) can be associated with the dry, thorn-scrub habitat that connected western North America with Florida (e.g., the extinct pygmy owl *Glaucidium explorator*, the extinct Old World vulture *Neophrontops slaughteri*, and an eagle *Aquila* sp.). Marine transgressions at the end of this period would have closed the Gulf Coast corridor again and submerged the peninsula by as much as 60%, as in the previous period. At that time, most of these species disappear from the record in Florida including wetland and terrestrial taxa.

By the early and middle Pleistocene, 1.6–1.0 Ma, wetland aquatic and coastal taxa again dominate the originations and extinctions. Sea level fluctuations were occurring, but were not as dramatic as in the previous periods. Perhaps because of this, originations and extinctions are more balanced here than in any other period (Fig. 3), though wetland taxa again suffer the most by the end of the period with 22% disappearing at that time. Interestingly, this period also sees a brief reappearance of alcids (diving seabirds) in Florida with two specimens recovered at Leisey Shell Pit. These fossils are too fragmentary for positive identification, but are similar in size and characters to the living Rhinoceros Auklet (*Cerorhinca monocerata*). It may have entered Florida waters during a cooling period in the early Pleistocene as has occurred in the Holocene with other alcid species including the Great Auk (*Pinguinus impennis*) and Common Murre (*Uria aalge*) which were identified from archaeological sites that date to periods of cooler climates than today [19]. The next period of the Pleistocene, 1.0–0.3 Ma, is the most poorly known, but avian taxa from this record indicate a re-expansion of the Gulf Coast corridor had occurred with the origination of more species with subtropical and Neotropical affinities, as well as two western species, the Rough-legged Hawk (*Buteo lagopus*) and Golden Eagle (*Aquila chrysaetos*).

The late Pleistocene (0.3–0.01 Ma) is by far the best known of all the time periods in the Plio-Pleistocene with dozens of fossil localities throughout Florida representing many different communities. At least three sea level changes are known from this period with the last, the Wisconsin which peaked at 18,000 B. P., causing sea levels to fall by as much as 80 m and possibly up to 120 m [20]. This latter event re-expanded the Gulf Coast corridor one last time and allowed entrance of many more subtropical and western taxa into the peninsula. At least

30% of originations at this time are from these regions. Most of these species, however, disappear from the record by the end of the Pleistocene.

This dynamic history of the Florida peninsula illustrates how climate and sea level change can impact avian communities and the appearance of many new species, as well as their extinction. This record also serves as a model that can be tested with future additions to the fossil record in Florida. However, because of Florida's low topography and location along the Gulf Coast corridor, originations and extinctions there have been magnified compared to other regions in North America. How then were Plio-Pleistocene events affecting avian communities in other regions of North America where a comparable fossil record can be found? In western North America, numerous cave sites have provided a rich record of birds that date primarily to the late Pleistocene allowing examination of the impact of the Pleistocene/Holocene transition that can be compared to the Florida record. Moreover, two caves in Colorado are now providing a rare glimpse on how high-elevation communities responded to climate change before and after the Last Glacial Maximum (LGM).

High-elevation communities in the Rocky Mountains, Colorado

Over a dozen cave sites in the Rocky Mountain and desert west have provided a rich fossil record of birds and mammals dating to the terminal Pleistocene. A recent review of avian communities represented in these sites [21] reveals that these faunas not only indicate mixed communities of birds and mammals characterized the late Pleistocene, but reflect an extensive habitat of steppe-tundra and subalpine forest that stretched along the Rocky Mountain region from Wyoming to southern New Mexico, as well as westward into Idaho, Utah, and Nevada. The mixed assemblages indicate that avian species now associated with boreal habitats (e.g., Boreal Owl *Aegolius funereus*, Snowy Owl *Nyctea scandiaca*, rosy finch *Leucosticte* spp.) co-occurred with species of more southern and warmer environments (e.g., California Condor *Gymnogyps californianus*, Prairie Falcon *Falco mexicanus*, sage grouse *Centrocercus* spp.). These 'disharmonius' or 'nonanalog' faunas include mammal [22–23] as well as plant communities [24]. What is missing from this record, though, is information on communities prior to the LGM and exactly when these nonanalog communities first formed. Two cave sites in west-central Colorado are helping to answer these questions.

Porcupine Cave is located at an elevation of 2900 m in Park County, Colorado, and was excavated beginning in the mid 1980s, first by the Carnegie Museum of Natural History followed by the Denver Museum of Natural History. This cave has numerous rooms and chambers filled with fossiliferous sediments with excellent preservation of bone and teeth. Biochronology of rodent remains from these deposits indicate their ages range form early to late Pleistocene or ~2.0–0.78 Ma [25–26]. Bird remains from these deposits are comprised of over 200 bones representing at least 45 taxa [27]. Interestingly, none of these taxa represent extinct species and only one, the Far Eastern or Eurasian Curlew (*Numenius madagascariensis* or *N. arquata*) exhibits an unusual range extension and is the first fossil record of a large curlew representing an Asian or European species from North America. All other taxa from the cave, however, are typical for a nonanalog tundra-steppe community with species that represent alpine (e.g., Snowy Owl, rosy finch), sagebrush (Greater Sage-grouse *Centrocercus urophasianus*), and forested (woodpeckers) habitats today. This record, however, does lack species of more southern and warmer environments that often occur in late Pleistocene assemblages (e.g., vultures). The persistence of small mammal communities throughout the record at Porcupine Cave led to the proposal [26] that climate change had little impact here as compared to other regions of North America. The avian assemblage at this site supports this conclusion as well.

One new site in Colorado, Cement Creek Cave in Gunnison County, also is located at an elevation of 2900 m and is providing a unique glimpse at changes in high-elevation bird and mammal communities before and after the LGM. Unlike Porcupine Cave, this site has a rich fossil record so far dating to two periods of the late Pleistocene: pre-LGM communities at ~40,000 to 50,000 B. P., and those dating after the LGM from 12,000 B. P. to well within the Holocene. Thus, this site can test the model presented in [26] regarding resilience in high-elevation montane communities with climate change. Cement Creek Cave was only extensively excavated in summer 2007 and analyses are ongoing. To date, the record appears to be dominated by small mammals, especially rodents with some well preserved remains of shrews. Previous analysis of fossil shrews from this and one other site in Colorado indicate steppe-tundra habitat dominated high-elevation regions there at that time [28]. Birds and mammals identified from the deposits so far continue to be associat-

ed with this habitat and include ptarmigan (*Lagapus* sp.), grouse (*Dendragapus* sp.), marmot (*Marmota* sp.), pika (*Ochotona princeps*), and Snowshoe Hare (*Lepus townsendii*). Although it is too soon to know if this community persisted from pre- to post-LGM, early indications are that it did. High-elevation communities are currently considered to be particularly sensitive to climate change. However, the fossil record at Porcupine and Cement Creek Caves seems to indicate that major climatic events in the past facilitated formation of nonanalog alpine communities, but did not cause major extinctions. When the Pleistocene ended and modern communities formed, most of these high-elevation species persisted with new distributions. Whether or not these species can continue to survive with current climate change and rapid warming remains to be seen.

CONCLUSIONS

This summary has provided information on the fossil record of birds in three regions of North America ranging in age from early Pliocene to late Pleistocene. These records indicate that modern birds began evolving as early as the early Pliocene and during a period of climatic stasis. Once the Ice Ages began at 2.5 Ma, though, originations and extinctions of birds were more evident. Climate change was especially important in the origination and extinction of birds in Florida, where sea-level changes have had a considerable impact. The record there counters uninformed arguments by those who believe that climate change over the past 2.5 Ma has not had a major impact on species extinctions [29]. In high-elevation regions, though, climate change did more to rearrange community structure than cause extinctions, with most alpine species surviving major glaciation events. While many gaps in the fossil record still exist in North America, the changes in avian communities associated with climate change, including originations, extinctions, speciation and the evolution of migratory behavior, provide a model that can be tested with additions to the fossil record.

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