

Glacial cycles and the tempo of avian speciation

Irby J. Lovette

Laboratory of Ornithology, Cornell University, 159 Sapsucker Woods Road, Ithaca, NY 14850, USA

How old are most species of North American birds? A longstanding debate centers on whether Pleistocene events caused substantial avian diversification. Two new syntheses of speciation times by Johnson and Cicero, and Weir and Schluter provide compelling evidence of recent Pleistocene speciation, whereas diversification rate analyses by Zink *et al.* suggest that most speciation events occurred earlier. Although these results are seemingly contradictory, when considered together they provide a robust and complementary perspective on the tempo of avian diversification in North America.

Introduction

The climate cycles of the past two million years repeatedly transformed the North American landscape as the continent oscillated time and again between cold glacial and warmer interglacial periods. Although the advance and retreat of the Pleistocene ice sheets, and the shifts in habitats that they induced, are well documented, did they simultaneously cause extensive speciation? A longstanding debate centers on the timing and relative pace of diversification in various groups of North American organisms. Nowhere has this been more contentious than in studies of birds. Early workers postulated that most of the species diversity that we see today originated during a rapid burst of late Pleistocene diversification, but subsequent work has shown conclusively that any such recent speciation occurred against a background of substantial pre-Pleistocene diversity. Three recent surveys [1–3] based on different methods of comparing speciation patterns will revive this debate while simultaneously pointing to its probable resolution.

Beginning during the 1940s [4], the idea that the glacial cycles of the Pleistocene caused allopatric speciation by subdividing populations into disconnected or isolated refugia dovetailed with the emphasis of the Modern Synthesis on geographical modes of speciation. Many genera of North American birds include closely related taxa that are represented by eastern and western forms. This common east–west pattern is concordant with the hypothesis that these forms represent sister taxa that first separated during a Late Pleistocene glacial advance, particularly as many such pairs now have hybrid zones in intermediate regions of probable secondary contact. As the avian fossil record is relatively depauperate, these distributional patterns had an unusually pervasive influence on thinking about the causes of avian speciation,

leading, by the early 1980s, to almost universal agreement that most of the diversification among extant North American birds occurred during the second half of the Pleistocene. Concurrently, several explicit hypotheses linking geographical patterns of bird distributions with particular glacial periods were developed and refined. The most influential of these was promoted by Robert Mengel [5], whose illustrations of successive glacial advances budding off western species from an eastern ancestor are familiar from numerous textbooks of evolutionary biology and biogeography.

Molecular challenges to Pleistocene speciation

This prevailing paradigm of Late Pleistocene speciation was turned on its head during the 1990s, when mitochondrial divergences among species were dated using molecular clock techniques. Surprisingly, the level of differentiation within many genera of North American birds was found to be much larger than that predicted by the Late Pleistocene speciation model [6–8]. In the most influential such study, John Klicka and Robert Zink [9] compared mitochondrial divergence between 35 east–west species pairs that were previously suggested to have split during the Late Pleistocene. By assuming a mean rate of mtDNA divergence of $2\% \text{ MY}^{-1}$, the authors found that the common ancestor of only one east–west pair dated to the Late Pleistocene, whereas ten pairs originated much earlier in the Pleistocene and 24 pairs in the late Pliocene or before. Based on the resulting histogram of divergence values (Figure 1a), Klicka and Zink concluded that most North American avian speciation events occurred long before the most recent glacial cycles. Although the Klicka and Zink study was challenged on several methodological grounds [10,11] and estimating speciation times from molecular divergence has several potential sources of error [12], the striking preponderance of pre-Pleistocene divergence that they reported was difficult to discount, and their new pre-Pleistocene speciation model found wide acceptance. Under this new paradigm, most diversification in the North American avifauna pre-dates the climate cycles of the Pleistocene.

Three new syntheses

One potential bias in Klicka and Zink's study was that they measured divergences between taxa that previous workers had explicitly proposed as Pleistocene species pairs, whereas subsequent phylogenetic studies have shown that many of these pairs are not each other's closest relatives. This effect of this bias is to increase the mean age of the speciation events being tallied. A new

Corresponding author: Lovette, I.J. (ijl2@cornell.edu).

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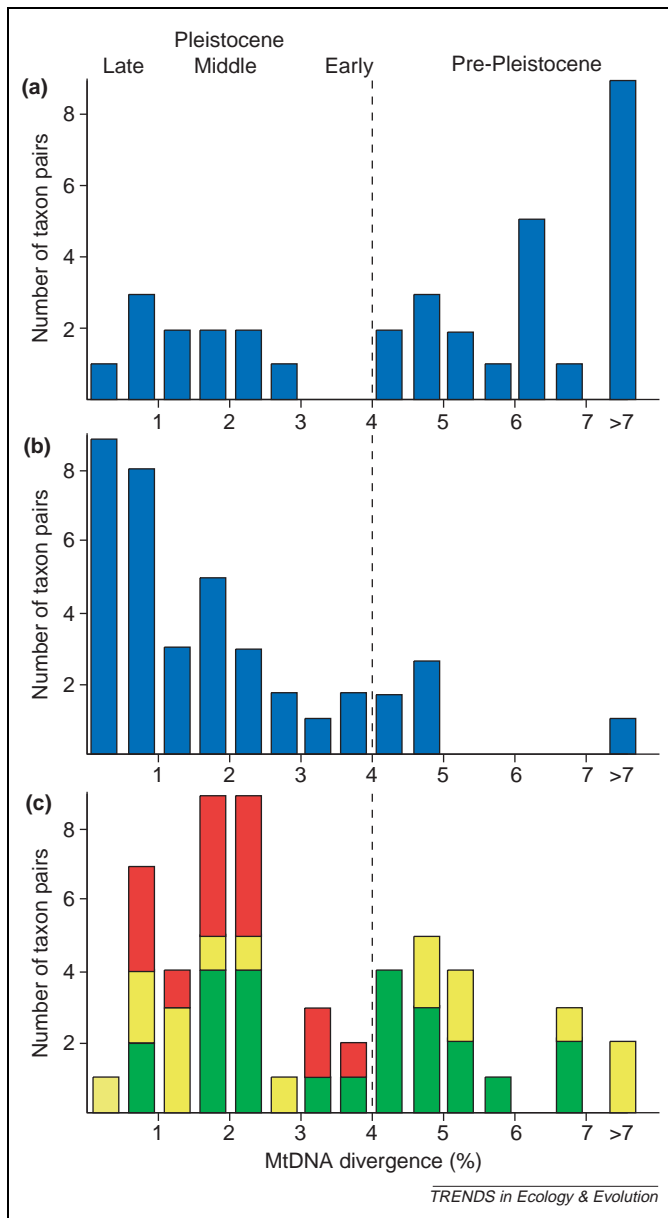


Figure 1. The timing of the most recent speciation events in North American birds based on mitochondrial DNA divergence between closely related species. (a) In 1997, an influential study by Klicka and Zink [9] rejected the prevailing late Pleistocene speciation paradigm by showing that many putative sister species diverged substantially earlier. (b) Subsequent phylogenetic studies have clarified many relationships among North American taxa. Johnson and Cicero [1] recently updated the pairwise comparison approach using only well established sister taxa, and showed that many of these most recent divergences are recent. (c) Weir and Schluter [2] partitioned speciation times along a latitudinal gradient and found that boreal species pairs (red bars) tend to have split much more recently than have species pairs at lower latitudes (sub-boreal species, yellow bars; neotropical species, green bars), a pattern that implicates the high disturbance regime of the Pleistocene glacial cycles in generating avian species diversity at northern latitudes. An important caveat to all of these surveys is that, although the revised comparisons provide new evidence for substantial avian speciation during the Pleistocene, most speciation events in the North American avifauna are not included in these comparisons, because they occurred earlier and link older and more differentiated lineages. Reproduced, with permission, from [1–3].

synthesis by the late Ned Johnson and Carla Cicero [1] follows the Klicka and Zink methodology of pairwise comparisons, but examines only pairs of species that independent and comprehensive phylogenetic surveys have now shown to be sister taxa. Johnson and Cicero's resulting histogram of pairwise divergences differs

strikingly from the pattern seen in Klicka and Zink's earlier study: in the new set of comparisons, most of the 39 sister taxa appear to have diverged during the Pleistocene and, in contrast to Klicka and Zink's study, 17 pairs date to the most recent 500 000 years (Figure 1b). This revised and expanded list of young species shows that the Pleistocene had a non-trivial role in the species-level diversification of birds.

Was diversification during the Pleistocene caused by glacial vicariance *per se*, or by the continent-wide climate shifts that accompanied each glacial advance? In a parallel study, Jason Weir and Dolph Schluter [2] similarly used pairwise genetic divergence comparisons to contrast these two potential mechanisms of avian diversification. The authors reasoned that vicariance caused by glacial advances would have had the largest impact on the most northerly breeding species, particularly those birds that breed in the expansive boreal forest that extends today from Maine to Alaska and that was repeatedly subdivided into separate refugia during glacial maxima. East–west species pairs occur in many boreal super-species complexes and previous studies of phylogeographical patterns have revealed east–west genetic structure in some of these [13–15]; however, Weir and Schluter are the first to compare the timing of speciation events across a latitudinal gradient that spans the boreal zone to the Neotropics. Their comparisons identified a strong latitudinal trend in the ages of speciation events: all of the speciation events among boreal taxa date to the Pleistocene, whereas only half of the splits between equivalent sub-boreal or neotropical species were that recent (Figure 1c). The authors conclude that Pleistocene glacial vicariance was directly responsible for an elevated speciation rate in boreal lineages compared with groups that had diversified over a longer time span.

These two new surveys provide compelling evidence that the Pleistocene had a role in augmenting the present-day diversity of the North American avifauna, but the original Pleistocene paradigm of the 1940s–1980s assigned most of the diversification within North American genera to the Pleistocene epoch. The fact that some North American bird species diversified recently is unsurprising, given that speciation is likely to be an ongoing process in any diverse group of organisms; a more refined approach seeks to identify when and where diversification has been most extensive. Broader comparisons based on phylogenies of entire avian genera accordingly reveal that Pleistocene-era nodes account for only a small proportion of the total species diversity of North American birds [6–8,16–17]. Formally testing the relative contribution of the Pleistocene requires dating all speciation events within these North American clades. Zink and his collaborators [3] have examined a new compendium of lineage-through-time plots for eight such avian groups, all of which show a preponderance of pre-Pleistocene or early Pleistocene diversification as well as a slowdown in the net rate of diversification over the course of the Pleistocene. The addition of this lineage-through-time perspective thereby brings balance to the question of the relative role of Pleistocene speciation in the diversification of North American birds: some taxa did separate as recently

as the late Pleistocene, but most of the lineages that are currently considered to be species diverged much earlier.

Whether the rate of diversification really changed during this period remains an open question: as Zink *et al.* [3] discuss, the apparent Pleistocene slowdown in speciation rate could be caused by a real decline in net diversification, or by the taxonomic artifact of considering recently separated lineages to be conspecific and thereby excluding them from analysis. Resolving this issue will require mapping the temporal distribution of all nodes in trees regardless of taxonomic designations, from the most recent splits among populations to the deepest nodes separating genera and families.

Conclusions

Considered in concert, these new syntheses show that the answer to the Pleistocene speciation debate is simply a matter of degree. We now know that some of the most closely related North American species pairs split during the Pleistocene, and that Pleistocene events similarly separated many populations that we currently consider conspecific, causing substantial intraspecific phylogeographical diversification [11,18]. The northernmost species pairs tend to have the most recent nodes, suggesting that Pleistocene climate cycles contributed directly to the present-day avian diversity of North America. At the same time, comparisons based solely on these most recent sister taxa show us only the tail of the distribution of speciation times, whereas comparisons of entire avian clades reveal that most present-day taxonomic species split from their extant relatives at a much earlier period. The recognition that many species of North American birds have had long tenures as independent lineages is especially poignant for the many such taxa that are now declining precipitously in the face of rapid anthropogenic disturbances, after having successfully weathered several million years of repeated climate change.

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Do some corals like it hot?

Erik E. Sotka¹ and Robert W. Thacker²

¹Grice Marine Laboratory, College of Charleston, 205 Fort Johnson Road, Charleston, SC 29412, USA

²Department of Biology, University of Alabama at Birmingham, 1300 University Boulevard, Birmingham, AL 35294-1170, USA

Global increases in sea temperatures threaten coral reef resilience because thermal stress can cause corals to bleach; that is, to lose their photosynthetic microalgal

symbionts. Recent evidence suggests that some corals associate with genotypes of microalgae that resist future thermal stress, however, these genotypes might provide less energy for growth when thermal stresses are curtailed. Coral reef resilience depends on whether phenotypic and genotypic changes in host-symbiont

Corresponding author: Sotka, E.E. (sotkae@cofc.edu).

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