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COMMENTS

THE TEMPO OF AVIAN DIVERSIFICATION: A COMMENT ON JOHNSON AND CICERO

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Abstract.—Johnson and Cicero (2004) claimed that inspection of a distribution of uncorrected mitochondrial DNA avian sister-taxon distances illustrated that the late Pleistocene was an important time for avian speciation. They believed this finding to be at odds with conclusions of Klicka and Zink (1997). However, both studies document recent speciation events. More germane to the discussion is what is meant by an ''important'' time for speciation, which we take to mean above some baseline diversification rate. We constructed a null distribution of sister-taxon distances based on a model of constant speciation and extinction rates. The empirical distribution of sister-taxon distances in Johnson and Cicero (2004) did not differ from the null model. Therefore, our analysis of Johnson and Cicero's data suggests that the late Pleistocene was no more important for avian speciation than any other time during this time period.

Key words.—Diversification rate, late Pleistocene, null models, sister species, speciation.

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In a recent paper, Johnson and Cicero (2004) claimed that inspection of a distribution of uncorrected mitochondrial DNA (mtDNA) divergence values for a suite of avian sister taxa revealed that the Pleistocene, including the most recent two glacial cycles, was an important time for speciation in birds. They interpreted this result to be at odds with the conclusions of Klicka and Zink (1997). Here, we emphasize the following points: (1) the occurrence of late Pleistocene divergence dates (for taxa both above and below the species level) has not been questioned in any previous study, and (2) the distribution of sister-taxon distances should be tested against a null model before drawing conclusions about the ''importance'' of particular time periods for divergence and speciation.

As Johnson and Cicero (2004) note, one area of intense interest in evolutionary biology has been the influence of glacial cycles during the Quaternary on speciation of temperate zone organisms. Mayr (1970, p. 334) wrote ''Evolutionists agree on the overwhelming importance of Pleistocene barriers in the speciation of temperate zone animals.'' In birds, many speciation events have been linked to particular glacial cycles. For example, Hubbard (1973) suggested that evolution of some North American arid-land birds proceeded in a two-step fashion, with initial isolation into refugia during the Illinoian glacial period (190,000–125,000 years ago), subsequent range expansion, and a second bout of isolation during the Wisconsinian (100,000–18,000 years ago), followed by range expansion into current distributions. Such a hypothesis leads to the prediction that species isolated during the last glacial advance (Wisconsinian) should be extremely similar genetically.

Our earlier study (Klicka and Zink 1997) reported mtDNA divergences between specific pairs of avian taxa suggested to have evolved in this manner by taxonomists such as Hubbard (1973) and Mengel (1964). We found that mtDNA distances between these pairs of species seemed anomalously large (mean = 5.1%) for extremely recent speciation events. We concluded that many species pairs traditionally hypothesized to be of very recent origin in fact originated much earlier, some as early as the late Pliocene. We did not discount the potential isolating effects of glaciers, nor claim that the Pleistocene played no role in songbird diversification. Nevertheless, Johnson and Cicero (2004, p. 1127) concluded: ''In contrast, our results support the conclusion that the Pleistocene was an important time for divergences of North American sister species, and that the entire epoch—including the last two glacial cycles (<250,000 years ago)—was involved.'' This conclusion clearly mirrors ours (Klicka and Zink 1997, pp. 1666, 1668): ''Our data reflect a protracted history of speciation throughout the Pleistocene and Pliocene'' and that evidence for Late Pleistocene diversification in songbirds would more likely be found ''among geographically segregated conspecific populations and subspecies . . . .'' The data presented by Johnson and Cicero supported this view in that 15 of the 32 songbird species pairs they examined were until recently (coinciding with the advance of modern molecular methods) considered to be conspecifics (American Ornithologists' Union 1983). More germane to the topic is what is meant by an ''important'' period for speciation.

Johnson and Cicero based their interpretation of ''important'' on the seemingly high number of recent speciation dates in their histogram of divergence values (they used divergence and speciation interchangeably, although they only plotted divergences between what they considered to be sister species). To conclude that the late Pleistocene was an important time for speciation requires (1) sampling sister taxa irrespective of whether they are classified as phylogroups, subspecies, or species; and (2) having a null hypothesis. The reasons are twofold: (1) sampling from alternative taxonomies based on different species concepts can bias the distribution of divergences, and (2) a histogram of divergences between sister taxa should contain a relatively large number of recent divergences because speciation and extinction remove the signatures of older speciation events (between sister species). Johnson and Cicero (2004, p. 1127) noted this latter pattern empirically: ''our distribution was significantly non-

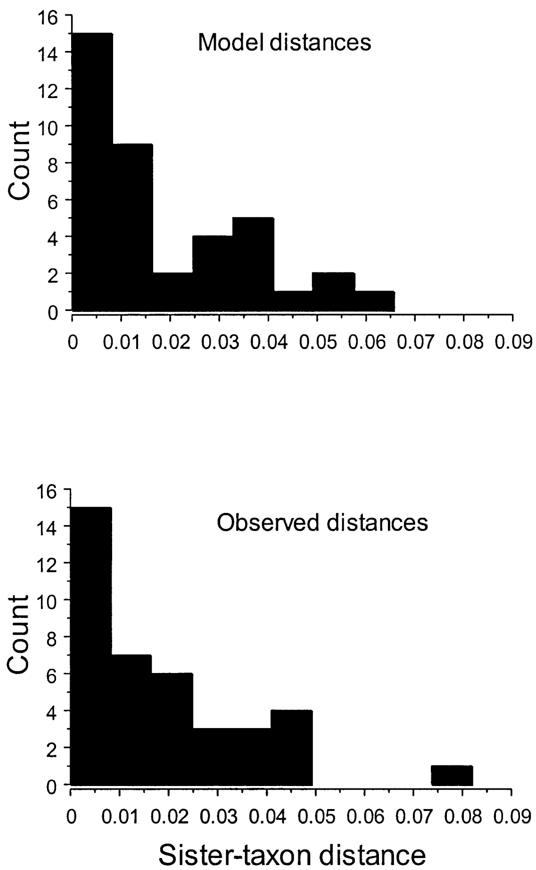

FIG. 1. Plots of sister-taxon distances. The upper distribution was one of 100 random samples of sister-taxon distances derived from phylogenetic trees constructed with equal speciation and extinction rates. The lower plot shows the distribution of avian sister-taxon distances from Johnson and Cicero (2004). The two distributions are not significantly different (Kolmogorov-Smirnov test, $P = 0.99$).

normal ($D = 0.159$, $P > 0.05$) with values strongly skewed toward younger (i.e., Pleistocene) mtDNA divergence times'' but they did not recognize its significance. The seemingly high number of recent divergences could simply be an artifact of the process of phylogenetic diversification.

Zink et al. (2004) initiated development of null models for distributions of sister-taxon differences given three scenarios: constant speciation/extinction rates, accelerated recent extinction (Zink and Slowinski 1995), and accelerated recent speciation. Perhaps the most appropriate null model here is one of constant speciation and extinction rates. If this null model cannot be falsified, one cannot infer that late Pleistocene was any more important for speciation than prior times. For example, Zink et al. (2004) were unable to falsify a model of constant speciation/extinction rates for verified sister taxa of birds at various taxonomic ranks (conspecific phylogroups, subspecies, species); although many recent divergences were observed, they were not in excess of expectation.

To evaluate Johnson and Cicero's claim that their data illustrated the importance of the Pleistocene, we compared their distribution of sister-taxon values (their table 1 and figure 1) against a distribution of sister-taxon values derived from simulations based on a phylogenetic model of constant speciation-extinction rates (details are provided in Zink et al. 2004). In brief, we simulated phylogenetic trees and tallied branch lengths connecting sister taxa ($n = 308$). Distributions from multiple simulations were statistically similar, irrespective of the values set for speciation and extinction rates (R. M. Zink, unpubl. data). We then randomly selected (with replacement) 100 sets of 39 simulated sister-taxon values to match the 39 pairs of empirical values in Johnson and Cicero's table 1. Of 100 Kolmogorov-Smirnov tests of the observed values versus the random ones, none differed (average $P = 0.77$, range 0.15–0.99). An example of one such comparison is shown in Figure 1; note the relatively high proportion of recent divergences. Therefore, the distribution of values in Johnson and Cicero's table 1 does not differ from a random distribution of values from a model of constant speciation and extinction.

If one assumes that an ''important'' time for speciation means that speciation events occurred in the late Pleistocene, all previous studies agree (Klicka and Zink 1997, 1999; Avise and Walker 1998; Lovette 2005; Weir and Schluter 2004). If ''important'' is taken to mean ''above some baseline rate,'' Johnson and Cicero's own data suggest that the late Pleistocene is no more important for speciation than any other time during the last several million years. Furthermore, nothing in Johnson and Cicero (2004) obviates Klicka and Zink's (1997) conclusion that many specific species pairs previously assumed to have evolved as a result of isolation during the last two glacial cycles are much older.

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