The Pliocene-Pleistocene transition had dual effects on North

American migratory bird speciation

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32   **Abstract**

33   Paleo-environmental change is thought to substantially influence biological
34   evolution. In particular, fragmentation of the geographical distributions of vertebrate
35   faunas and subsequent speciation events occurred frequently due to glacial advances
36   after the Pliocene-Pleistocene transition 2.5 million years ago (Ma). However, the
37   effects of glacial advances on speciation between migratory and sedentary birds have
38   not been systematically evaluated. Here, we conducted phylogenetic meta-analysis of
39   14 closely related pairs of the North American migratory species and 25 closely related
40   pairs of the North American migratory and neotropical sedentary species and estimated
41   their divergence times using cytochrome *b*. Whereas divergence events between
42   migratory species were mostly in the Pleistocene (median 1.51 Ma) as previously
43   reported, many divergence events between the migratory and sedentary bird species
44   appear to date back to the Pliocene (median 2.77 Ma). These speciation patterns
45   indicate that the Pliocene-Pleistocene transition may have accelerated speciation
46   between migratory bird species, but did not accelerate that between migratory and
47   sedentary species through counteracting mechanisms.

48

49   **Keywords**

50   glacial cycles; ice sheets; phylogeny; divergence time; mitochondrial DNA;

51   cytochrome *b*

52

1. Introduction

Paleo-environmental change substantially influences biological evolution (Webb and Bartlein, 1992). Systematic evaluation of effects of past environmental change on speciation is important for predicting the effects of future environmental changes on the biodiversity (Pearson and Dawson, 2003; Provan and Bennett, 2008). Phylogenetic methods have been used to infer the impacts of paleo-environmental changes on species distribution, genetic differentiation, and speciation (Avise et al., 1998; Cicero and Johnson, 1998). Because much DNA sequence data have been archived, studies combining phylogenetic meta-analysis and paleo-environmental analysis hold promise in exploring the interplay between paleo-environmental changes and biological evolution (Claramunt and Cracraft, 2015).

The Pliocene-Pleistocene transition 2.5 million years ago (Ma) represents one of the most fundamental climatic changes in geologic history. This transition was marked by an increase in the pace of glacial and interglacial cycles as well as an increase in the area of continental ice sheets, manifesting in more rapid and larger climatic and environmental oscillations (Lisiecki and Raymo, 2005). These changes had a major impact on the biodiversity. In particular, glacial advances southward were

70 believed to have promoted speciation events by fragmenting the geographical
71 distributions of vertebrate faunas at northern latitudes (Mengel, 1970), and this
72 hypothesis is supported by phylogenetic analyses (Bermingham et al., 1992; Weir and
73 Schluter, 2004; Lovette, 2005).

74   Many organisms, including birds, insects, fish, and mammals, migrate as an
75 adaptation to seasonal and geographical variations in resource abundance (Dingle and
76 Drake, 2007). Evolutionary transitions from residency to migration or vice versa, as
77 well as changes in patterns of migration, have occurred frequently in these organisms
78 (Alerstam et al., 2003) and promoted speciation events (Winker, 2000). Birds show
79 striking evidence of frequent evolutionary transitions: closely related species include
80 residents and short-distance and long-distance migrants (Alerstam et al., 2003),
81 although the evolution of migration systems apparently involve costs associated with
82 the migratory process in terms of time (e.g. losses of prior occupancy advantages),
83 energy, and mortality (e.g. increased exposure to parasites). These variations are
84 sometimes observed even between different populations of a single species (Alerstam
85 et al., 2003; Milá et al., 2006), where some bird species travel extraordinary distances
86 during their annual migratory journeys (>10,000 km; Alerstam et al., 2003). Therefore,

evolution of migratory birds has been of special interest for a long period (Salewski and Bruderer, 2007). The evolution of migratory systems can be promoted by ecological and biogeographic factors like seasonality, spatiotemporal distributions of resources, habitats, and predation and competition in winter and breeding seasons (Lundberg and Alerstam, 1986; Alerstam et al., 2003). Because these factors must have been influenced by past climatic changes, comprehensive examination of the evolution of migratory birds in the context of paleo-environmental records are crucial (e.g. Voelker et al., 2013).

Evolution of migratory species can occur in three ways: speciation of migratory species, loss of migratory behavior in migratory species, and gain of migratory behavior in sedentary species. In the first case, migratory species develop new migratory routes to facilitate colonization of new areas, resulting in geographic isolation of breeding sites and subsequent speciation (Mengel, 1970). Previous phylogenetic analyses suggested that glacial cycles during the Pleistocene modified migratory paths (Ruegg and Smith, 2002) and are responsible for sister-species level genetic divergences between migratory bird species (Avice et al., 1998; Johnson and Cicero, 2004; Boulet and Gibb, 2006). Weir and Schluter (2004) and Lovette (2005)

104 showed that most coalescence events between North American migratory birds were in
105 the Pleistocene, suggesting that their speciation was accelerated by range fragmentation
106 associated with the onset of northern hemisphere glacial cycles in the Pleistocene. In
107 the second and third cases, migratory species become sedentary and vice versa, either
108 *de novo* (Cox, 1985) or by the loss of migratory behavior (Bruderer and Salewski,
109 2008; Kondo et al., 2008). Regarding the ongoing debate of how and when migratory
110 species originate (Salewski and Bruderer, 2007; Zink, 2011), there are two main
111 hypotheses. The *southern home* hypothesis assumes that *de novo* bird migration arises
112 when sedentary tropical species gradually extended their ranges into northern
113 temperate areas, where a superabundance of summer resources exists, and then evolved
114 to escape from high-latitude winter environments (Cox, 1985; Salewski and Bruderer,
115 2007). Conversely, the *northern home* hypothesis assumes that migratory birds left
116 high-latitude areas to tropical areas, evolving to tropical sedentary birds (also known as
117 *migratory drop-off*) when the global climate became cold by making high-latitude
118 environments especially severe (Bruderer and Salewski, 2008; Winger et al., 2012,
119 2014). Both the sedentary-origin and migratory-origin hypotheses are supported by
120 phylogenetic studies (Outlaw et al., 2003; Voelker et al., 2013; Winger et al., 2012,

2014).

In the southern home hypothesis, advance and recession of ice sheet during the Pleistocene glacial cycles are assumed to have promoted the evolution of migratory bird species (Cox, 1985, Milá et al., 2006, Helbig, 2003). On the other hand, in the northern home hypothesis, global cooling during the Pleistocene is assumed to have promoted the evolution of tropical sedentary birds. Therefore, whether the northern or southern hypothesis is the case, divergences between the North American latitudinal migratory and neotropical sedentary (or less migratory) birds may have been promoted during the Pleistocene; however, this hypothesis has not been systematically examined. Here, we combined phylogenetic meta-analysis of speciation within North American latitudinal migratory and neotropical sedentary (or less migratory) birds with analysis of their geographical distributions and paleo-environmental data.

2. Material and methods

Species lists containing closely related North American latitudinal migratory and neotropical sedentary (or less migratory) birds were created based on literature survey across 18 papers that used mitochondrial DNA cytochrome *b* (cyt *b*) sequences

for phylogenetic analyses (Table 1). Cyt *b* was selected because an avian universal evolutionary rate is available for this gene (Weir and Schluter, 2008). Their cyt *b* gene sequences and those of the related species were retrieved from NCBI GenBank (Benson et al., 2012). Their accession numbers are available in the *Supplementary Material*. For each group of the closely related species, we created a multiple alignment of the nucleotide sequences using MAFFT 7.058 (Katoh et al., 2005) with default settings and reconstructed molecular clock phylogenies (linearized maximum likelihood trees) using MEGA 5.2 (Tamura et al., 2011) with the best-fit evolution models. Likelihood ratio tests (Huelsenbeck and Rannala, 1997) did not reject the molecular clock assumption at the 5 % significance level in all cases except for pairs of *Vireo gilvus* vs *V. leucophrys* and *Toxostoma rufum* vs *T. longirostre*/*T. guttatum* (the molecular clock assumption was not rejected in all cases at a 1 % significance level). The most recent divergence times between the closest pairs of (i) different North American migratory species and/or (ii) North American migratory and neotropical sedentary species were then estimated by applying the previously reported evolutionary rate of avian cyt *b* genes: 2.10 %/million years (Myr) or 1.05 %/Myr per lineage (Weir and Schluter, 2008).

To evaluate whether the Laurentide and Cordilleran ice sheets in North America promoted the divergence of migratory birds by range fragmentation, we also overlaid the geographical distribution of the North American migratory birds onto that of the ice sheet. We obtained the breeding ranges of the migratory birds using Birds of North America Online (Rodewald, 2015), where information of 11 pairs was available (that of *Calcarius ornatus* was obtained from the NatureServe website instead (NatureServe, 2006)). The areas of the Laurentide and Cordilleran ice sheets were reconstructed based on the compilation of geological records of the last glacial maximum (Dyke, 2004).

3. Results

First, we investigated whether the divergences between North American latitudinal migratory and neotropical sedentary birds occurred frequently in the Pleistocene. Table 1 contains the estimated divergence times of 14 closely related pairs of the North American migratory species and 25 closely related pairs of the North American migratory and neotropical sedentary species. Sequence divergences among the former pairs ranged from 0.30 to 2.71 % (median 1.58 %) and those among the

latter ranged from 0.23 to 8.06 % (median 2.91 %). Accordingly, we estimated that the divergence times of the former pairs ranged from 0.28 to 2.58 Ma (median 1.51 Ma) and those of the latter ranged from 0.22 to 7.68 Ma (median 2.77 Ma). Notably, whereas 12 out of the 14 pairs of the North American migratory species diverged during the Pleistocene (past 2.5 Myr), only 10 out of the 25 pairs of the North American migratory and neotropical sedentary species did so (Figure 1A). Binomial tests confirmed the significance of the deviation from the uniform divergence-time distribution during the past 5 Myr for the former pairs ($P = 0.035$), but not for the latter pairs ($P = 0.424$). This conclusion was not affected when we removed species pairs that diverged before the Pliocene (i.e., before 5 Ma) from the dataset. A Wilcoxon test also confirmed significant difference between the divergence times of the migratory-migratory and migratory-sedentary species pairs ($P = 0.018$).

To examine if the expansion of the Laurentide and Cordilleran ice sheets could actually cause geographic fragmentation of North American migratory birds in the Pleistocene, the breeding ranges of the migratory species pairs that diverged during the Pleistocene were overlain onto the areas of the Laurentide and Cordilleran ice sheets (Figure 2). The geographical distribution of the bird pairs overlapped with the glacial

areas in 11 out of the 12 cases, suggesting that the expansion of the Laurentide and Cordilleran ice sheets could have caused fragmentation of their original breeding range.

4. Discussion

The phylogenetic meta-analysis revealed that the speciation rate between North American migratory species accelerated in the Pleistocene. This trend shows good consistency with a previous study that reported acceleration of speciation between migratory birds in the Pleistocene (Weir and Schluter, 2004). The geographical distribution of the North American migratory birds is also consistent with the hypothesis that the expansion of the Laurentide and Cordilleran ice sheets caused fragmentation of their original breeding ranges. First, the geographical distribution of the bird pairs overlapped with the glacial area in 11 out of the 12 cases, suggesting that the glacial advances influenced their geographic distribution. Second, the geographic distribution of the bird pairs overlapped in eight of the 11 cases. In general, overlap in geographic distribution can restore gene flow that cancels prior divergence. However, if the geographic isolation induced by enlarged continental ice sheets lasted long enough (figure 1B), subsequent gene flow could be completely eliminated due to

206 differentiated reproduction systems associated with behavior or habitat preference.
207 Lundberg and Alerstam (1986) argued that longitudinal segregation of breeding
208 populations could be caused by factors such as asymmetric winter and breeding
209 competition rather than the ice sheet advance. However, the frequently overlapped
210 wintering areas of the analyzed migratory bird pairs may not support this scenario
211 because their model assumed different wintering areas.

212   Divergence between North American migratory and neotropical sedentary
213 sister species, on the other hand, did not accelerate in the Pleistocene (Figure 1). This
214 was unexpected because the Pleistocene glacial cycles are thought to have also
215 promoted generation or loss of migratory behavior and subsequent speciation. Why did
216 the speciation between the migratory and sedentary species not accelerate in the
217 Pleistocene, in contrast to that between the migratory species? If the southern home
218 hypothesis is adopted, our results suggest that the glacial cycles did not promote the
219 evolution of migratory birds from sedentary birds. The larger size of the Laurentide and
220 Cordilleran ice sheets could have acted as a counteracting mechanism that inhibited
221 such speciation by reducing areas available for novel breeding sites. However, we
222 assume that this effect was limited because the observed acceleration of speciation

223 between the migratory bird species indicates that there still remained many areas for
224 novel breeding sites. Another notable change in North America at the Pliocene-
225 Pleistocene transition was that temperature difference between the high and low
226 latitudes became much larger than that in the Pliocene (figure 1C). The larger
227 temperature difference would have formed an "ecological barrier" (Henningsson and
228 Alerstam, 2005) that required larger evolutionary jumps to adapt to new habitats for
229 breeding, and could specifically counteract the effect of the promoted speciation
230 between the migratory and sedentary birds. Alternatively, unstable environment in the
231 Pleistocene may have also prevented geographical isolations between intraspecific
232 migratory and sedentary populations. As an example of migratory behavior being
233 sensitive to environmental changes, the common whitethroat (*Sylvia* or *Curruca*
234 *communis*), a small warbler that breeds in Europe and overwinters in West Africa, can
235 show a collapse of migratory populations because of marked declines of rainfall in its
236 migratory route (Cox and Moore, 2010). If the northern home hypothesis is adopted,
237 the temperature difference and unstable environment may also have acted as a
238 counteracting mechanism that inhibited speciation. In addition, competition with
239 neotropical sedentary species in the Pleistocene may also have inhibited the

colonization of migratory birds in tropical areas, which could have served as refugia in glacial periods. It may be notable that divergences between migratory and sedentary birds are expected to have occurred frequently in cold, high-latitude environments in the Pleistocene due to migratory drop-off but such a trend was not observed in the present dataset. Finally, it should be noted that evolutionary history of migratory birds could be actually complex because of many factors such as range contraction or expansion, latitudinal range shifts, and isolation in different refugia. Phylogenetic analyses of very closely related groups might provide keys to resolving those complex factors. However, phylogenetic analysis often fails in estimating closely related phylogenetic relationships (Kondo et al., 2008). Phylogenetic analysis using whole mitochondrial genome sequences might be useful in overcoming such obstacles (Hirase et al., 2016).

Conclusion

In summary, our results indicate that the Pliocene-Pleistocene transition may have accelerated speciation between migratory bird species, but did not accelerate that between migratory and sedentary species likely through counteracting mechanisms.

257 Environmental change can have profound impacts on biodiversity. As genetic sequence
258 data are accumulating at an ever-increasing pace, we expect that combining studies of
259 phylogenetic meta-analysis and paleo-environmental analyses will become more
260 important in teasing out the effects of environmental change on biodiversity.

261

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413

Figure Captions

Figure 1

A. Forest plot of estimated divergence times between the closest pairs of the North American migratory species (upper) and those of the North American migratory and neotropical sedentary (or less migratory) species (below). B. Global stack of deep-sea foraminiferal oxygen isotope records for the last 5 Myr, obtained from deep-sea sediments (Lisiecki and Raymo, 2005). The fluctuations mainly represent global ice volume changes. C. Differences in sea surface temperatures (SSTs) between the high-latitude (site 1014: 32°50'N, 119°59'W, Dekens et al., 2007) and the average of the low-latitude (sites 846: 3°6'S 90°49'W, Lawrence et al., 2006 and 1237: 16°0.4'S, 76°22.7'W, Dekens et al., 2007) sites. The window size is a hundred thousand years. Note that the data is missing from 4.4 to 4.6 and 4.9 to 5.0 Ma.

Figure 2

Breeding ranges of the closely related species pairs of the North American migratory birds that diverged during the Pleistocene. Gray color shows the areas covered by the Laurentide and Cordilleran ice sheets during the last glacial period (Dyke, 2004).

Figure 2

Table 1

Table 1 Species pairs analyzed in this study and their estimated divergence times

Family name	Species pair	Nucleotide substitution model	Sequence divergence per lineage (%)	Estimated time (Ma)	Reference
<i>North American migratory species pairs</i>					
Anatidae	<i>Bucephala islandica</i> vs <i>B. clangula</i> (Barrow's goldeneye vs Common goldeneye)	TN	1.65	1.57	Oates and Principato (1994)
Apodidae	<i>Chaetura pelagica</i> vs <i>C. vauxi</i> (Chimney swift vs Vaux's swift)	HKY+G	2.71	2.58	Price et al. (2004)
Calcariidae	<i>Calcarius pictus</i> vs <i>C.ornatus</i> (Smith's longspur vs Chestnut-collared longspur)	HKY+G	1.65	1.57	Klicka et al. (2003)
Turdidae	<i>Catharus fuscescens</i> vs <i>C. minimus</i> (Veery vs Grey-cheeked thrush)	HKY+G	0.52	0.49	Outlaw et al. (2003)
Emberizidae	<i>Melospiza lincolni</i> vs <i>M. georgiana</i> (Lincoln's sparrow vs Swamp sparrow)	HKY	1.51	1.44	Carson and Spicer (2003)
Emberizidae	<i>Pipilo maculatus</i> vs <i>P. erythrophthalmus</i> (Spotted towhee vs Eastern towhee)	HKY+I	0.30	0.28	DaCosta et al. (2009)
Emberizidae	<i>Zonotrichia albicollis</i> vs <i>Z. leucophrys</i> (White-throated sparrow vs White-crowned sparrow)	TN+G	2.23	2.12	Carson and Spicer (2003)
Icteridae	<i>Euphagus carolinus</i> vs <i>E. cyanocephalus</i> (Rusty blackbird vs Brewer's blackbird)	HKY+G	2.70	2.57	Powell et al. (2008)
Icteridae	<i>Sturnella neglecta</i> vs <i>S. magna</i> (Western meadowlark vs Eastern meadowlark)	TN+G	2.45	2.33	Lanyon and Omland (1999)
Parulidae	<i>Geothlypis tolmiei</i> vs <i>G. philadelphia</i> (MacGillivray's warbler vs Mourning warbler)	HKY	1.14	1.09	Lovette et al. (2010)
Parulidae	<i>Oreothlypis virginiae</i> vs <i>O. luciae</i> (Virginia's warbler vs Lucy's warbler)	HKY+G	0.75	0.71	Lovette et al. (2010)
Parulidae	<i>Setophaga occidentalis</i> vs <i>S. townsendi</i> (Hermit warbler vs Townsend's warbler)	HKY+G	0.46	0.44	Lovette et al. (2010)
Parulidae	<i>Setophaga petechia</i> vs <i>S. pensylvanica</i> (American yellow warbler vs Chestnut-sided warbler)	HKY+G	2.47	2.35	Lovette et al. (2010)
Vireonidae	<i>Vireo cassinii</i> vs <i>V. solitarius</i> (Cassin's vireo vs Blue-headed vireo)	HKY	1.35	1.29	Cicero and Johnson (1998)
Median value (<i>n</i> = 14)			1.58	1.51	
<i>North American migratory vs neotropical sedentary (less migratory) species</i>					
Apodidae	<i>Chaetura pelagica</i> / <i>C. vauxi</i> vs <i>C. chapmani</i> (Chimney swift/Vaux's swift vs Chapman's swift)	HKY+G	3.75	3.57	Price et al. (2004)
Caprimulgidae	<i>Caprimulgus carolinensis</i> vs <i>C. rufus</i> (Chuck-will's-widow vs Rufous nightjar)	TN+G	3.69	3.51	Han (2006)
Caprimulgidae	<i>Caprimulgus vociferus</i> vs <i>C. arizonae</i> / <i>C. saturatus</i> (Eastern whip-poor-will vs Mexican whip-poor-will/Dusky nightjar)	TN+G	4.13	3.94	Lovette et al. (2012)
Cardinalidae	<i>Piranga ludoviciana</i> vs <i>P. bidentata</i> (Western tanager vs Flame-colored tanager)	HKY+G	3.01	2.87	Burns (1998)
Columbidae	<i>Zenaida asiatica</i> vs <i>Z. meloda</i> (White-winged dove vs West Peruvian dove)	HKY+G	2.87	2.73	Johnson and Clayton (2000)
Columbidae	<i>Zenaida macroura</i> vs <i>Z. graysoni</i> (Mourning dove vs Socorro dove)	HKY	0.48	0.46	Johnson and Clayton (2000)
Emberizidae	<i>Pipilo maculatus</i> / <i>P. erythrophthalmus</i> / <i>P. chlorurus</i> vs <i>P. ocai</i> (Spotted towhee/Eastern towhee/Green-tailed towhee vs Collared towhee)	HKY+I	2.82	2.68	DaCosta et al. (2009)
Emberizidae	<i>Zonotrichia albicollis</i> / <i>Z. leucophrys</i> vs <i>Z. capensis</i> (White-throated sparrow/White-crowned sparrow vs Rufous-collared sparrow)	TN+G	4.40	4.19	DeCosta et al. (2009), Carson and Spicer (2003)
Hirundinidae	<i>Petrochelidon fulva</i> vs <i>P. rufocollaris</i> (Cave swallow vs Chestnut-collared swallow)	HKY	0.90	0.85	Sheldon et al. (2005)
Hirundinidae	<i>Stelgidopteryx serripennis</i> vs <i>S. ruficollis</i> (Northern rough-winged swallow vs Southern rough-winged swallow)	HKY+G	3.46	3.30	Sheldon et al. (2005)
Icteridae	<i>Icterus bullockii</i> vs <i>I. pustulatus</i> (Bullock's oriole vs Streak-backed oriole)	HKY	1.47	1.40	Jacobsen et al. (2010)
Icteridae	<i>Icterus galbula</i> vs <i>I. abeillei</i> (Baltimore oriole vs Black-backed oriole)	HKY	0.23	0.22	Jacobsen et al. (2010)
Icteridae	<i>Molothrus ater</i> vs <i>M. bonariensis</i> (Brown-headed cowbird vs Shiny cowbird)	HKY	0.66	0.63	Lanyon and Omland (1999)
Icteridae	<i>Quiscalus quiscula</i> vs other Quiscalus species (Common grackle vs other Quiscalus species)	HKY+G	2.43	2.31	Powell et al. (2008)
Icteridae	<i>Sturnella neglecta</i> / <i>magna</i> vs <i>S. bellicosa</i> / <i>S. militaris</i> / <i>S. loyca</i> (Western meadowlark/Eastern meadowlark vs Peruvian meadowlark/Red-breasted blackbird/Long-tailed meadowlark)	TN+G	8.06	7.68	Lanyon and Omland (1999)
Mimidae	<i>Toxostoma rufum</i> vs <i>T. longirostre</i> / <i>T. guttatum</i> (Brown thrasher vs Long-billed thrasher/Cozumel thrasher)	HKY+G	3.59	3.42	Lovette et al. (2012)
Parulidae	<i>Cardellina rubrifrons</i> vs <i>C. ruber</i> / <i>C. versicolor</i> (Red-faced warbler vs Red warbler/Pink-headed warbler)	HKY+G	2.44	2.33	Lovette et al. (2010)
Parulidae	<i>Oreothlypis virginiae</i> / <i>O. luciae</i> / <i>O. ruficapilla</i> vs <i>O. crissalis</i> (Virginia's warbler/Lucy's warbler/Nashville warbler vs Colima warbler)	HKY+G	1.32	1.26	Lovette et al. (2010)
Parulidae	<i>Setophaga discolor</i> vs <i>S. vitellina</i> (Prairie warbler vs Vitelline warbler)	HKY	1.26	1.20	Lovette et al. (2010)
Parulidae	<i>Setophaga occidentalis</i> / <i>S. townsendi</i> vs <i>S. adelaide</i> (Hermit warbler/Townsend's warbler vs Adelaide's warbler)	HKY+G	3.10	2.95	Lovette et al. (2010)
Parulidae	<i>Setophaga pinus</i> vs <i>S. pityophila</i> (Pine warbler vs Olive-capped warbler)	HKY+G	2.91	2.77	Lovette et al. (2010)
Turdidae	<i>Catharus fuscens</i> / <i>C. bicknelli</i> / <i>C. minimus</i> vs <i>C. frantzii</i> (Veery/Bicknell's thrush/Grey-cheeked thrush vs Ruddy-capped nightingale-thrush)	HKY+G	3.86	3.67	Outlaw et al. (2003)
Turdidae	<i>Catharus guttatus</i> vs <i>C. occidentalis</i> (Hermit thrush vs Russet nightingale-thrush)	HKY+G	3.53	3.36	Outlaw et al. (2003)
Tyrannidae	<i>Empidonax oberholseri</i> vs <i>E. affinis</i> (American dusky flycatcher vs Pine flycatcher)	HKY+G	0.30	0.28	Johnson and Cicero (2002)
Vireonidae	<i>Vireo gilvus</i> vs <i>V. leucophrys</i> (Warbling vireo vs Brown-capped vireo)	GTR	3.01	2.87	Johnson et al. (1988)
Median value (<i>n</i> = 25)			2.89	2.75	