

## S19-1 Origins and timing of avian migrant evolution in the New World

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**Abstract** A variety of data, including taxonomic and ecological information, confirm that the majority of long-distance land bird migrants in the New World originated from populations of tropical species. Phylogenetic distances from tropical relatives indicate that, for some species, migration had its roots in the distant past while in others it evolved very quickly and recently, judged by movement data for species introduced into the New World within the past 200 years. Long distance migrants constitute a fairly small portion of the avifauna of the Western Hemisphere. However, populations of species that undergo regular seasonal movements between intra-continental sites, areas, or regions make up a much larger percentage. In fact, data are only now being gathered that will allow determination of the extent to which the majority of tropical birds are migratory. Preliminary data indicate that two factors facilitate the evolution of migration: 1) two separate environments where fitness differs seasonally for the members of a species, and 2) the ability to move between the two environments. When these conditions are met, migration is likely to evolve because birds possess a number of appropriate adaptations, such as homing ability and energy storage capacity which allow them to capitalize on the conditions. Evolution of these adaptations is probably as old as the Class Aves itself, because these adaptations are favored in any dispersing animal. Thus, migration is probably as old as movement and seasonality, and long-distance migration is probably as old as seasonal variation in habitat quality and flight.

**Key words** Birds, Origin, Avian migration, Evolution, New World

### 1 Introduction

Nearctic avian land bird migrants are Western Hemisphere species that breed in the north temperate and boreal regions of the Western Hemisphere, and winter, all or in part, in the neotropics (Rappole et al., 1995). The purpose of this paper is to present an analysis of information relevant to three critical questions regarding these species: (1) in which geographical region did the majority of these species originate? (2) when did this process occur? and (3) what circumstances favored evolution of migratory behavior?

### 2 Geographical origin of Nearctic migrants

A range of data, including taxonomic and ecological information, confirm that the majority of Nearctic avian land bird migrants originated from populations of tropical species (Mayr, 1946). Thus, 48% of Nearctic migrants have conspecific populations that are resident breeders in the tropics, e.g. the red-eyed vireo (*Vireo olivaceus*), yellow warbler (*Dendroica petechia*), and peregrine falcon (*Falco peregrinus*), while 78% have congeners that are resident breeders in the tropics (Rappole, 1995). Several Nearctic migrants are members of families composed almost entirely of resident tropical species, such as the tanagers, Thraupidae, with four Nearctic migrants and 250 tropical residents.

Ecological information provides additional evidence for the neotropical origins of many Nearctic migrants. Migrants winter in all major neotropical habitats, where they integrate

as members of the avian communities there; and many have demonstrated fidelity to specific winter sites in a wide variety of habitats from one year to the next (Rappole et al., 1995). As an example of such fidelity, a Kentucky warbler (*Oporornis formosus*) was captured in rain forest understory by mist net on 28 December 1973, banded and released 1.5 km south of Tuxtla Biological Station in southern Veracruz, Mexico. This bird was recaptured within 50 m of its original capture point on 5 December 1980, still carrying its leg bands, presumably having completed seven round-trips from its Mexican, tropical wintering site and a breeding site somewhere in the eastern United States (Rappole, unpubl. data).

Members of many species, such as the northern waterthrush (*Seiurus noveboracensis*) establish and defend individual territories throughout the wintering period (Schwartz, 1964; Rappole and Warner, 1980), a phenomenon that has been documented for at least 75 species of Nearctic avian migrants (Rappole, 1995). Other Nearctic migrants, such as the chestnut-sided warbler (*Dendroica pensylvanica*) and golden-cheeked warbler (*Dendroica chrysoparia*), join mixed-species flocks during the wintering period in neotropical habitats, remaining with them throughout the winter period (Greenberg, 1984; Hutto, 1987; King and Rappole, 2000).

### 3 Timing of the origin of Nearctic migration

Most long-distance Nearctic land bird migrants are derived from tropical ancestors. Some clearly split from their

tropical relatives in the distant past. The migratory wood thrush, *Hylocichla mustelina*, for example, is the sole member of its genus, although clearly related to members of the turdid genus *Catharus*, which has seven tropical members and five Nearctic migrants (Winker and Rappole, 1988). Thus it seems likely that migration in this species evolved hundreds of thousands of years ago. Similarly, the closest apparent relative of the American redstart (*Setophaga ruticilla*) is the whistling warbler, *Catharopeza bishopi* (Lovette and Bermingham, 2002), a tropical resident of the West Indian island of St. Vincent, and not other Nearctic migrants of the family Parulidae. This suggests distant — and so, ancient — derivation from a tropical relative.

Such taxonomic information indicates that migration evolved long ago for many Nearctic migrants, particularly in the parulid warblers. The recent distributional history of other species, such as the cattle egret (*Bubulcus ibis*), shows nevertheless that migration can evolve rapidly. This species first arrived in South America in the late 1800s. The first individuals were recorded in the United States in the early 1950s, yet long-distance migrant populations now breed as far north in the Nearctic region as southern Canada (Telfair, 1994).

Long distance migrants, that is, species moving more than 1 000 km between breeding and wintering areas, constitute only a small portion of the avifauna of the Western Hemisphere (Rappole, 1995). However, short-distance migrants with populations that undergo regular, seasonal movements between intra-continental sites, areas or regions make up a much larger percentage. In hummingbirds, for example, as many as 40% of the 328 species undertake some seasonal movement — whether altitudinal, latitudinal, or long-distance (Rappole and Schuchmann, 2003). Only 13 of these species are Nearctic migrants, while an additional 15 are long-distance austral migrants to the temperate zone of southern South America.

The remaining 102 seasonal shifters undertake migratory movements within the tropics themselves. Such intra-tropical migration is difficult to document, requiring long-term data that shows consistent seasonal disappearance of populations from one area and coincident appearance at another. Assessment is further complicated by the fact that some of the population may not even move at all (Vega and Rappole, 1994; Rappole et al., 1997; Winker et al., 1997). Nevertheless, intra-tropical migration is probably a very common phenomenon, which future research may demonstrate is a rapidly-evolving response to seasonal change in critical resource distribution (Levey and Stiles, 1992; Rappole and Tipton, 1992).

## 4 Factors favoring evolution of migratory behavior

Two factors appear to favor evolution of migratory behavior. In the first, two separate environments are needed where fitness differs seasonally for members of a species; the second requires species to have the ability to move

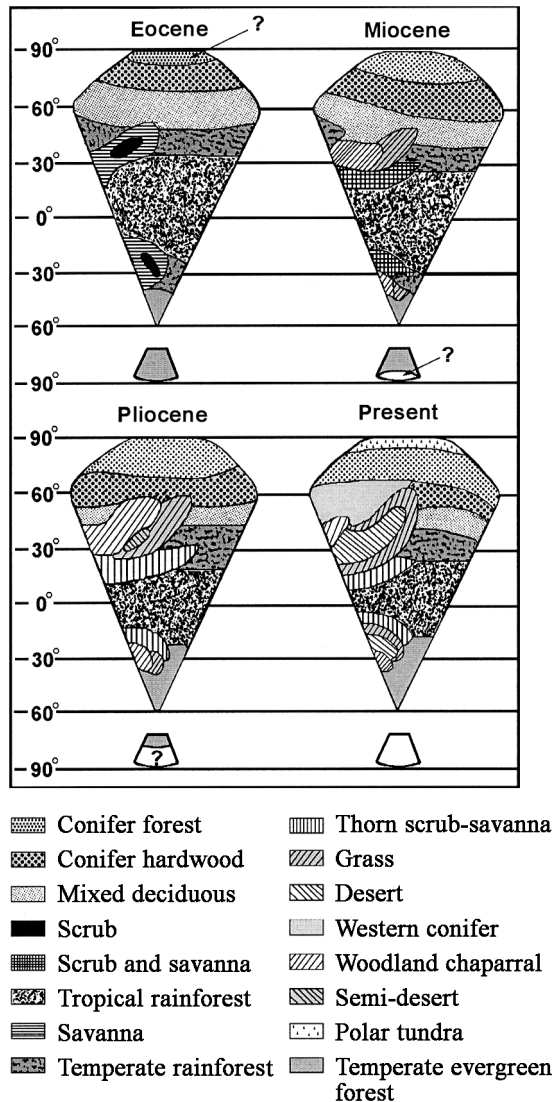
efficiently between the two environments (Rappole, 1995). When these conditions are met, migration is likely to evolve because birds possess adaptations that allow them to capitalize on these factors: hyperphagia, which enables birds to take in food in excess of their immediate needs, storage of readily released energy reserves in the form of deposited fat, flight, and homing ability. Evolution of these adaptations are probably as old as the Class Aves, because they are adaptations that are advantageous to any dispersing animal.

So migration is probably as old as bird movement and phenological shifts; and long-distance migration is probably as old as seasonal variation in habitat quality and flight. Seasonality depends on the tilt of the earth's axis, and thus seasonal habitats are probably as old as terrestrial vegetation. Fernandez (2002) reports at least five major Ice Ages based on percent of the earth's surface covered by ice: the Late Cenozoic (1 mybp), Gondwanan (280 mybp), Ordovician (450 mybp), Varangian (680 mybp) and Sturtian (750 mybp), with smaller fluctuations throughout the Tertiary (1.6–66.4 mybp). Seasonal habitats, such as deciduous phanerogam forest, go back at least to the Eocene epoch of the early Tertiary nearly 60 million years ago, prior to the appearance of many modern avian families in the fossil record (Fig. 1; Udvardy, 1969).

That Holarctic climates were much warmer, on average, during the Tertiary is well known, with subtropical conditions prevailing as far north as 50 degrees latitude. Groups considered tropical in terms of habitat requirements, e.g., potoos (Nyctibiidae, Caprimulgiformes) and trogons (Trogoniformes), occur in the fossil record of Holarctic habitats from the Eocene and Oligocene epochs of northern Europe (Mayr, 1999, 2001; Kristoffersen, 2002), along with apparently ancestral forms of other tropical-centered groups, e.g., the colies (Coliiformes) and parrots (Psittaciformes) (Mayr and Daniels, 1998; Dyke and Waterhouse, 2001). In fact, it seems possible that, even though some modern avian families had not yet arisen, significant numbers of migrants were present, especially among frugivores for reasons elucidated by Levey and Stiles (1992). Some habitats at northern latitudes were seasonal, and were not separated from the tropics by vast stretches of disconnecting desert or sea as they are now, circumstances presumably facilitating evolution of migratory habits.

## 5 Conclusions

Most Nearctic land bird migrants appear to have originated from tropical resident populations, with origins dating back as much as several million years. Nevertheless, recent evolution of a migratory or nomadic habit in some species demonstrates that migratory propensity is extremely responsive to selection. The principal conditions favoring the evolution of migration appear to be seasonal environments and a facility for movement which allows individuals to increase fitness relative to sedentary individuals. Climatic, seasonal, and consequent habitat change are ancient phenomena, dating back to the beginning of life; and dur-



**Fig. 1** Principal habitats of the Eocene (37–58 MYA), Miocene (5–24 MYA), Pliocene (2–5 MYA) and Holocene (present). Temperate, seasonal environments were extensive in these epochs. Based on material in Udvardy (1969) and Axelrod (1952).

ing the period of evolution of modern birds, there is evidence that paleohabitats in the Tertiary included such seasonal environments as temperate deciduous and coniferous forest. These Tertiary environments in the Nearctic were probably inhabited seasonally by migrant birds, perhaps even including such species as trogons and potoos which are resident in the tropics today.

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## References

Axelrod D, 1952. Variables affecting the probabilities of dispersal in geologic time. *Bull. Amer. Mus. Nat. Hist.* 99: 177–188.

- Dyke G, Waterhouse DM, 2001. A mousebird (Aves: Coliiformes) from the Eocene of England. *J. Ornithol.* 142 (1): 7–15.
- Fernandez L, 2002. The paleoclimate record and climate models. University of Michigan Global Change Project: [http://www.sprl.umich.edu/GCL/Notes-1998-Fall/climate\\_rec.html](http://www.sprl.umich.edu/GCL/Notes-1998-Fall/climate_rec.html).
- Greenberg R, 1984. *The Winter Exploitation System of Bay-Breasted and Chestnut-Sided Warblers in Panama*. Berkeley, CA: University California Publ. Zool., Vol. 116.
- Hutto RL, 1987. A description of mixed-species insectivorous bird flocks in western Mexico. *Condor* 89: 282–292.
- King DI, Rappole JH, 2000. Mixed-species foraging flocks in montane pine forests of Middle America. *Condor* 102: 664–672.
- Kristoffersen AV, 2002. An early Paleogene trogon (Trogoniformes) from the Fur Formation, Denmark. *J. Vertebrate Paleontol.* 22: 661–666.
- Levey DJ, Stiles FG, 1992. Evolutionary precursors of long-distance migration: resource availability and movement patterns in Neotropical landbirds. *Amer. Nat.* 140: 467–491.
- Lovette IJ, Bermingham E, 2002. What is a wood warbler? Molecular characterization of a monophyletic Parulidae. *Auk* 119: 695–714.
- Mayr E, 1946. History of the North American bird fauna. *Wilson Bull.* 58: 2–41.
- Mayr G, 1999. A new trogon from the Middle Oligocene of Céreste, France. *Auk* 116: 427–434.
- Mayr G, 2001. Comments on the osteology of *Masillapodargus longipes* Mayr, 1999 and *Paraprefica major*, Mayr 1999, caprimulgiform birds from the Middle Eocene of Messel (Hessen, Germany). *Neues Jahrb. Geol. Paläontol. Monatsb.* 2001: 65–76.
- Mayr G, Daniels M, 1998. Eocene parrots from Messel (Hessen, Germany) and the London Clay of Walton-on-the-Naze (Essex, England). *Senckenbergiana Lethaea* 78: 157–177.
- Rappole JH, 1995. *Ecology of Migrant Birds: a Neotropical Perspective*. Washington, D.C.: Smithsonian Institution Press.
- Rappole JH, Morton ES, Lovejoy TE, Ruos JS, 1995. *Nearctic Avian Migrants in the Neotropics*, 2nd edn. Front Royal, VA: Conservation and Research Center, Smithsonian Institution.
- Rappole JH, Ramos MA, Warner DW, Oehlenschläger RJ, Winker K, Zink RM, 1997. Aves migratorias neárticas. In: Gonzalez Soriano E, Dirzo R, Vogt R ed. *Historia Natural de los Tuxtlas*. Mexico City, Mexico: Univ. Nac. Autónoma de Mexico, 545–556.
- Rappole JH, Schuchmann K-L, 2003. The ecology and evolution of hummingbird population movements: a review. In: Berthold P, Gwinner E, Sonnenschein E ed. *Avian Migration*. Berlin: Springer, 39–51.
- Rappole JH, Tipton AR, 1992. The evolution of avian migration in the Neotropics. *Ornitología Neotropical* 3: 45–56.
- Rappole JH, Warner DW, 1980. Ecological aspects of avian migrant behavior in Veracruz, Mexico. In: Keast A, Morton ES ed. *Migrant Birds in the Neotropics: Ecology, Behavior, Conservation, and Distribution*. Washington, D.C.: Smithsonian Institution Press, 353–394.
- Schwartz P, 1964. The northern waterthrush in Venezuela. *Living Bird* 3: 169–184.
- Telfair RC, 1994. Cattle egret (*Bubulcus ibis*). In: Poole A, Gill F ed. *The Birds of North America*, No. 113. Philadelphia, PA: The Academy of Natural Sciences.
- Udvardy MDF, 1969. *Dynamic Zoogeography*. New York: Van Nostrand Reinhold.
- Vega JH, Rappole JH, 1994. Composition and phenology of an avian community in the Rio Grande Plain of Texas. *Wilson Bull.* 106: 366–380.
- Winker K, Escalante P, Rappole JH, Ramos MA, Oehlenschläger RJ, Warner DW, 1997. Periodic migration and lowland forest refugia in a “sedentary” Neotropical bird, Wetmore’s Bush-Tanager. *Conserv. Biol.* 11: 692–697.
- Winker K, Rappole JH, 1988. Taxonomic relationships between the genera *Hylocichla* and *Catharus*. *Auk* 105: 392–394.