

NEOTROPICAL BIRD MIGRATION DURING THE ICE AGES: ORIENTATION AND ECOLOGY

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ABSTRACT.—Reconstruction of breeding habitat of North American Neotropical migrants 18,000 years ago and 9,000 years ago indicated major shifts in both location and composition of plant communities relative to present conditions. Increased vegetation in xeric areas may have compensated, at least in part, for the reduction in breeding habitat due to glaciation. Autumnal flights of Neotropical passerine migrants flying on constant headings from North America to Central and South America were simulated under present wind conditions and for winds during periods of glaciation at 18,000 and 9,000 years ago. The 155° average headings currently observed for Atlantic migrants were found to function well during periods of glaciation and may have been more generally useful during those times than at present.

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CYCLES OF QUATERNARY GLACIATION during the last 1.6 million years have influenced the development of present routes of both Neotropical and Paleotropical migration (Moreau 1972, Gauthreaux 1982). North American Neotropical migrants were most clearly affected because most of their present breeding grounds were covered by a permanent ice cap only 18,000 (radiocarbon) years ago (18 kya) and because the ecology of North America has undergone several major changes during the period of deglaciation (Imbrie and Imbrie 1979, Emery et al. 1988, Webb 1988). Modern species assemblages or plant formations are of recent origin in North America. Most developed after early Holocene warming: modern tundra first appeared at about 8 kya, boreal forest at 7 kya, and modern mixed forest at 6–8 kya. Only modern prairie, first appearing about 10 kya, and modern deciduous forest (12 kya) existed during periods of significant glaciation (Webb 1988). After their first appearance, plant formations increased in area and approached their present distributions only in the past 4,000 years (Van Devender 1986, Webb 1988). The present distributions of plant taxa were relatively rare events during the Quaternary and, like the interglacial periods with which they are associated, have existed for only 10% of the 100,000-year glacial/interglacial cycles (Ruddiman and Raymo 1988). These findings pose two major problems for the study of the evolution of bird migration. What behavior would allow bird species to track changes in habitat over thousands of years, while preserv-

ing the fitness of current bird populations over their short lifetime? Would the orientation system(s) used by birds under present conditions have been effective under past conditions?

We examine whether fixed-heading orientation would be sufficient to guide Neotropical migrants during periods of glaciation. We first estimate breeding habitats of Neotropical migrants in North America at 18 kya (full glaciation) and at 9 kya (partial glaciation). We then simulate migratory flights at fixed headings for these birds in order to examine the constraints posed on orientation at those times in the past. The Neotropical migrants we discuss are a subset of the type A Neotropical migrants defined by the Research Working Group of Partners in Flight (1992). We consider only autumnal (southward) migration. We exclude diurnal migrants such as raptors, which are clearly influenced by local topography, and exclude birds moving southwest within North America. We focus on shorebirds and passerines flying south to southeast from North America to Central and South America. We refer to this subset of birds as Neotropical migrants.

Several lines of evidence, including radar and radio-telemetry observations of migration, the experimental manipulation of captive birds, and simulated migratory flights, suggest that at least some songbirds and shorebirds guide long-distance migrations by maintaining a fixed compass heading. Drift by winds produces a variable track, but by selecting synoptic weather conditions for take-off, the great majority of birds

can move reliably between breeding and wintering areas each year (Williams and Williams 1978, 1990, Alerstam 1981, Stoddard et al. 1983, Cochran and Kjos 1985, Alerstam et al. 1986, Richardson 1991, Williams 1991). Direction and some cue for the cessation of migration (distance, time, latitude, or habitat) appear to be genetically encoded (Wiltschko and Wiltschko 1978, Gwinner 1986, Berthold 1988, 1990). One or more such vectors direct first-year birds to the general location of stopover and wintering areas, where they then search for suitable habitat. In subsequent years, birds return to these local habitats using familiar landmarks or some other orientation system operational within the areas specified by the coded vector (Wiltschko and Wiltschko 1978, Williams and Williams 1990, R. Wiltschko 1992). A variety of approaches have shown that such fixed headings could be maintained by use of a compass based on the sun, stars, wind, or magnetic field of the earth (Able 1980, Alerstam 1981, Wiltschko and Wiltschko, 1988).

Although birds may use other techniques for orientation (Rabøl 1978, Able 1980, Wiltschko and Wiltschko 1988, 1991, Richardson 1991, Wallraff 1991, R. Wiltschko 1992), orientation by a fixed compass heading is consistent with available data for Neotropical migrants moving south to southeast across North America to Central and South America (Williams et al. 1977a, 1977b, Williams and Williams 1978, 1990, Williams 1985). Radar observations of Neotropical migrants over the Caribbean, Bermuda, and over the North American eastern coast revealed average headings close to 155° (relative to true north) at all sites with no significant change of headings to compensate for wind drift (Williams and Williams 1978, Williams 1985). In simulations birds move southeast across North America and over the western North Atlantic, where they encounter northeast trade winds that drift them westward to Central and South America. The best available sample of the radar observations is from Antigua in the Caribbean. At Antigua the average heading was 153°, with an angular (standard) deviation of 26.9° (Williams and Williams 1978, Williams 1985). Mean headings observed at other windward islands, Bermuda, and Miami ranged from 151° to 157° (Williams 1985). Airspeeds at Antigua showed two peaks, one at 45 km/h, presumably passerines, and one at 75 km/h, presumably shorebirds (Williams 1985).

METHODS

We used the mapped pollen data from Webb (1988) and Overpeck et al. (1992) to estimate bird habitats. We labeled these habitats as desert, prairie, tundra, coniferous forest, mixed forest, and deciduous forest to describe structural features, but do not imply present species assemblages for each region in the past (Baker 1983, Webb et al. 1987, Thompson 1988, Webb 1988). We set the southern limit of breeding habitat for Neotropical migrants as the southern limit of killing frost and set no northern continental limit. Breeding habitat includes all forest types, wetlands, prairie and tundra, but excludes desert and permanent ice. We considered Arctic coastal and North Slope areas as suitable habitat for shorebirds, but not Neotropical passerine migrants.

To simulate migratory flights, we first created a wind matrix for North America representative of those winds actually used by Neotropical migrants. We then simulated flights through these wind fields with an iterative computer program. Finally, we modified the wind matrix to estimate conditions during glaciation and repeated the simulations with these wind conditions.

The methods for creation of a wind matrix under present conditions are described in detail in Williams (1991). The 5° latitude × 5° longitude matrix for present conditions was an average wind velocity for those North American weather systems known to have supported major autumnal migrations of passerines and shorebirds moving to the south and southeast as observed by radar. Weather systems associated with such movements were determined from radar observations in: Alberta (Richardson and Gunn 1971); Wisconsin (T. C. Williams and J. M. Williams unpubl. 1979 report to Office of Naval Research); Ontario and Quebec (Richardson 1972); and along the North American eastern coast (Drury and Keith 1962, Richardson 1972, 1979, 1980, Williams et al. 1977a, 1977b, Williams 1991). At all sites, south or southeast migrations likely to contain significant numbers of Neotropical migrants occurred west of a cold front, when barometric pressure was rising or steady and when winds were northerly, westerly or calm (see Richardson 1978). The concurrence of these factors was then considered to be criteria for identifying weather systems likely to produce Neotropical migratory flight in areas or at times when we lacked radar observations. South and southeast migration that occurs under other, less-predictable conditions was excluded (Richardson 1978, 1990).

The wind matrix for current conditions was created by averaging 774 wind measurements taken at 850 mb (ca. 1,500 m altitude), and 595 surface-wind measurements. This gave an estimate of winds close to the average altitude of migrant birds over continental areas (Eastwood 1967, Able 1970, Williams et al. 1977a). Wind data from 500 mb (ca. 5,000 m) were used to modify surface data when 850 mb data were lacking. Flight at 5,000 m is rare over continental areas, al-

though it has been documented for shorebirds initiating transoceanic flight (Richardson 1979). Flight at these altitudes at a constant heading has been simulated over eastern North America by Williams (1991), but is not included in our simulations.

Matrix values for present winds in areas not penetrated by North American weather systems were determined as follows. Winds over the western North Atlantic were average wind velocities, recorded at the altitude of birds, during radar observations of moderate or heavy autumnal bird migration in those areas (Williams et al. 1977a, 1977b, McClintock et al. 1978, Williams 1985). Prevailing winds were used over oceans south of 30°N. We limited our wind matrix to latitudes 10°S to 70°N and longitude 50°W to 130°W because we lacked adequate radar observations in South America and the Arctic.

Parameters for heading and airspeed used in the simulations were derived from more than 2,000 radar tracks of migrants obtained over Antigua for five migratory seasons. For the simulation we used a heading of $155^\circ \pm 25^\circ$. Simulated airspeed was 35 km/h (10 m/s), about one standard deviation below the mean airspeed of late season (passerine) migrants observed with radar at Antigua, and represents the slowest migrants likely to make the Atlantic crossing (Stoddard et al. 1983).

Winds at 9 kya and 18 kya were estimated by modifying the present wind-velocity matrix in relation to the National Center for Atmospheric Research Community Climate Model (NCAR CCM) simulation for North America at 9 kya and 18 kya as given in Kutzbach (1987). NCAR CCM simulations were available for January and July for these periods. A model for modification of the simulated wind patterns was obtained by comparison of present winds observed during southeast migrations with present simulated storm tracks, high- and low-pressure centers, and resultant winds for January and July. Simulated resultant winds along the present simulated January storm track approximated winds observed during autumnal migration more closely than did those of present July simulations. The average location of January and July high-pressure centers and the average velocity of January and July trade winds corresponded to those observed during present autumnal Neotropical migrations. We obtained January storm tracks, average location of stable high- and low-pressure centers, and resultant winds for January and July, from NCAR CCM simulations for 9 kya and 18 kya and substituted these values in the model derived from present simulations to obtain a $5^\circ \times 5^\circ$ matrix of estimated winds used by autumnal Neotropical migrants at 9 kya and 18 kya.

RESULTS

The climates of glaciated North America were unlike any today and this condition led to veg-

etation and faunas without analog in today's plant and animal communities (COHMAP 1988, Overpeck et al. 1992). Analyses of past pollen distributions show that the major tree taxa responded independently to past changes in climate. Major pollen-producing trees in both Europe and North America show changes in distribution that are independent of other taxa (Huntley and Webb 1989). The scant data on Quaternary avian distribution also indicate that birds utilized habitats dissimilar from their current species associations (Gauthreaux 1980).

Since associations among plant taxa were ephemeral during the Quaternary, we used physical and structural factors to identify breeding areas for long-distance migrants. Summers had to be sufficiently warm and wet to provide a large insect and fruit food source, and winters sufficiently cold to greatly reduce these food sources. Severe weather conditions during the nonbreeding season in these areas would severely limit the resident populations of birds, mammals and parasitic insects, thus reducing competition, predation, and parasitism for breeding migrants (see Cox 1985). Below we give habitat and migratory-route reconstructions for 18 kya and 9 kya and compare these with the present conditions. In each case we begin with a description of simulated climate and paleoecology to locate likely breeding habitat and then consider the effects of constant heading orientation on Neotropical migration under these conditions.

18,000 years ago.—Glaciation has been the predominant climate condition for North America for more than 80% of the past 900,000 years (Ruddiman and Raymo 1988). At the height of glaciation much of the present breeding area of Neotropical migrants north of 45°N was covered by ice up to 3,300 m thick (Fig. 1C). The principal exceptions were Alaska which was largely ice-free, and possible ice-free areas in the Canadian far north and between the eastern and western ice domes. Both summer and winter temperatures south of the ice were 2° to 10°C lower than present. Unglaciated areas in Alaska, as well as in northwestern, north-central, and southeastern United States, were drier than at present; the Northeast and Southwest had wetter summers than present (Kutzbach 1987, COHMAP 1988).

Lowering of sea level by about 100 m exposed large areas of new land. We suggest that substantial additional habitat was available to Neo-

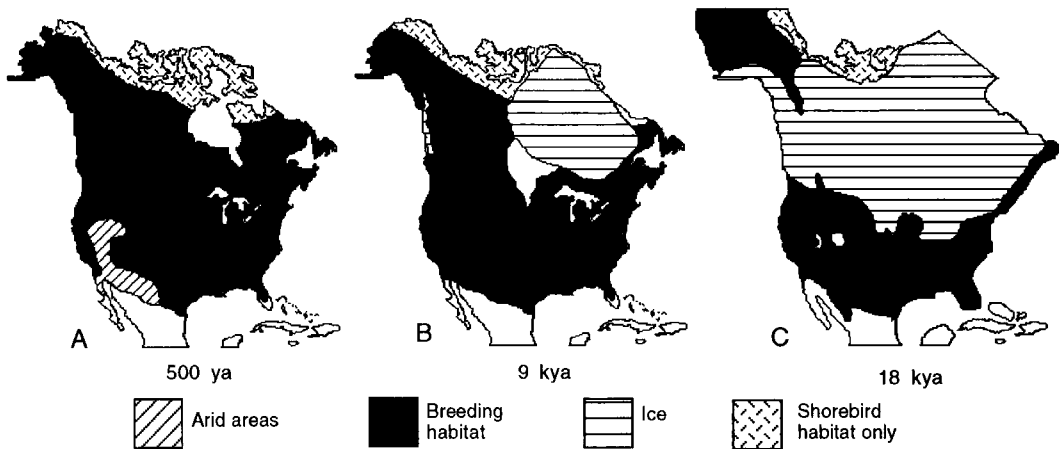


Fig. 1. Estimated breeding habitat for passerine and shorebird Neotropical migrants based on criteria given in text. Stippled area would support major shorebird breeding populations, but probably not passerines. Northern extent of breeding areas 9 kya and 18 kya assumes ice-free Arctic coastal areas and tundra structure similar to present. At 18 kya, land area was continuous with eastern Siberia and ice cap extended northeast to cover Greenland; these areas have been truncated. Margins of ice caps and coastlines from Denton and Hughes (1981) and from COHMAP (1988). Glacial lakes shown: Agassiz (9 kya), and Lahontan and Bonneville (18 kya).

tropical migrants along the east and west coasts of North America, and in the Caribbean and Gulf of Mexico (see Fig. 2C). The extent of this habitat is difficult to estimate as areas near the ice would have been depressed due to its mass (Denton and Hughes 1981, Peltier 1987), and Caribbean areas were subject to tectonic forces that may have depressed land areas (Aubry et al. 1988). As suggested by Emery (1967), the nature of these lands either could have been estuarine, where sea level dropped below the continental shelf, or bay and wetlands, where the seas were shallow. Vegetation in these areas of the exposed continental shelf was similar to that on nearby continental margins (Emery 1967).

Pollen distributions from eastern North America 18 kya show a great reduction in deciduous forests compared to present. A pine forest with some deciduous trees covered the southeastern United States and probably much of the area of the exposed eastern continental shelf (Emery et al. 1967, Jacobson et al. 1987). An open woodland with deciduous trees, grasses and prairie forbs covered the area of the United States gulf states. Sedges and forbs indicating open to treeless vegetation, dominated the northeastern United States. South of the ice in the midwestern United States, enough spruce trees grew to yield a vegetation similar to park-

land (Jacobson et al. 1987). Northwestern North America consisted of a subalpine open woodland grading into tundra in ice-free Alaska (Barnosky et al. 1987, Engstrom et al. 1990). In mountainous areas, the tree line was depressed 1,200 to 500 m, with alpine vegetation below glaciated summits (Baker 1983). The increased precipitation and lower temperatures in the Southwest created large shallow lakes, such as Lake Bonneville (Fig. 1C). Present scrub and desert areas in the United States were a mixed woodland. The Mexican highlands were drier than at present (Baker 1983, Van Devender 1986, COHMAP 1988).

The total breeding habitat available for Neotropical migrants appears to have been less than at 500 years ago (ya) due to glaciation of almost all of the present northern breeding range (Fig. 1). This loss may have been compensated somewhat by the addition of excellent habitat in greatly expanded coastal areas, in areas near pluvial lakes, and in the increased woodland areas of the Southwest. With reduced opportunities for migration, some species may have become resident in expanded Caribbean land areas. During periods of maximum glaciation, species that at present breed in boreal forest may have been able to compete successfully in the generally coniferous, cooler habitats over much of the continental United States. There

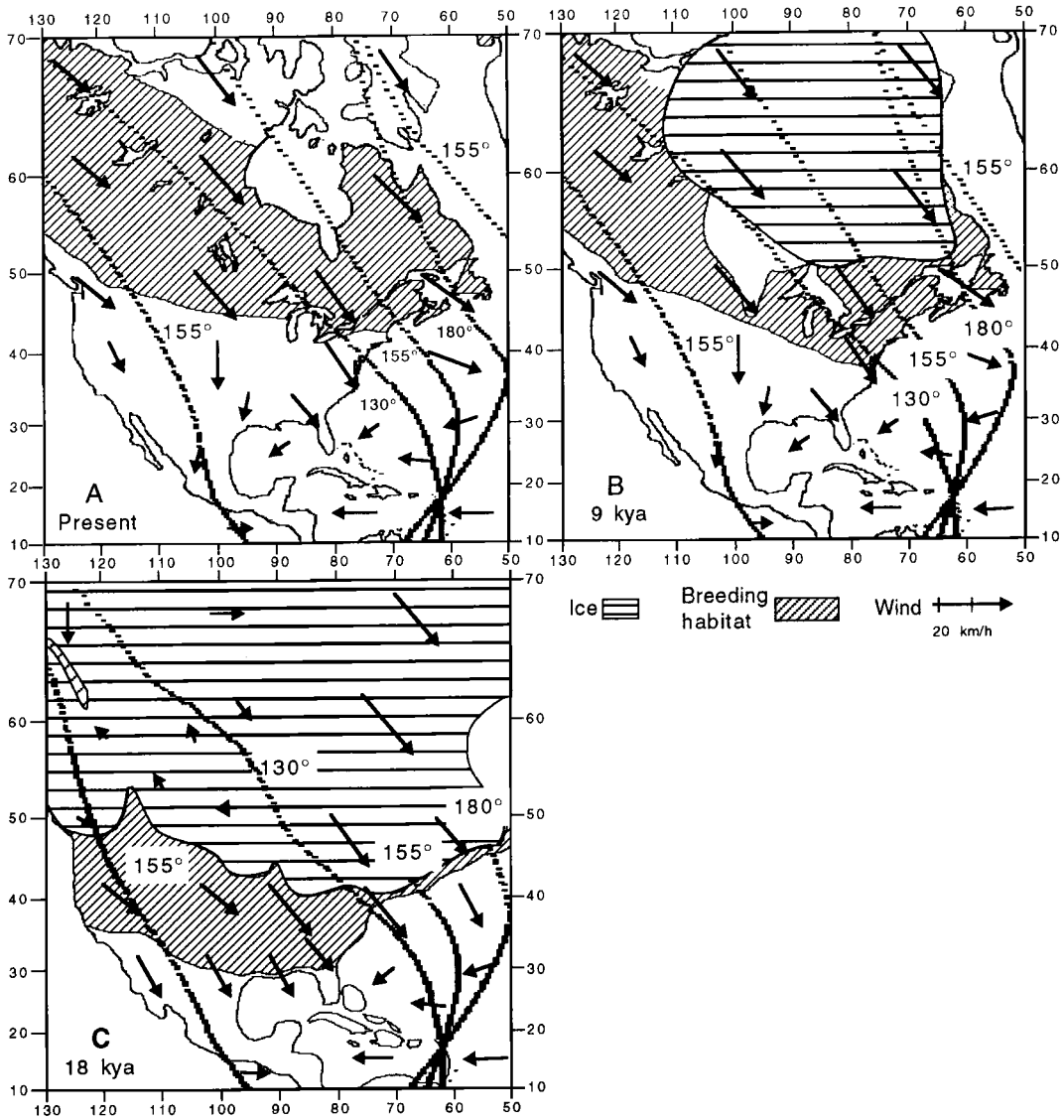


Fig. 2. Simulated migration routes and breeding habitats for hypothetical Neotropical migrant passerine moving from breeding grounds in North America to wintering areas in northern South America at three time periods: Present, 9 kya, and 18 kya. Simulated tracks of birds flying at airspeed of 35 km/h (10 m/s) with fixed headings as indicated; position plotted at 1-h intervals. Representative winds of the 5° × 5° wind matrix used for simulations shown by solid arrows. (A) For present conditions, winds are average for synoptic conditions selected by present autumnal migrants moving southeast over eastern North America. Breeding habitat shown meets criteria described in text. For simulations at (B) 9 kya and (C) 18 kya: winds and breeding habitats estimated from global climate simulations; area of ice cap from Denton and Hughes (1981). All panels show tracks of birds passing over island of Antigua on average heading observed in Caribbean (155°) and for 130° and 180°. Tracks also shown for birds using headings of 155° from extreme eastern and western portions of breeding area. Additional breeding areas exist(ed) north and west of geographical limits of figures. Degrees of latitude and longitude given at panel margins. Mercator projection distorts relative areas and distances, but shows direction of tracks and winds accurately.

may have been considerable habitat for birds such as Blackpoll Warblers (*Dendroica striata*) in Alaska 18 kya, depending on the northward extension of conifers into the tundra of that period and the composition of the tundra, which differed from that of today (Webb 1988, Engstrom et al. 1990). Much of the Nearctic was probably ice free in summer and was suitable breeding habitat for nonpasserine migrants (Johnson and Herter 1990).

To facilitate comparisons of past and present migration routes, we simulated the breeding area of a hypothetical Neotropical migrant passerine that today moves from Canada and Alaska to South and Central America (Fig. 2). The breeding area of this migrant is similar to that of the taxa that Mengel (1970) termed taiga wood-warblers. Alaskan areas (shown in Fig. 1) are not included in Figure 2. At 18 kya (Fig. 2C), the breeding area was shifted far to the south of the present distribution (Fig. 2A). The northeastern portion of the range of the hypothetical migrant was restricted to a narrow strip of exposed continental shelf between the ice and the sea. An alternative interpretation of breeding area is to restrict the wood-warbler to the much smaller areas of spruce located in the midwestern states.

In this and the following simulations, we first investigate whether the headings of $155^\circ \pm 25^\circ$ that reliably bring birds over Antigua on their way to South America at present would have been functional in the past. We also plot tracks with a heading of 155° departing from the western and eastern limits of the hypothetical breeding range to see if these headings are broadly applicable in North America. In Figure 2 we use an airspeed of 35 km/h (10 m/s), equal to the slowest passerines currently migrating over Antigua. Previous work has shown birds with low airspeeds to be the most constrained in their use of fixed-heading orientation (Stoddard et al. 1983, Williams 1991). We also simulated flights at airspeeds of 75 km/h (21 m/s) near the average for shorebirds flying over Antigua. These simulated tracks (not shown in Fig. 2) were less deflected from their heading and took less time to complete their flight (see Stoddard et al. 1983, Williams 1991). Tracks are shown from the most northerly point, but tracks initiated from a more southerly point will follow the same path, given that there is no effect of previous experience in the simulation.

Wind patterns at 18 kya were greatly affected

by the ice cap. A large high-pressure center dominated winds over central Canada creating relatively light wind in this area. The average storm track split into two. A northern track, arched up over north-central Canada and down along the northeastern coast, creating strong northwest winds in northeastern Canada. A southern branch of the storm track crossed the southern United States at about 40°N and then turned north along the coast to join the northern track. The southern storm track created strong northwest winds behind cold fronts over most of North America between 30°N and 50°N (Fig. 2C). These winds were more favorable for southeast migration in the western and central United States than are present wind conditions (Fig. 2A; Kutzbach 1987). Birds continuing fixed heading flight over the Atlantic encountered northeast trade winds south of Bermuda, which drifted them westward toward Central and South America. Simulated migrants moving along the west side of Central America found similar but less extensive west winds which drifted them eastward toward South America (Fig. 2C).

At 18 kya both passerines and shorebirds passing over Antigua could have used the same constant headings as they do today (Fig. 2 A and C). Passerines on headings of 155° to 180° would have arrived from the narrow northeastern seacoast, as there were no suitable passerine habitats north of 50°N in eastern North America. Passerines on headings of 130° could have come from as far as Alaska. Birds breeding north of the ice 18 kya would make two nonstop migrations. The first, over the ice cap, would take about 90 h for the slowest passerines (35 km/h) and about 50 h for shorebirds (75 km/h). The over-water flight would have taken about the same time as at present, up to 110 h for slow passerines and 60 h for shorebirds.

Of particular interest are flights from Alaska on headings centered around 155° (the most westerly track in Fig. 2C), and flights from the area bracketed by the eastern and western 155° tracks in Figure 2C. These areas constituted the great majority of breeding area 18 kya, and Figure 2C shows that fixed heading flights at about 155° , coupled with favorable winds at 18 kya, could have provided a rapid and efficient route to wintering areas in South America, Central America and the Caribbean. For the great majority of migrants to South America, these tracks would have taken birds over the (probably)

much expanded land areas of the Caribbean and Central America, a logical initial route between North and South America. Migrants at this time might have used fixed headings not to make long flights over open ocean or inhospitable arid lands, but to direct movements over well-vegetated continental areas or to guide relatively short flights over water between land areas.

9,000 years ago.—Nine thousand years ago a reduced North American ice cap covered northeastern North America (Fig. 1B), but was rapidly receding. As perihelion (closest approach to the sun) occurred in July, summers were warmer than at present except for areas near the ice. Simulated January temperatures indicated the distribution of killing frost would be similar to the present (Kutzbach 1987). Ice-free coastal areas probably existed along the northern and eastern margins of the ice due to the advection of warmer air above a stable anticyclone over the ice cap. In the Northwest (including Alaska) the North Central, and the Northeast, summers were drier than at present. Due to a strengthened summer monsoon, the southern United States were significantly wetter than present. The average storm track dipped southward from western Canada to well below the Great Lakes and then ascended northward along the eastern United States coast and out to sea. This pattern provided strong northwest winds west of cold fronts over most of the continent (Fig. 2B). Weaker winds were found in the Southwest and winds during migration were more northerly in the south-central United States than along the storm track (Fig. 2B). Thus, winds over the southern United States generally were less favorable than 18 kya. The relatively small ice cap reduced sea level about 10 m below present (Kutzbach 1987). This probably resulted in an increase in lagoon and wetland habitat in areas of continental shelf that were exposed (Emery 1967). The melting ice created extensive inland lakes such as lake Agassiz (Fig. 2B). Winter temperatures were similar to those at present.

Deciduous forests dominated eastern North America, but the association of taxa differed from the present (Jacobson et al. 1987). A mixed coniferous-hardwood forest extended north from the Great Lakes. Prairie forbs, sedges, and grasses were found in central North America, but were associated with pines and spruces in the north and with deciduous trees in the south. Pollen distributions and macrofossils from

packrat (*Neotoma*) middens from western North America indicate closed-canopy coniferous forests in coastal regions and at higher elevations of the northwest, with grasslands in the drier lower elevations (Baker 1983). The flora of the southwestern United States was similar to the present, but forests extended further upward in altitude due to warmer temperatures and further downward due to wetter summers. Forest habitat covered a larger area than at present in most areas (Thompson 1988). Deserts, such as the Chihuahu Desert, were grasslands due to the increased summer monsoon (Van Devender 1986).

Most of ice-free North America would have been excellent breeding habitat for migrants. The additional forest and grassland in the Southwest probably increased breeding populations of passerines and some shorebirds in that area compared to present conditions, while winters would have been sufficiently cold to favor migrants over residents. Loss of coastal and wetland habitats under the ice cap (Fig. 1B) may have been equaled by a gain in similar habitat along the exposed continental shelf, around glacial lakes, and along the multitudes of rivers and streams draining the melting ice cap. Species currently nesting in tundra may have found structurally similar although warmer habitats in the Southwest and near the melting ice. Tundra and coniferous forest habitats were probably reduced compared to present conditions, but there may have been a slight increase in mixed forest and deciduous forest habitats compared to the present. A general shift in breeding habitat to the south and west is likely, due to increased moisture in the Southwest and elimination of habitat in the Northeast under the ice cap.

The breeding area of the hypothetical migrant in Figure 2B is similar to that for present conditions except for areas of permanent ice. The southern boundary extends further south than at present in the eastern United States due to greater presence of confers in that area 9 kya.

At 9 kya, the headings of migrants observed at present over Antigua would have brought birds from much the same areas of ice-free North America as they do today (Fig. 2B). Birds breeding north of the ice 9 kya would have taken less than 45 h to cross the ice, even for the slowest passerines (35 km/h), while the over-water flight would take up to 110 h as at present.

Headings observed at present in the Carib-

bean could have been used from almost all North American breeding areas 9 kya. The retreat of ice in the eastern portion of North America and the shift in the center of breeding distribution to the north and east would have resulted in a greater percentage of birds moving over the Atlantic at 9 kya than during periods of full glaciation.

500 years ago.—The present time is one of maximum deglaciation. Boreal forest and tundra replaced most of the remaining ice cap, providing further habitat for Neotropical migrants. Grasslands and desert expanded in the Southwest and central United States due to a drier climate (Kutzbach 1987, Thompson 1988, Webb 1988, Thompson et al. 1993). The total area available for breeding as judged by our criteria, increased relative to 9 kya (Fig. 1A and B), but the removal of tree species from prairie areas, the retreat of forest areas in the Southwest and the increase in desert in the Southwest, may have reduced the density of Neotropical passerine migrants that could be supported by these habitats. Northern shorebird habitat appears to be near maximum at 500 ya (Järvinen and Väisänen 1978). Total populations of boreal passerines and shorebirds at 500 ya may have been near maximum for the entire glacial cycle (given that present habitat for Neotropical migrants has been greatly reduced by human activity from the levels at 500 ya). Winds, winter temperatures, and average storm tracks at present are similar to those at 500 ya and 9 kya (Kutzbach 1987).

The expansion of habitat in the north and east in the past 9,000 years and the reduction in habitat in the Southwest resulted in a north-eastward shift in the center of breeding distributions. The usefulness of fixed-heading orientation for Neotropical migrants is more constrained at 500 ya (and at present) than at any other time in the glacial cycle. Birds departing from the eastern portion of the breeding grounds on headings less than 155° (illustrated by the most eastern track in Fig. 2A) would fly too far east over the Atlantic to make landfall in South America (Stoddard et al. 1983). Birds departing the far western breeding range over the Pacific on headings greater than 155° also would fail to make landfall in South America. Thus, although fixed-heading orientation would be successful from all of the breeding range, permissible headings are severely restricted in the eastern portions and somewhat restricted in the far western portions of that range.

DISCUSSION

Changes in climate during the most recent deglaciation of North America resulted not only in major changes in the area covered by vegetation, but also in the species composition of plant formations. During the past million years, present conditions were rare, representing not the norm, but the extreme development of boreal forest and desert habitats. During the remaining time, glaciation covered much of the northern breeding areas currently used by Neotropical migrants. Our analysis indicates that increased vegetation in southern and coastal areas may have compensated for some of this loss if northern species could compete effectively in these habitats. The present expansion of tundra and taiga in North America is exceptional, and the abundance of species exploiting those areas was reduced significantly during periods of glaciation.

The fauna of North America reacted to climate change in a variety of ways. Some animals, such as southern reptiles, showed little change in distribution during the past 20,000 years, instead they adapted to the changing conditions of the area (Van Devender 1986). Although there are few avian fossils from the Quaternary (Gauthreaux 1980), it is probable that birds, due to their high mobility and observed common occurrence of vagrancy, changed distribution with the migration of plant species over North America. This conclusion is consistent with the observed low rate of Quaternary speciation in birds as compared with mammals (Mengel 1964). Gauthreaux (1980) and Huntley and Webb (1989) independently concluded that the movements of birds and of trees differed only in the time scale of their migrations. As a description of the phenomenon this is true, but birds are able to direct their migrations, while trees are not. Thus, the type of orientation system used by birds in migration may well have implications for changes in avian species distribution.

Flexibility in habitat selection would benefit birds during periods of major changes in plant formations. Habitat selection by birds includes both inherited preferences and reaction to proximate factors (Hutto 1985, Sherry and Holmes 1985). Selection of both breeding and wintering sites appears directly influenced by competition (Cody 1985, Cox 1985, Sherry and Holmes 1988, 1989, Holmes et al. 1989, Sherry 1990). Our analysis agrees with that of Cox (1985); habitat selection in Neotropical migrant birds is more

likely to be the result of interspecific competition than dependence on specific plant species or plant associations. Such specific dependence would be difficult to reconcile with relatively stable avian species in the face of major changes in vegetation. Our estimates of breeding habitats indicate that Neotropical migrants, even those presently restricted to boreal forest breeding areas, would have not have fluctuated as greatly in abundance as did the plant species which they now exploit. During periods of maximum glaciation, sufficient additional habitat was available in presently unsuitable areas to compensate at least in part for the loss of areas covered by ice. If this view is correct, the present observed reduction in Neotropical migrant populations (Hagan and Johnston 1992, Gill 1994) could be greater than that due to glaciation.

Fixed-heading orientation, coupled with differential reaction to weather as a stimulus for migration, appears well suited to coping with changing Quaternary ecology. Although the exact routes would vary from year to year, our simulations indicate that such a system would reliably direct birds over oceans, ice caps, and continental areas. Despite the major shifts in breeding distribution shown in Figure 1, the southeast headings shown in Figure 2 continued to bring the great majority of migrants to Neotropical wintering areas at all times tested. Some cue indicating cessation of migration must be specified as well as direction. If this is distance or time as suggested by Gwinner (1986), then this parameter would have to change for birds making longer flights. If the cue were instead a function of latitude, as would be the case for the elevation of the sun or stars, or inclination of the geomagnetic field (see Wiltschko and Wiltschko 1992), the system could function at all times in the Quaternary without change. Rather than directing birds to a specific location, this orientation system would bring them to a large general area more than 100 km in diameter (Williams 1991). Birds would then have to search within this area for suitable habitat (Williams and Williams 1978, 1990, Wiltschko and Wiltschko 1978, 1991).

Radar observations of Neotropical migration reveal both large-scale broadfront migrations as predicted for fixed-heading orientation and (usually under other weather conditions) flights of large numbers of birds in directions inappropriate for the seasonal migration (Drury and Keith 1962, Gauthreaux and Able 1970, Wil-

liams et al. 1977a, 1981). These latter flights may constitute the search phase of orientation and, rather than being the result of errors, may be a specific adaptation to Quaternary conditions (Richardson 1982, gives alternative interpretations).

Searching for suitable habitat, necessitated by a fixed-heading orientation, may itself have been adaptive during periods of rapid climate change. Both birds and mammals could track the changes in plant distribution during the Quaternary, yet most bird species survived, while many mammal species did not (Cox 1985, Sutcliffe 1985). An effective system for discovering new, often distant habitats and reevaluating old ones may have made a crucial difference. Current studies indicate that, for several species of passerine and shorebird migrants, successful adults return to the same breeding, stopover, and wintering areas, while first-year birds and unsuccessful adult breeders disperse widely (Sherry and Holmes 1985, 1989, Myers et al. 1987, Johnson et al. 1989). In most cases, birds that have found recently opened, underutilized breeding sites, wintering areas, or stopover sites could easily recoup the cost of a few hours of flight.

Present rather than past conditions appear to pose the greatest stress on a fixed-heading orientation system in our simulations. Considering that for 80 to 90% of the past 900,000 years North America has been in a state of glaciation (Van Devender 1986, Ruddiman and Raymo 1988), present conditions might be considered to be a rare period in avian evolution, posing a relatively brief stress on a system largely evolved under different conditions. Our simulations suggest that constant-heading orientation with a mean heading of 155° could have evolved during periods of full glaciation. At that time it would have guided flights from breeding areas in southern North America over the Caribbean Sea and Gulf of Mexico to wintering grounds in the Caribbean Islands, Central America, and South America. As the ice retreated, the same orientation system would direct birds on longer and longer over-water flights. During subsequent glaciations, the system also would serve to cross the ice caps themselves, as is currently observed over Greenland (Alerstam et al. 1986). The over-water and over-ice flights would result in energy savings and reduced risk of predation compared to flights around the ice caps or around seas (Williams et al. 1977a, Johnson and Herter 1990, Williams and Williams 1990)

Orientation by means of a fixed southeast heading is not the only system used by Neotropical migrants (in the broad sense; Richardson 1991). Birds moving south to southwest through North America to Central America would have to use south to southwest headings, and Richardson (1979) observed large numbers of shorebirds departing the Canadian Maritime coast on headings too far east to allow successful flight to South America without a change in orientation. Laboratory experiments with orientation cages indicate multiple vectors consisting of fixed heading and distance segments for Palearctic-African and Australian migrations (Wiltshko and Wiltshko 1991, Munro et al. 1993). Genetic analyses of these vectors show that avian populations can shift both direction and distance significantly in only a few generations (Berthold 1990). These experiments suggest an alternative to our hypothesis of a relatively fixed, general heading; bird species could follow the displacement of specific plant species or species associations or specific invertebrate fauna (Hutton 1984). In this view, migration is accomplished by route-specific instructions, and the present migratory routes of birds reflect the past as well as present location of the critical habitats for that bird species. Each successive stage of glaciation would require altering the genetic system for the migratory route or at least the addition of a new segment to the encoded route. Some anomalies in present migration routes could be explained by the persistence of all or portions of past migration routes in the species' genetic code (Rabøl 1978, Sharpe 1978, Gill 1994). Our analysis of North American vegetation history, the probable benefits of less precise orientation systems, and the demonstration of the efficacy of a simple fixed-heading system suggest that such route-based, population-specific orientation systems should be rare in Neotropical migrants (as defined for our simulations). This conclusion is supported by the circular normal distributions of headings around a southeast mean observed for Neotropical migrants over the western North Atlantic Ocean (Williams 1985). The relatively broad spread of headings around this mean ($SD > 25^\circ$) is consistent with birds facing uncertain conditions in both winter and breeding areas. We suggest that a more precise orientation system (including one with less variation in fixed headings) would not benefit migrants.

If it is true that a generalized orientation sys-

tem, such as fixed-heading orientation, allows a species to track habitat changes over thousands of years, we still must account for its selective advantage during the reproductive lifetime of a bird. Behaviors that are beneficial to a species are not favored in evolution unless they are also beneficial to the individual (Krebs and Davies 1987). A generalized, nonspecific orientation system coupled with extensive habitat search must also have raised the average migrant's fitness above that of a system which reliably returned it to its natal location and to specific stopover and wintering areas. A general characteristic of Quaternary ecology is that local habitats change relatively rapidly both in space and in time. Fires, floods, storms and severe seasonal weather create a fluctuating patchwork of species associations and successional stages. Raw data from pollen-core sites show that plant associations consisted of a matrix of species changing irregularly from site to site. Only when many sites are averaged do we find continuous variation over large areas (Baker 1983, Jacobson et al. 1987). Palynological analysis on a high-resolution time scale shows many rapid changes in species composition at a single site, some changes being as rapid as historic deforestation from intensive, widespread lumbering (Jacobson et al. 1987). Records of lake or river sediments, shoreline positions, water temperatures, snowfall amounts, and volcanic or organic ash deposits all show variations at the finest discernible time intervals that are comparable to many of the average variations at intervals of hundreds or thousands of years (Kutzbach 1981, Street-Perrott and Smith 1983, Kutzbach and Street-Perrott 1985, Jacobson et al. 1987, Engstrom et al. 1990, Gear and Huntley 1991, Koltermann and Gorelick 1992, Wang and Lewis 1992). Climate simulations and studies of Neotropical areas suggest similar variation for wintering areas of migrants (COHMAP 1988). South America and the Amazon basin appear to have supported unstable associations of species swept at intervals by fire and flood as recently as a few thousand years ago (Meggers 1975, Colinvaux 1987). Under such conditions, it appears that the same factors of unstable climate and competition that favor habitat search at present would also have been effective in increasing fitness in the past. An average individual shift of as little as 0.5 km per year is sufficient to account for a population shift of 10,000 km in 20,000 years. We conclude that fixed-heading

orientation and search within a goal area would benefit avian populations during the lifetime of an individual and would also allow a species to track large-scale vegetation changes over thousands of years.

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