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# BIRD MIGRATION AT DIFFERENT LATITUDES IN EASTERN NORTH AMERICA

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ABSTRACT.—We attempt to quantify the relationship between migration and latitude in the avifauna of eastern North America. Progressing northward up the east side of the continent, the proportion of breeding species that moves south for the winter increases steadily, from 12% at 25°N (southern Florida) to 87% at 80°N (Ellesmere Island), a mean increase of 1.4% for every degree of latitude. Conversely, the proportion of wintering species that moves north for the summer decreases with latitude, from 52% at 25°N to none at 70°N, a mean decrease of 1.1% for every degree of latitude. These relationships hold despite the fact that 24% of all species breeding in eastern North America leave the area completely in fall to winter south of 25°N, mostly in Central and South America (including the Caribbean Islands). These trends are similar to those in western Europe, but at any given latitude an average of 17% more breeding species leave for the winter in eastern North America, and 10% more wintering species leave for the summer. This difference is attributed to climate, in that at any given latitude temperatures are cooler in eastern North America than in Europe. We argue that relationships between migration and latitude exist because latitude is a good surrogate measure of factors likely to more directly influence migration, such as climate and daylength, which in turn control the amplitude of seasonal changes in food supplies. *Received 2 August 1995, accepted 3 November 1995.*

WE EXAMINE THE PROPORTIONS of all bird species breeding at successive latitudes in eastern North America that move south for the winter. We also examine the proportions of all species wintering at successive latitudes that move north to breed. The study follows a similar analysis for the avifauna of western Europe (Newton and Dale 1996), enabling a comparison between the two regions. The relationship between migration and latitude has been previously examined only in fairly general terms (Lack 1954, Slud 1976, Alerstam 1991), or for particular groups of birds (MacArthur 1959, Willson 1976, Herrera 1978). These earlier studies do not reveal the broad latitudinal picture that we discuss for the entire avifauna, summer and winter. The main relevance of our paper is in understanding the role of migration in influencing the distribution patterns of birds, and the resulting diversity gradients.

## METHODS

We adopted the same procedure as in our earlier analysis for European birds (Newton and Dale 1996). Using maps of the breeding and wintering ranges of eastern North American birds given by Godfrey (1966), Scott (1987), Root (1988), and Price et al. (1995), we recorded the distribution of relevant species, summer and winter, in an approximately 1,000-km wide band spanning 60° of latitude (25° to 85°N) lying along the eastern edge of North America and adjacent coastal areas. The band extended from Florida to Ellesmere Island (Fig. 1).

Within this band, we calculated for each successive 5° of latitude the numbers of bird species present: (1) year-round, (2) in summer only, and (3) in winter only, including only species that occurred within 1° on either side of each latitude line. From these figures, we examined changes in the latitudinal distribution of birds in eastern North America between summer and winter. We also calculated the proportion of species breeding at each latitude that moved south for the winter, and the proportion of species wintering at each latitude that moved north for the summer. Some 374 regularly occurring species were included in the analysis (not vagrants), the criterion for acceptance being a range map in Scott (1987). The list included a few introduced species, such as House Sparrow (*Passer domesticus*) and European Starling (*Sturnus vulgaris*), that have become established over wide areas, but excluded those found only in restricted locations.

Only species that abandoned a given latitude com-

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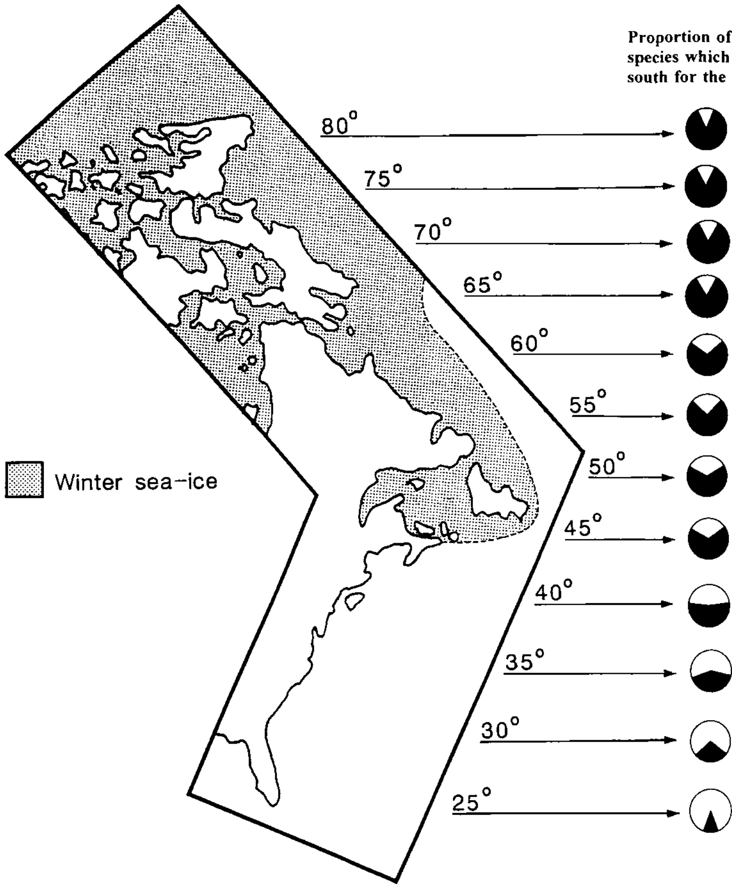


FIG. 1. Map of eastern North America showing proportions of breeding birds at different latitudes that migrate south for the winter.

pletely for the winter or summer were classed as migrants at that latitude, whether they moved short distances within North America or longer distances elsewhere. Species that at any given latitude were partial migrants were classed as resident at that latitude because they could be found there year-round (though some may have moved from inland to coast or from mountain to valley). The breeding latitudes for seabirds were based on locations of nesting colonies, recognizing that some pelagic species might forage hundreds of kilometers from their colonies during the breeding season. Each species was placed in one of three categories according to whether its main winter habitat was land, freshwater, or coastal marine. This last category included both shorebirds and seabirds, and will hereafter be referred to as coastal. Some species in this category occupied a different habitat in summer, most shorebird species moving to inland terrestrial habitats and most sea duck species to freshwater. They were classed as coastal for the analyses because the emphasis was on winter distribution.

## RESULTS

Of the 374 species found regularly within the area considered, 69 (18%) are present throughout their latitudinal range year-round, and the remaining 305 (82%) are completely migratory in part or all of their respective ranges (Table 1). Eighty-three (22%) species breed in eastern North America and leave the area completely for the winter, mostly moving either to Central or South America and nearby coastal areas (including the Caribbean Islands; 78 species) or to western North America (Yellow-billed Loon [*Gavia adamsii*], Pacific Loon [*G. pacifica*], Thayer's Gull [*Larus thayeri*]) or Africa (Northern Wheatear [*Oenanthe oenanthe*], Common Ringed Plover [*Charadrius hiaticula*]). Conversely, 22 species that do not breed in the area considered move in for the winter, either from farther west or northwest on the continent (17 species), from

TABLE 1. Migratory status of 374 bird species in eastern North America.

| Migratory status | All species | Coastal species | Freshwater species | Land species |
|---|---|---|---|---|
| Resident[a] | 69 | 6 | 5 | 58 |
| Breeding only[b] | 81 | 17 | 2 | 62 |
| Wintering[c] | 22 | 14 | 5 | 3 |
| Migrating within North America[d] | 191 | 60 | 36 | 95 |
| Summering but not breeding[e] | 11 | 11 | 0 | 0 |
| Total number of species | 374 | 108 | 48 | 218 |

[a] Present over full latitudinal range year-round, but may include some partial migration in which part of population moves within year-round range.

[b] Breeds in eastern North America, but entire population winters elsewhere.

[c] Winters in eastern North America, but entire population breeds elsewhere.

[d] Present in parts of eastern North America year-round, but latitudinal distribution changes between summer and winter.

[e] Seabirds that breed outside area considered here but are present off eastern North America in summer (see Table 2).

Iceland and northwestern Europe (Great Skua [*Catharacta skua*], Lesser Black-backed Gull [*Larus fuscus*], Black-headed Gull [*L. ridibundus*], Eurasian Wigeon [*Anas penelope*]), or from Greenland (Dovekie [*Alle alle*]). The populations of several species that both breed and winter in eastern North America are augmented in winter by birds from other breeding areas in Greenland or western Canada. Finally, 11 seabirds occur regularly off eastern North America in summer but do not breed there; seven species breed in neighboring or more distant areas in the Northern Hemisphere (including Manx Shearwater [*Puffinus puffinus*], which also breeds in small numbers in eastern North America), and four species breed in the Southern Hemisphere in the austral summer and migrate north to spend the northern summer (= austral winter) in the North Atlantic (Table 2). The main distributional patterns found among eastern North American birds are elaborated in the Appendix.

*Latitudinal trends in species numbers.*—The number of breeding species in eastern North America increases progressively with latitude from 110 at 25°N (in southern Florida) to 210 at 40°N (near Chesapeake Bay), and then declines progressively to 30 at 80°N (on Ellesmere Island; Fig. 2A). Baffin and Ellesmere islands extend northward from latitude 70°N and are so large and close to other land areas that their isolation is unlikely to account for much of the decline in species numbers at high latitudes. Indeed, species numbers on Baffin Island are no different than those on the nearby mainland. However, some seabird species extend much farther north in western Greenland than in eastern Canada, notably the Razorbill (*Alca torda*; 70° vs. 60°N) and the Atlantic Puffin (*Fratercula arctica*; 80° vs. 55°N).

The low species numbers in Florida may be partly attributable to the peninsula effect (in which species numbers decline from base to tip) and partly to the lack of montane habitats, which occur over much of the latitudinal range farther north. In quadratic regression analyses, latitude accounted for 59% of the variance in overall species numbers in summer (compared with 90% in western Europe), 57% for landbirds alone, 77% for freshwater birds, and only 6% for coastal birds (Table 3). The decline in species numbers from 40°N northward is apparent within each major vegetation zone, including boreal coniferous forest and tundra.

In summer, the largest number of coastal species also occurs in mid latitudes, at 45° to 65°N. This is mainly due to the peak at these latitudes in number of seabird species (rather than shorebirds), which coincides with a similar peak in zooplankton biomass at >500 mg · $m^{-3}$ (Food and Agricultural Organization 1982). Presumably, it is zooplankton on which seabird numbers ultimately depend.

In winter, the latitudinal trend in species numbers is more marked than in summer, and approximately linear, as species numbers decline progressively from 203 at 25°N to 4 at 80°N (Fig. 2B). Of the four species that can be found in winter at 80°N, the Rock Ptarmigan (*Lagopus mutus*) is the same as in Europe at that latitude. The other three—Gyrfalcon (*Falco rusticolus*), Snowy Owl (*Nyctea scandiaca*), and Common Raven (*Corvus corax*)—are absent altogether from Svalbard, which covers this latitude in western Europe. In contrast to Europe, no seabirds occur in winter at 80°N in eastern North America, presumably because of the greater extent of pack ice in North America.

In winter, latitude alone accounts for 95% of the variance in overall species numbers, and for 92 to 95% of the variance in the numbers of species of different habitat categories (Table 3). Unlike the situation in summer, the latitudinal trend in winter is apparent in every biome, with species numbers at successive 5° latitudes declining from 203 to 194 within the southern evergreen zone, from 156 to 86 within the eastern deciduous forest, from 58 to 32 within boreal conifer forest, and from 19 to 4 within the tundra zone. The rate of decline in species numbers with latitude is approximately the same in landbirds, freshwater birds, and coastal birds, although very few land and freshwater birds occur north of 50°N in winter. Seabirds that extend in winter north beyond 55°N include the Razorbill, Black Guillemot (*Cepphus grylle*), Dovekie, and Ivory Gull (*Pagophila eburnea*). These species also winter farthest north among seabirds in Europe, making use of gaps in the pack ice, but it is uncertain to what extent they move south during the period of complete darkness.

The relative contributions made to the total avifauna by birds of different habitats change markedly with latitude. In particular, coastal birds increase in representation from 20 to 67% of total breeding species in summer over the latitudinal range 25° to 80°N, and from 27 to 67% of total species numbers in winter over the range 25° to 65°N, and landbirds and freshwater birds decline in proportion accordingly. In the northern parts of their winter range, where freshwater is frozen, aquatic species are more or less confined to the coast. Examples include Ring-necked Duck (*Aythya collaris*), Lesser Scaup (*A. affinis*), and Ruddy Duck (*Oxyura jamaicensis*), all of which also occur inland farther south.

Comparison of the summer and winter species distributions (Fig. 2) reflects the marked southward shift of many species between summer and winter. In the south, at 25° to 35°N, more species are present in winter than in summer, but from 40° northward, summer species increasingly outnumber winter ones. The same situation holds in western Europe, the switch again occurring at 35° to 40°N. At 70°N in eastern North America, summer species outnumber winter ones by more than six to one, and at 80°N by more than seven to one.

*Proportion of migrants at different latitudes.*—The proportion of breeding species that moves

TABLE 2. Seabirds that regularly occur off eastern North America in spring and/or summer but breed elsewhere.[a]

| Species | Latitudinal range | Main season of occurrence | Nearest breeding areas |
|---|---|---|---|
| Black-capped Petrel (*Pterodroma hasitata*) | 25–30°N | Spring-summer-fall | Caribbean Islands |
| Cory's Shearwater (*Calonectris diomedea*) | 25–50°N | Summer-fall | East Atlantic and Mediterranean |
| Greater Shearwater (*Puffinus gravis*) | 25–65°N | Spring | Tristan da Cunha, South Atlantic |
| Sooty Shearwater (*Puffinus griseus*) | 25–60°N | Summer | Southern South America |
| Manx Shearwater (*Puffinus puffinus*) | 35–50°N | Summer-fall | East Atlantic: Azores, Europe, Iceland |
| Audubon's Shearwater (*Puffinus lherminieri*) | 25–35°N | Summer-fall | Caribbean Islands |
| Wilson's Storm-Petrel (*Oceanites oceanicus*) | 25–60°N | Summer | Southern Ocean |
| Masked Booby (*Sula dactylatra*) | 25°N | Year-round | Caribbean Islands |
| Brown Booby (*Sula leucogaster*) | 25°N | Year-round | Caribbean Islands |
| Magnificent Frigatebird (*Fregata magnificens*) | 25°N | Summer | Marquesas Key off Florida; Caribbean Islands |
| South Polar Skua (*Catharacta maccormicki*) | 25–55°N | Spring-summer-fall | Antarctic |

[a] Other species of accidental occurrence include Yellow-nosed Albatross (*Diomedea chlororhynchos*), Black-browed Albatross (*D. melanophris*), Little Shearwater (*Puffinus assimilis*), Band-rumped Storm-Petrel (*Oceanodroma castro*), White-faced Storm-Petrel (*Pelagodroma marina*), White-tailed Tropicbird (*Phaethon lepturus*), Red-billed Tropicbird (*P. aethereus*), and Red-footed Booby (*Sula sula*).

TABLE 3. Regression relationships between species number (or percent migrants) and latitude. Presence of a quadratic term means that relationship is significantly better fitted by a curve than a line, though in all such cases a linear model also gives a significant fit.[a]

| | Independent variables | | |
|---|---|---|---|
| Dependent variable | Latitude ($x$) | Latitude[2] ($x^2$) | Variance explained ($100r^2$) |
| **All birds** | | | |
| Species number in summer | −2.63 | | 59 |
| Species number in winter | −12.18 | 0.08 | 95 |
| Percent migrants among summer species | 4.33 | −0.03 | 98 |
| Percent migrants among winter species | −3.22 | 0.03 | 87 |
| **Landbirds** | | | |
| Species number in summer | −2.23 | | 57 |
| Species number in winter | −6.39 | 0.04 | 93 |
| Percent migrants among summer species | 5.42 | −0.05 | 96 |
| Percent migrants among winter species | −1.75 | | 91 |
| **Freshwater birds** | | | |
| Species number in summer | −0.45 | | 77 |
| Species number in winter | −1.63 | | 92 |
| Percent migrants among summer species | 3.05 | | 90 |
| Percent migrants among winter species | −0.26 | | 15 |
| **Coastal birds** | | | |
| Species number in summer | 0.05 | | 06 |
| Species number in winter | −1.23 | | 95 |
| Percent migrants among summer species | 1.48 | | 86 |
| Percent migrants among winter species | −0.55 | | 26 |

[a] Analyses omit Southern Hemisphere seabirds that pass the austral winter (= northern summer) in North American waters.

south for the winter increases from about 12% at 25°N to 75% at 60°N (treeline) and 87% at 80°N, a mean increase of 1.4% of species for every degree of latitude (Fig. 3, Table 3). Over most of the latitudinal range, the relationship is approximately linear, but the rate of increase reduces beyond 45°N (Fig. 3). This change of slope is attributable entirely to the pattern in landbirds, among which the proportion of migrants among breeding species does not increase much beyond 45°N (Fig. 3). This is in contrast to freshwater and coastal birds in which the proportion of migrants continues to increase to the northern limits of distribution. On a quadratic regression analysis, latitude accounted for 98% of the variance in this proportion overall, and for 86 to 96% among the birds of different habitats (Table 3). The relationship between the proportion of species migrating south for the winter and the latitude of the breeding area differed significantly between birds of different habitats (landbirds vs. freshwater birds, $F = 25.4$, df = 1 and 16, $P < 0.001$; landbirds vs. coastal birds, $F = 8.1$, df = 1 and 20, $P < 0.01$; freshwater birds vs. coastal birds, $F = 13.6$, df = 1 and 16, $P < 0.01$), with the steepest regression slope for freshwater birds and the shallowest for landbirds. The converse of these relationships is shown in Figure 3 as the proportions of all bird species wintering at different latitudes that move north for the summer. This proportion is greatest in the south, affecting 52% of species wintering at 25°N, and declines linearly northward, affecting 21% of species at 60°N (mostly seabirds) and none at 70° to 80°N, a mean decline of about 1.1% of species per degree of latitude to 70°N. Latitude again accounts for a large proportion of the variance, but not in all groups (on linear regression analysis, 87% overall and 91% among landbirds, decreasing to 26% in coastal birds and only 15% among freshwater birds; Table 3). These relationships held despite the fact that 24% of all species breeding in eastern North America leave the area completely to winter south of 25°N. The relationship between the proportion of species migrating north to breed and the latitude of the wintering area differed significantly between birds of land and freshwater habitats, with a steeper regression slope for landbirds ($F = 13.9$, df = 1 and 8, $P < 0.01$).

*Comparison with western Europe.*—There are some striking parallels between eastern North America and western Europe, notably the pro-

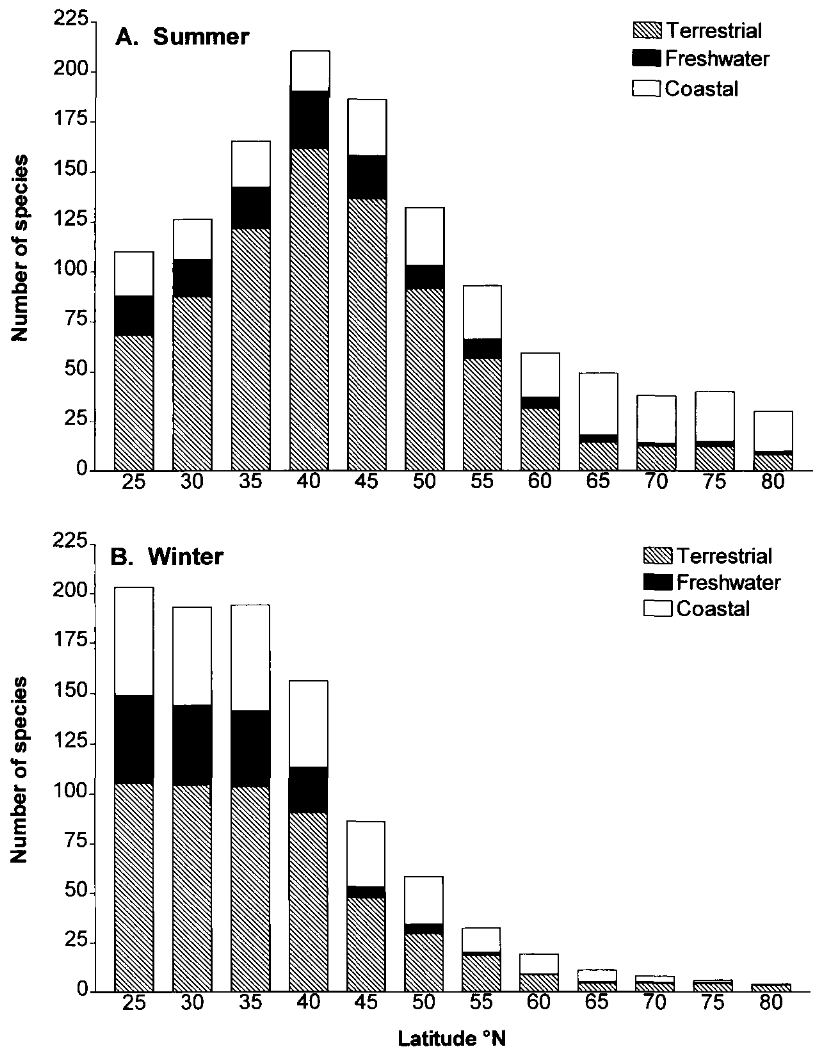


FIG. 2. Number of bird species breeding (A) and wintering (B) at successive latitudes in eastern North Amerca.

gressive increase in summer migrants, and decrease in winter migrants, with increasing latitude. On both continents, the proportion of migrants among breeding species increases with latitude (Fig. 4). The slopes of the regression lines do not differ significantly between continents but the intercepts do ($F = 27.5$, df = 1 and 19, $P < 0.001$). At any one latitude, an average of about 17% more of the local breeding species leaves for the winter in North America than in Europe. This difference reflects the climatic difference between the eastern and western sides of the Atlantic in that, over most of the latitudinal range, winters at any given latitude are colder in eastern North America than in western Europe. A similar pattern holds in winter, when on both continents the proportion of migrant species in the local wintering avifauna decreases linearly with latitude (Fig. 4). Again, the slopes of the regression lines do not differ significantly between continents, but the intercepts do ($F = 9.9$, df = 1 and 16, $P < 0.01$). Throughout the latitudinal range, the proportion of wintering species that leaves for the summer averages around 10% greater in eastern North America than in western Europe.

## DISCUSSION

The trend for species numbers to decrease with increasing latitude is well established in many types of organisms (Fischer 1960, Pianka

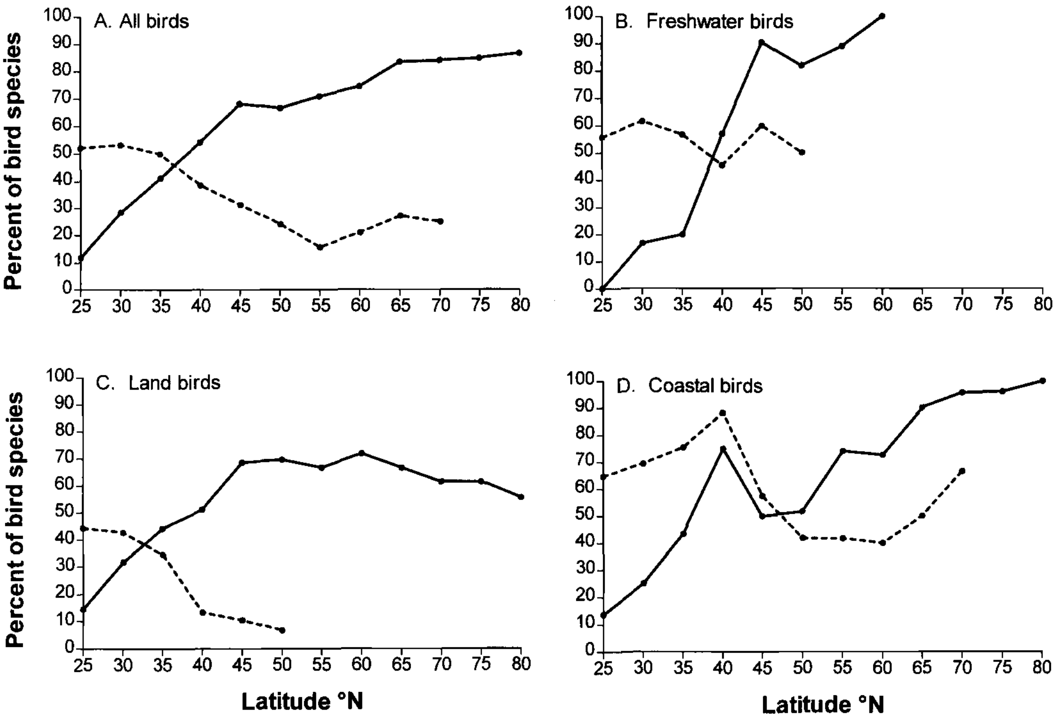


FIG. 3. Proportions of bird species present at successive 5° latitudes in summer that migrate south for winter (continuous line), or in winter that migrate north to breed (dotted line). The two lines are not mirror images of each other because some birds leave eastern North America completely for summer or winter.

1966, Stevens 1989), including birds in North America (Cook 1969, MacArthur 1972, Tramer 1974). In eastern North America in summer, the numbers of breeding species increase between 25° and 40°N, and only then decline northward. The increase between 25° and 30°N refers to the Florida peninsula, and if counts had been made in the wider land areas farther west (i.e. northern Mexico), they would have shown greater species numbers in this latitudinal zone and a progressive decline from 25°N northward (MacArthur 1972). The decline in eastern North America from 40° northward is not apparent in all bird taxa, and forest passerines, in particular, show the reverse trend (Rabenold 1993).

In winter in eastern North America, a northward decline in species numbers is apparent over almost the whole latitudinal range, particularly beyond 35°N. The seasonal difference in distribution patterns reflects the withdrawal of many species from northern regions in winter. Although the precise patterns differ between birds of land, freshwater, and coastal habitats, it would be misleading to place too much emphasis on these differences, because categorization was based on winter (vs. summer) habitats and was inevitably somewhat arbitrary. Many shorebirds classed as coastal on their winter habitats would have been more appropriately classed as landbirds in summer. It is the overall pattern in the avifauna as a whole that is most meaningful. The basis for the latitudinal trend in migration was discussed in our earlier paper, and attributed to a northward increase in the amplitude of seasonal change in food supply (Newton and Dale 1996), following MacArthur (1959), Rabenold (1993), and others.

In both western Europe and eastern North America, roughly one-fourth of the breeding species (23 and 24%, respectively) leave the region completely for the winter, mostly for regions to the south—Central and South America, or Africa, as the case may be. Although most North American species migrate within the New World, two species (Northern Wheatear and Common Ringed Plover) that breed in the Canadian Arctic cross the Atlantic to winter in the

Old World. The assumption is that these species colonized North America from the Old World, via Greenland, and retained their ancestral wintering range. This long migration would be unlikely to persist unless it were favored by selection. The same holds for several species that have colonized Alaska from Asia and still return to wintering areas in the Old World. In contrast, several species that breed in the Old World, such as Eurasian Wigeon, Black-headed Gull, and Lesser Black-backed Gull, now winter regularly in small numbers in eastern North America, perhaps representing the start of a new migration route or colonization of North America.

One of the puzzling features in eastern North America is that, among landbirds, the proportion of total migrants among breeding species does not increase beyond 50°N. This latitude roughly corresponds with the boundary between the eastern deciduous and boreal coniferous forests. Many boreal species live on tree seeds and can stay in some numbers at high latitudes in most winters. This is true of at least half of all passerine species that breed between 50° and 60°N.

Over most of the latitudinal range of eastern North America (as in Europe), some species move south for the winter, while a smaller number of different species from farther north moves in. Above 35°N, the fall emigrants exceed the immigrants so that, at any one latitude, total species numbers are lower in winter than in summer. Below 35°N, the reverse holds and winter species outnumber summer ones. Still, however, more species leave eastern North America completely for the winter than for the summer. Some of those that emigrate totally spend at least part of the winter south of the equator where the seasons are reversed (Terborgh 1989). Thus, they gain the benefits of summer food supplies at both ends of their migration. The same is true for the species that breed in the Southern Hemisphere during the austral summer and then spend the nonbreeding period in the Northern Hemisphere (although still in the tropics).

Considering that about 24% of eastern North American breeding species leave the region completely for the winter, many reaching areas south of the equator, it is striking that only four species (all seabirds) make such a long reverse journey, breeding in the Southern Hemisphere and moving north as far as North America for the southern winter (= northern summer). The same is true in Europe. This difference between north and south, both in the Old World and the New World, may have arisen because the land areas in the Northern Hemisphere are so much greater than those in the south. Birds from a wide longitudinal span in northern North America move southward by migration into progressively narrowing land areas, a process of compression that could force them far to the south. In contrast, birds migrating north from southern South America face ever-widening land areas, so perhaps they can all be accommodated nearer their breeding areas. The reverse situation holds for pelagic seabirds, which have greater sea areas in the south. Thus, perhaps it is no surprise that the only four Southern Hemisphere species that extend in large numbers to North American latitudes during their nonbreeding period are pelagic.

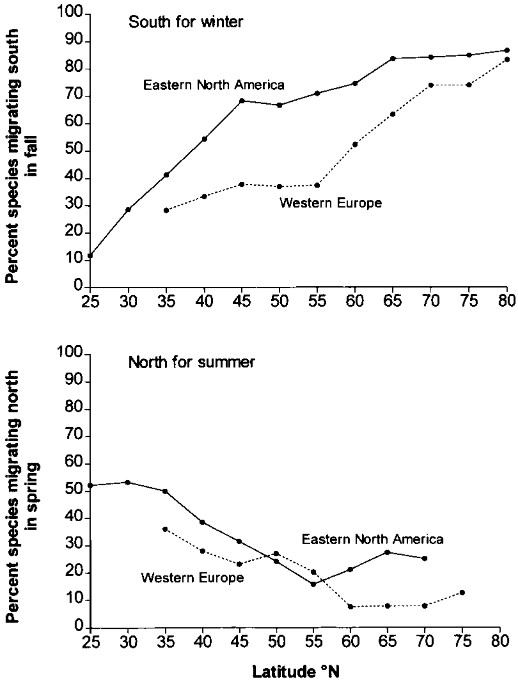


FIG. 4. Proportion of breeding bird species ($y$) at different latitudes ($x$) in eastern North America and western Europe that migrate south for the winter (upper) or north for the summer (lower). For southward migration in eastern North America, $y = -75.05 + 4.33x - 0.03x^2$; $r^2 = 0.98$. In western Europe, $y = 41.49 - 1.03x + 0.02x^2$; $r^2 = 0.97$. For northward migration in eastern North America, $y = 123.72 - 3.22x + 0.03x2$; $r^2 = 0.87$. In western Europe, $y = 55.65 - 0.66x$; $r2 = 0.81$. In the first three relationships, a quadratic equation gave a significantly better fit than a linear one.

Several pelagic seabirds that breed in western Europe can be seen regularly off eastern North America in summer. They are presumably prebreeders, as confirmed for Manx Shearwaters by band recoveries of second-year birds (Perrins et al. 1973). If the equivalent dispersal occurred in reverse, with North American breeding birds reaching European waters in summer, it could be detected only by banding or telemetry, for no pelagic species breed in eastern North America that do not also breed in Europe. Any birds seen in European waters are thus presumed to derive entirely from European breeding colonies.

The total number of species comprising the local avifauna (summer and winter) and the proportion of migrants (summer and winter) were correlated with latitude. In fact, in most analyses, the correlation with latitude was so strong that no other factor included in the same regression model could have accounted statistically for much of the variance in species numbers. This is not to imply that latitude as such has any direct influence on species numbers or on the proportion of migrants. Nevertheless, latitude clearly is a useful surrogate measure that integrates day length, climatic variables, and other variables, all of which influence directly the seasonal changes in avian food supplies on which migration depends (Lack 1954, MacArthur 1959, Herrera 1978, Terborgh 1989, Newton and Dale 1996). The ultimate cause of the latitudinal variation in migration almost certainly is the amplitude of the seasonal variation in food availability, and the extent to which the abundant food supplies of summer are reduced by winter severity. In any one region, the food types available in winter clearly influence which species stay and which ones leave (Newton 1995).

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## LITERATURE CITED

ALERSTAM, T. 1991. Bird migration. Cambridge University Press, Cambridge.

COOK, R. E. 1969. Variation in species density of North American birds. Systematic Zoology 18: 63-84.

FISCHER, A. G. 1960. Latitudinal variation in organic diversity. Evolution 14:64-81.

FOOD AND AGRICULTURE ORGANIZATION. 1982. Atlas of the living resources of the seas. Food and Agriculture Organization, Rome.

GODFREY, W. E. 1966. The birds of Canada. National Museum of Canada Bulletin No. 203, Ottawa.

HERRERA, C. M. 1978. On the breeding distribution pattern of European migrant birds: MacArthur's theme re-examined. Auk 95:496-509.

LACK, D. 1954. The natural regulation of animal numbers. Clarendon Press, Oxford.

MACARTHUR, R. H. 1959. On the breeding distribution pattern of North American migrant birds. Auk 76:318-325.

MACARTHUR, R. H. 1972. Geographical ecology. Patterns in the distribution of species. Harper and Row, New York.

NEWTON, I. 1995. The contribution of some recent research on birds to ecological understanding. Journal of Animal Ecology 64:675-696.

NEWTON, I., AND L. DALE. 1996. Relationship between migration and latitude among west European birds. Journal of Animal Ecology 65:137-146.

PERRINS, C. M., M. P. HARRIS, AND C. K. BRITTON. 1973. Survival of Manx Shearwaters *Puffinus puffinus*. Ibis 115:535-548.

PIANKA, E. R. 1966. Latitudinal gradients in species diversity: A review of concepts. American Naturalist 100:33-46.

PRICE, J., S. DROEGE, AND A. PRICE. 1995. The summer atlas of North American birds. Academic Press, London.

RABENOLD, K. N. 1993. Latitudinal gradients in avian species diversity and the role of long-distance migration. Current Ornithology 10:247-274.

ROOT, T. 1988. Atlas of wintering North American birds. University of Chicago Press, Chicago.

SCOTT, S. L. (Ed.). 1987. Field guide to the birds of North America, 2nd ed. National Geographic Society, Washington, D.C.

SLUD, P. 1976. Geographic and climatic relationships of avifaunas with special reference to comparative distribution in the Neotropics. Smithsonian Contributions to Zoology No. 212.

STEVENS, G. C. 1989. The latitudinal gradient in geographical range: How so many species coexist in the tropics. American Naturalist. 133:240-256.

TERBORGH, J. 1989. Where have all the birds gone? Princeton University Press, Princeton, New Jersey.

TRAMER, E. J. 1974. On latitudinal gradients in avian species diversity. Condor 76:123-130.

WILLSON, M. F. 1976. The breeding distribution of migrant birds: A critique of MacArthur (1959). Wilson Bulletin 88:582-587.

APPENDIX. Types of latitudinal distribution patterns found among eastern North American birds.

R. Present year-round throughout whole latitudinal range. Examples: Ruffed Grouse (*Bonasa umbellus*), Limpkin (*Aramus guarauna*), Great Horned Owl (*Bubo virginianus*), Common Raven (*Corvus corax*), Carolina Wren (*Thryothorus ludovicianus*).

B-R. Present only during summer breeding season in the north of range, year-round in the south. Examples: Turkey Vulture (*Cathartes aura*), Red-tailed Hawk (*Buteo jamaicensis*), Common Moorhen (*Gallinula chloropus*), Killdeer (*Charadrius vociferus*), Black Skimmer (*Rynchops niger*), Common Grackle (*Quiscalus quiscula*).

R-W. Present year-round in the north of range, only during winter in the south. Example: Evening Grosbeak (*Coccothraustes vespertinus*).

B-R-W. Present only during the summer breeding season in the north of range, year-round at intermediate latitudes, and during winter only in the south. Examples: American Black Duck (*Anas rubripes*), Cooper's Hawk (*Accipiter cooperii*), Sharp-shinned Hawk (*Accipiter striatus*), Cedar Waxwing (*Bombycilla cedrorum*), Dark-eyed Junco (*Junco hyemalis*), Song Sparrow (*Melospiza melodia*).

B-W. Summer breeding range beginning immediately to the north of winter range. Examples: Red-breasted Merganser (*Mergus serrator*), House Wren (*Troglodytes aedon*), Rusty Blackbird (*Euphagus carolinus*).

B-P-W. Summer breeding range separated geographically from winter range by a gap in which species occurs only on migration. Examples: Tundra Swan (*Cygnus columbianus*), Black-bellied Plover (*Pluvialis squatarola*), American Tree Sparrow (*Spizella arborea*), Lapland Longspur (*Calcarius lapponicus*).

B. Present in summer breeding season only. Examples: Swallow-tailed Kite (*Elanoides forficatus*), Chimney Swift (*Chaetura pelagica*), Long-tailed Jaeger (*Stercorarius longicaudus*), Barn Swallow (*Hirundo rustica*), Red-eyed Vireo (*Vireo olivaceus*).

W. Present only in winter. Examples: Great Skua (*Catharacta skua*), Black-headed Gull (*Larus ridibundus*), Lesser Black-backed Gull (*Larus fuscus*), Ivory Gull (*Pagophila eburnea*), Eurasian Wigeon (*Anas penelope*).

S. Breeds in the Southern Hemisphere during the austral summer, and moves to the Northern Hemisphere during the austral winter (= northern summer). Examples: Great Shearwater (*Puffinus gravis*), Sooty Shearwater (*Puffinus griseus*), Wilson's Storm-Petrel (*Oceanites oceanicus*).

P. Occurs only on passage migration, breeding and wintering elsewhere. Example: Hudsonian Godwit (*Limosa haemastica*).

V. Vagrant only, occurring mainly or entirely during migration periods. Examples: Curlew Sandpiper (*Calidris ferruginea*), Northern Lapwing (*Vanellus vanellus*), Fieldfare (*Turdus pilaris*).

R = resident (found year-round); B = breeding, W = wintering, P = on passage, or migration; S = Southern Hemisphere species "overwintering" in the Northern Hemisphere during the northern summer; V = vagrant.