

ECOLOGICAL AND DISTRIBUTIONAL ANALYSIS OF NORTH AMERICAN BIRDS

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Lönnerberg (1927) and Mayr (1946) have made the principal attempts to analyse the North American avifauna from the point of view of faunal history. Both being taxonomists, their emphasis was on the distributional history of the taxa and on their possible dispersal routes. In most instances they had to restrict their considerations to the family and subfamily level. The scarcity of avian fossils and the great geological time span they covered warranted this restriction.

Mayr, and implicitly Lönnerberg, were seriously criticized by Wolfson (1955), who states that the interpretations of Mayr would also fit a distributional theory based on the assumption of the drift of continents. Savile (1956), however, countered most of Wolfson's arguments.

These few discussions, however valuable they are, have barely started the zoogeographical analysis of North American birds. One field that deserves attention is the ecological grouping of the elements of this fauna, because such a grouping has its causes rooted in the past history of the fauna and of the habitat, and it permits certain deductions.

HABITAT GROUPS

My original effort in analysis compared the western North American avifauna with that of the western Palearctic region. My field knowledge of birds and their habitats is restricted mainly to these two areas. Later I was able to extend the analysis to the whole North American fauna on the basis of the rich literature available.

The method employed for the establishment of the ecological groups was the following: I went through the A.O.U. Check-list of North American birds and listed the breeding species of each family. For each species the breeding habitat has been defined, using the life history data collected by Bent (1919-1953), the regional faunistic literature of North America, and such ecological monographs as Miller's (1951) for California, and Munro and Cowan's (1947) for British Columbia.

I have tabulated the notes on the species in the form of a card index of the families. This material is deposited in the archives of the Department of Zoology, University of British Columbia, Vancouver, B.C.

Table 1 summarizes the results of this grouping for the non-passerine, and passerine families, respectively. In table 2 the ecological groups are listed, together with the number of species in each and the percentage which the group constitutes in the total number of breeding birds in North America. For each group the number of species common with Palearctic and Arctic Eurasia is given, as well as the ratio of these common elements in the total number of species of the group.

As far as the Palearctic fauna is concerned, it was not possible to complete an ecological analysis of the whole fauna, but, using the monographs of Hartert (1903-1922), Stegmann (1938), and Dementiev and Gladkov (1951-1954), I have drawn up a list of the species and genera that North America has in common with the Palearctic.

North America in my analysis extends, as is customary, from Greenland in the north-east south to the Mexican boundary of the United States. I have left out of the analysis certain southern species that occur only within this area in the lower Rio Grande Valley of Texas; also excluded are those West Indian birds that have their northern boundaries in southern Florida. These birds are representatives of more southern biomes.

Table 3 contains results for the breeding fauna of Europe similar to those given for North America in table 1. For the grouping of European birds I have used the breeding

fauna that is listed in Peterson, Mountfort, and Hollom (1954). The handbooks of Witherby, Jourdain, Ticehurst, and Tucker (1943-44), and Niethammer (1937-1942) were consulted for habitat data in the case of certain species. Table 4 lists the ecological groups of the European avifauna, in an arrangement similar to that of table 2.

I distinguish, for both continents considered, ten major ecological groups within the breeding avifauna. These mainly correspond to the biomes of the northern temperate regions. There is an additional group of unanalyzed birds. These latter species have either very wide ecological tolerance, and thus could not justly be included within any of the ten groups, or they have a very narrow habitat preference but occur in several biomes within the area. A good example of the first is the Raven (*Corvus corax*) and of the latter, the Kingfisher (*Megaceryle alcyon*). The groups are:

1. Arctic sea birds. Within the northern open habitats there is a distinct group of marine and shore species which feed in the pelagic or littoral zones and nest in coastal locations.

2. Tundra birds. Land and shore birds that nest in the tundra biome.

3. Taiga birds. The northern half of the temperate forest belt of North America harbors a distinct group of birds that is very closely associated with the northern coniferous forest belt, or with the muskegs within these forests. This fauna shows great affinity to that of the Palearctic biome of similar nature, the taiga.

4. Forest and woodland birds. Over one-third of the breeding birds in North America live in wooded habitats of diverse nature, that is, in coniferous, mixed and deciduous forests, woodlands, and their ecotones. A more refined subdivision of these faunas was not practical because there are many species that have a wide habitat preference in which often the presence of trees is the only common requirement.

5. Mediterranean scrub birds. Characteristic birds of the western chaparral, piñon-juniper, and related communities, of the eastern pine-oak scrubs in North America, and of similar formations such as macchia and mequis in Europe. These birds do not require high arboreal vegetation.

6. Desert birds. This group in North America is solely composed of birds of the desert scrub and sage brush, while the closest comparable group in the Palearctic is, as a whole, more adapted to the open, xeric habitats of true deserts.

7. Open grassland birds. Birds of all the open habitats, except those few on the alpine meadows, are included within this group.

8. Montane birds. Inhabitants of alpine meadows, and rocky, alpine or montane ledges form a very small group in North America. In Europe, on the other hand, the Tibetan fauna of Stegmann (1938) is a substantial element of the Palearctic avifauna, with disjunct type of ranges of the constituting species throughout the highest mountain peaks.

9. Temperate sea birds. Here belong all pelagic and marine littoral species of the temperate Atlantic and Pacific coasts. This group will not be discussed in this paper.

10. Limnic birds. All aquatic inland species and those of the wet succession zones (lakes, ponds, riversides, marshes, meadows, and freshwater littoral habitats) as long as the plant community is a member of a hydrosere and the bird does not require the presence of trees for its nesting.

COMPARISON OF THE TWO AVIFAUNAS

Comparing the North American avifauna with that of Eurasia, we find that slightly over one-fourth of the North American species are common to these two continents and that 43 per cent of the North American genera also are represented in arctic and temperate Eurasia (table 5).

Cuculidae				3									2
Tytonidae												1 (1)	1 (1)
Strigidae		1 (1)	3 (3)	10 (1)		1	2 (1)						10 (8)
Caprimulgidae				4		2							4 (1)
Apodidae				2							1		3 (1)
Trochilidae				13								1	9
Trogonidae				1									1
Alcedinidae												2	2
Picidae			2 (1)	18									10 (2)
Families: 41 (33)	36 (32)	41 (31)	26 (16)	80 (2)	3	11	13 (1)	4	30 (18)	78 (23)	9 (6)		184 (100)
Passerine Birds													
Tyrannidae			3	21	2	3							10
Alaudidae							1 (1)						1 (1)
Hirundinidae				4 (1)							4 (1)		7 (2)
Corvidae			1	7 (1)	3	1					1 (1)		7 (4)
Paridae			2 (1)	9 (1)		1							3 (1)
Sittidae			1 (1)	3									1 (1)
Certhiidae				1 (1)									1 (1)
Chamaeidae					1								1
Cinclidae												1	1 (1)
Troglodytidae				4 (1)		1				2	2		8 (1)
Mimidae				3	1	5							4
Turdidae			2 (2)	10							1 (1)		7 (5)
Sylviidae			3 (2)	1		1							3 (2)
Motacillidae		2 (2)					1				2 (2)		2 (2)
Bombycillidae			1 (1)	1									1 (1)
Ptilonotidae				1									1
Laniidae			1 (1)	1									1 (1)
Vireonidae				9	2								1
Parulidae			8	40	1	1				1			15
Icteridae			1	9		1	3			3			10
Thraupidae				4									1
Fringillidae		5 (3)	15 (5)	21	9	4	14	2 (1)		6			33 (8)
Families: 22 (14)	7 (5)	38 (13)	149 (5)	19	17	19	2 (1)		12	11 (5)			119 (31)
Total	63 (47)	36 (32)	48 (36)	64 (28)	229 (7)	22	29	32 (2)	6 (1)	30 (18)	90 (23)	20 (11)	303 (131)

¹ In each avifaunal group the number of species common with Eurasia is in parentheses.

The portion of the Holarctic passerines in the North American passerine species group is only 11 per cent, and even that of the genera common with the Palearctic amounts to only 23 per cent. Thus the passerines of the two continents, as was known long ago, are much less related than the nonpasserine birds. This situation may be explained by the substantial barrier that separated the two continents, which acted selectively on the dispersal of the passerines (primarily arboreal birds) and the nonpasserines, the majority of which are non-arboreal in North America. We shall see from the following discussion that an ecological and distance barrier has indeed been operating

Table 2
Analysis of North American Avifauna

Habitat group	Number of species	Per cent of total avifauna	Species in common with Eurasia	Per cent in common of total species in group
Arctic sea birds	36	5.9	32	86.5
Tundra birds	48	7.9	36	75.0
Taiga birds	64	10.6	28	43.8
Forest and woodland birds	229	37.9	7	3.1
Mediterranean scrub birds	22	4.0
Desert scrub birds	29	4.8
Open grassland birds	32	5.3	2	6.2
Montane birds	6	1.0	1	16.7
Temperate sea birds	30	5.0	18	62.0
Limnic birds	90	14.9	23	25.6
Unanalyzed birds	20	3.3	11	55.0

in the case of the montane, grassland, desert and scrub habitats (chiefly populated by birds of arboreal origin) and that the composition of the temperate forest fauna also indicates the presence of some kind of barrier in the latter part of the Tertiary. The nonpasserine avifauna of North American limnic habitats, on the other hand, shows a closer relationship with that of the Palearctic.

We cannot, however, state definitely the nature of such a selective barrier. Recent studies in comparative ethology of birds indicate that a barrier may be of intrinsic nature. On the one hand, the faculty of dispersal is dependent on the specific degree of *philopatry*, that is, the faithfulness to the previous breeding range. On the other hand, students of bird migration realize how important a "psychological" barrier a strange habitat (sea or grassland) is for a forest bird even during the routine annual migration. Until we obtain a general idea of the scope and importance of these behavior patterns in dispersal of passerine and other birds, their role in past distribution cannot be properly estimated.

According to present paleontological knowledge (Wetmore, 1955), a great number of the living bird genera had already evolved by early and middle Tertiary, and many species, especially of the nonpasserines, are also known from Tertiary fossils. In view of the great age of the nonpasserine forms, their dispersal even across water or other geographical or ecological barriers has been possible for a long time span. There are very few passerine fossils from the earlier part of the Tertiary (Howard, 1950). The assumption that the evolution of passerines is much more recent than that of the nonpasserine orders (Mayr and Amadon, 1951) is supported by the fact that passerines show much less interchange of species between North America and the Palearctic area.

A third possible cause of the discrepancy between the passerine and other bird

groups lies in the present apparently high rate of speciation in the passerines. The species-genus ratio within North American nonpasserines is 1.8, whereas for the passerines it is 2.3. The ratio for European nonpasserines is 2.0, for passerines, 2.4.

ARCTIC SEA BIRDS AND TUNDRA BIRDS

The similarity of the avifaunas is much the greatest between the two continents in the two ecological groups of the arctic. The present arctic habitats are circumpolar, and the radius of the Arctic Ocean is quite short, facilitating faunal exchange between the continents. Stegmann (1938) assumes that most of the arctic avifauna originated in the north of eastern Siberia and western Alaska, that is, in northern Beringia. This view agrees with that of Hultén (1937) who studied arctic and boreal plant distribution.

The main distribution centers of arctic sea birds are the North Atlantic and the North Pacific oceans and the Arctic Ocean north of Beringia, hence the high uniformity of the faunas on the continents concerned. The tundra was apparently divided into separate refuges during the Pliocene and Pleistocene ice ages, some of them lying north and others south of the glaciated area (Johansen, 1956). Isolation of these refuges from one another would account for many of the differences in species and genera.

TAIGA BIRDS

The affinities of the taiga (northern [boreal] coniferous biome) avifauna of North America can be expressed in the following figures: out of 40 genera 65 per cent (26) are in common with the Palearctic; out of 64 species 60 per cent (38) belong to Holarctic genera; out of 64 species 45 per cent (29) have a Holarctic range.

This group of birds includes 16 limnic nonpasserines, birds of the northern bogs, 11 of which occur in the Palearctic region. Although I did not analyse them further, they have been classified here because of the similarity of their range with those of the majority of the coniferous forest birds. The similarity is strengthened by the fact that all the 16 are widespread across the continent within the biome considered.

Several of the "taiga genera" have a predominantly western distribution, and their range includes the "Canadian" zone of the mountains in the southwest, as in *Strix*, *Nucifraga*, *Zonotrichia*. This is easy to understand, if we postulate that large taiga refuges could survive warm interglacials in this mountainous area. The majority of the dendrophilic taiga species are widespread across North America. *Strix nebulosa* does not reach the eastern limits of the taiga belt, and another six species are markedly western in their distribution. On the other hand, there are seven species with an eastern distribution area. Remarkably enough, these six western and seven eastern taiga birds form the bulk of the 15 dendrophilic taiga birds that belong to originally American families, namely the Tetraonidae, Parulidae, Tyrannidae, and Icteridae (North American and Pan-American elements of Mayr, 1946).

According to Stegmann (1938) the taiga birds of Holarctic distribution point toward affinities through the Bering Strait area. At Tertiary periods, and in the Quaternary, when the strait was dry, he postulates a continuous coniferous belt across the intercontinental land bridge, which served the dispersal of taiga birds as well. This, or these bridges, account for the high number of genera and species common to the Holarctic boreal forest. Stegmann shows also that the taiga fauna is richest in eastern Siberia which suffered least during the Pleistocene glaciations. There is a gradual impoverishment of the avifauna toward the west; only 28 of the 55 east Siberian taiga species reach the eastern border of Finland.

It is interesting that only 13 species of the foregoing 55 species reach North America, in spite of the much shorter distance from east Siberia, and in spite of the land bridge

Table 3
Ecological Groups of the European Avifauna Compared with the
Birds of North America¹

Nonpasserine Birds

Habitat group	Arctic sea	Tundra	Taiga	Forest	Scrub	Desert scrub	Grassland	Montane	Temperate sea	Limnic	Unanalyzed	Genera
Gaviidae			4 (4)									1 (1)
Podicipitidae										5 (3)		1 (1)
Procellariidae									4 (1)			1 (1)
Sulidae									1 (1)			1 (1)
Phalacrocoracidae									1 (1)	2 (1)		1 (1)
Pelecanidae										2		1 (1)
Ardeidae										9 (2)		6 (4)
Ciconiidae				1						1		1
Plataleidae										2 (1)		2 (1)
Phoenicopteridae										1		1
Anatidae	4 (4)	11 (5)	7 (5)						1	15 (6)		17 (13)
Aegypidae				1		1		2				4
Accipitridae			1 (1)	14 (1)			3	1 (1)		3 (1)	2 (2)	11 (7)
Falconidae		1 (1)	1 (1)	5				2			1 (1)	1 (1)
Tetraonidae		2 (2)	3					1				4 (1)
Phasianidae					3							4
Turnicidae					1							1
Gruidae										2		2 (1)
Rallidae										10 (1)		6 (4)
Otididae							3					2
Haematopodidae									1 (1)			1 (1)
Charadriidae	1 (1)	3 (2)								4 (3)		3 (2)
Scolopacidae		10 (6)	4	2						10 (1)		11 (6)
Recurvirostridae										2 (1)		2 (2)
Phalaropodidae		2 (2)										1 (1)
Burhinidae						1						1
Glareolidae						1	2					2
Stercorariidae	4 (4)											1 (1)
Laridae	6 (6)								6 (2)	12 (5)		8 (7)
Alcidae	5 (5)								1 (1)			4 (4)
Pteroclididae						3						2

Columbidae					4				1					2	(1)											
Cuculidae					2									2												
Tytonidae					1	(1)								1	(1)											
Strigidae	1	(1)	3	(3)	6	(1)	1		1	(1)				9	(8)											
Caprimulgidae					1		1	1						1	(1)											
Apodidae					1									1												
Alcedinidae														1												
Meropidae										1				1												
Coraciidae					1									1												
Upupidae					1									1												
Picidae				2	(1)	8								5	(2)											
Families:	35	(25)	20	(20)	30	(19)	25	(15)	48	(3)	6	7	12	(1)	8	(1)	15	(7)	80	(25)	5	(3)	129	(76)		
Passerine Birds																										
Alaudidae			1	(1)		1				4	4													6	(1)	
Hirundinidae											1		2								2	(2)		4	(2)	
Oriolidae						1																		1		
Corvidae				2		5	(1)	1					2								1	(1)		7		
Paridae				2	(2)	7		1													1			4	(1)	
Sittidae						2							1	(1)										1	(1)	
Certhiidae						2	(1)						1											2	(1)	
Troglodytidae						1	(1)																	1	(1)	
Cinclidae																							1	1	(1)	
Turdidae					3	7		3			1		3								1	(1)	1	(1)	8	(3)
Sylviidae					2	(1)	13	11			1										8			9	(1)	
Regulidae					1	(1)	1																	1	(1)	
Muscicapidae						4																		1		
Prunellidae						1							1											1		
Motacillidae			1	(1)		1			1		2	(1)	1								1	(1)	1	(1)	2	(2)
Bombycillidae					1	(1)																		1	(1)	
Laniidae						4	(1)	1																1	(1)	
Sturnidae						1		1			1													1		
Fringillidae			4	(3)	11	(5)	6	3		1	1		2	(1)						1				12	(8)	
Passeridae										2	2													2		
Families:	20	(15)			6	(5)	22	(10)	57	(4)	21	8	13	(1)	13	(2)				12	(2)	8	(5)	67	(25)	
Total	55	(40)	20	(20)	36	(24)	47	(25)	105	(7)	27	15	25	(2)	21	(3)	15	(7)	92	(27)	13	(8)	196	(101)		

¹ In each avifaunal group the number of species in common with North America is in parentheses.

Table 4
Analysis of European Avifauna

Habitat group	Number of species	Per cent of total avifauna	Species in common with North America	Per cent in common of total species in group
Arctic sea birds	20	4.8	20	100.0
Tundra birds	36	8.6	24	66.7
Taiga birds	47	11.6	25	53.2
Forest and woodland birds	105	25.2	7	6.7
Mediterranean scrub birds	27	6.5
Desert birds	15	3.6
Open grassland birds	25	6.0	2	8.0
Montane birds	21	5.0	3	14.3
Temperate sea birds	15	3.6	7	46.7
Limnic birds	92	22.2	27	29.3
Unanalyzed birds	13	3.1	8	61.5

available at times. However, these 13 species are all, without exception, members of the group of 23 most widespread taiga species that reach western Scandinavia as well. Therefore we have to postulate a long-lasting gap in communication between the Palearctic and Nearctic taigas, since none of the eastern endemic Siberian species reached Alaska. The communication has apparently been resumed only in quite recent time, since, besides the widespread Holarctic taiga birds, there is only a small group that got a foothold on the opposite side of the Bering Strait.

Amongst Palearctic birds pioneering North America, *Parus cinctus*, *Luscinia cyane-cula*, *Phylloscopus borealis*, *Emberiza rustica* are the taiga species, while *Motacilla alba* and *M. flava* are also known from wet and more open communities of this biome. *Oenanthe oenanthe* is ubiquitous while the exclusively tundra nester *Anthus cervinus* seems to be the most recent crosser and is known to nest only at Cape Wales opposite Siberia (Bailey, 1948). Only one taiga species is known that successfully crossed the strait the other way; this is the Gray-cheeked Thrush (*Hylocichla minima*) with a breeding population in Siberia. Judging from the small ranges on their new continent we may assume that at least most of these nine passerines crossed the strait during the recent postglacial time without a land bridge. Presumably a land bridge was not necessary for many an earlier Palearctic immigrant either.

Table 5
Relation of Passerine and Nonpasserine Birds in the North American Avifauna

		Genera	Species
North American avifauna	Total number of birds	303	605
	Number of nonpasserine birds	184	331
	Number of passerine birds	119	274
	Per cent of passerines in total number	39	45
Avifauna in common to North America and Eurasia	Total number of birds in common	131	159
	Per cent in common	43	26
	Number of nonpasserine birds in common	100	129
	Number of passerine birds in common	31	30
	Per cent of nonpasserines in common of total number of North American nonpasserines	54	39
	Per cent of passerines in common of total number of North American passerines	26	11

Summing up, the present (postglacial) infiltration of Eurasian taiga birds is apparently far separated in time from the earlier invasion (or invasions), as intermediate types of range are not present in North America. The homogeneity of the majority of ranges indicates in my opinion that the fauna is much older in North America than the recent glaciation.

On the other hand, it seems that most boreal forest birds of more southern (American) origin became members of this biome quite recently, probably during Pleistocene glaciations that superimposed the taiga belt on refuges of more southern types of forest communities. Therefore they were late, or retarded in their spreading, and are still limited to the western or eastern parts of the taiga belt, respectively. Detailed ecological and speciation studies are needed to reveal how stable their east-west limits are.

FOREST AND WOODLAND BIRDS

This large group, 38 per cent of the entire North American avifauna, shows an entirely different picture, as far as species and genus composition is concerned. The number of species that are common to the forest faunas of the old and new world is negligible—7 species, making only 3.1 per cent of the total (table 2). Twenty per cent of the species belong to genera that are of Holarctic distribution, and the number of these genera is also 20 per cent of the total number of forest bird genera.

These are the numerical facts. They necessitate the drawing of a sharp border between the northern coniferous forest biome, and the other forested biomes. The North American temperate forest and woodland communities have only some old affinities with the old world (Palearctic) avifauna that are expressed mainly on the family and sub-family level, as shown by Mayr (1946).

Knowing that the flora and mammal fauna of the northern temperate, coniferous and deciduous forests show far reaching similarities throughout their entire Tertiary evolution, we have to look for particular reasons that explain the striking paucity of avifaunal exchange between the northern continents. One possible reason could be the extinction of such temperate forest birds as a result of habitat discontinuity during the extremes of the glacial epochs. It would be worthwhile to examine the extent of the North American biomes during the Pleistocene, as Moreau (1955) did for the Palearctic habitats. Dillon (1956) shows that habitat restrictions in North America were considerable during the Wisconsin glaciation, and presumably they were also during the previous ones. However, because of the width of the southern, unglaciated part of the continent, mass extinction of temperate forest birds at such southern latitudes is not very likely.

It is therefore not likely that extinction alone could account for the small number of common elements. There must have been some kind of barrier that separated the two continents at the time when both were covered mainly with a uniform arctotertiary forest. We can clear the ground by first eliminating those barriers which could not have been operating.

Most obviously one may suppose that since middle Tertiary, when a gradual cooling of the polar area took place, this climatic barrier hindered the free intercommunication of the two northern continents, both in the Bering Strait and in the North Atlantic area. This cooling, however, did not mean permanent extermination of the forest in the north. It meant in fact the establishment of the taiga belt, consisting of the more adaptable (and already adapted) conifers of the northern arctotertiary forest. If this uniform taiga belt had persisted for a long time during the close of the Tertiary, its avifauna would have had much greater opportunity for interchanges between the two continents. However, most of the existing affinities in the taiga, as we have seen, are explainable by Quaternary connections during the interglacial periods. In other words, if the Bering

Strait area had been a continuous taiga belt for a longer time, excluding by its presence the intercommunication of the temperate forests, its ornithofauna would have been much more related than it is known to be, both on the generic and the specific level. Therefore the assumption of a climatic barrier raises more questions than it would solve.

We can also exclude distance as a factor hindering animal distribution in this instance. While the distance between the east Asiatic temperate forest and northwestern North America is considerable, the distance between the former and the western Palearctic is still greater. Yet these two deciduous forest areas of the Palearctic show so much similarity in their forest avifauna that the two could be considered as disjunct remnants of the common, arctotertiary temperate forests, separated by the Quaternary intrusion of the tundra and taiga and the central Asiatic dry belt. The European and Chinese forest faunas have 12 common species with continuous range and another 13 species or subspecies pairs with disjunct ranges. The almost complete lack of similarly related birds linking the east Asiatic forest and that of western North America would then indicate that the faunal connection between the two had been very remote.

An assumption that time prevented the mixing of the two faunas cannot stand, if we look again at the zoogeographic maps of either the Palearctic area or North America. Wherever there is no geographical or ecological barrier, neighboring faunas do mix to a great extent during a relatively short period of time. While it is certainly true that some species are less dynamic and are slow in their dispersal, the majority show a quick adjustment following even minor climatic fluctuations (Kalela, 1949).

It could also be thought that because of the narrowness of the connecting belt in Beringia the two faunas excluded each other by ecological competition, allowing only a slight infiltration into empty, vacant niches. We could very easily discard even this possibility on the following basis: In a postulated ecological competition of two balanced faunas, there certainly would be a number of species that were superior to the original ones and which would have replaced them in part of their habitat at least. However, no such occurrence is known. On the contrary, both areas have a host of vacant niches. This is reflected in the fact that life forms that are well evolved in the one are lacking in the other of the two faunas.

As examples of this may be mentioned the muscicapid flycatchers that are exclusively hole-breeders in the Palearctic whereas tyrannid flycatchers of the Nearctic are mainly open breeders. The hole-breeding swallow species are lacking on the Asiatic side of Beringia. The small Eurasian kingfisher exploits the minnow and small fry of the creeks, whereas the large North American *Halcyon* utilizes a larger size class of fish prey, yet neither one penetrated the empty niche on the other side of Beringia.

My chief argument is, however, that, if ecological competition be effective for a long period between species making the same demand, the result is not likely to be extinction, or exclusion from an area, but speciation (Lack, 1949; Mayr, 1949; Udvardy, 1951).

Climatic, ecological, time, and distance barriers excluded, I can only think of one possibility hindering faunal migration across Beringia and that is a water barrier. Large bodies of water are not easily crossed by land birds, especially by forest birds of relatively weak flying ability. The probabilities of crossing them successfully by homogeneous faunas is very slight and is dependent on geological time (Simpson, 1952). Occasional vagrancy and drifting affords the only chance for resident forest birds. While it is certainly true that drifting allowed effective population of oceanic islands, as remote as the Galápagos or the Hawaii group, the drift-dispersal established unbalanced faunas with great possibilities of subsequent local speciation. Other examples, like the avifaunal barriers of water gaps along Wallace's line (Mayr, 1944), or the failure of drift-visitors of the North American avifauna to establish themselves in Europe since

the Pleistocene, strengthen the assumption that a water barrier would be an effective means of preventing the mixture of temperate forest faunas across Beringia.

To coordinate this assumption with the known history of the Bering bridge (Simpson, 1947; Axelrod, 1952) is difficult, since, besides Recent times, the period with "decreased intermigration" of mammals are the early Pliocene and the late Oligocene.

The same argument can be applied for an Atlantic land connection of the two continents. The dissimilarity of the forest avifauna alone excludes the existence of an early or middle Tertiary land bridge, such as the followers of the continental drift theory (Wolfson, 1955) maintain. We have to contend, however, with the assumption that Greenland might have been connected with Iceland (Lindroth, 1956, presents new zoogeographical evidence) and the latter certainly has been in land connection with northern Eurasia as late as the Pleistocene. The lack of species common to the two areas that might have used this route during interglacial periods suggests strongly a water gap, or water gaps, even in this area.

Lastly, a consideration is necessary of each of the seven species that occurs throughout the temperate forests of Holarctica. *Accipiter gentilis*, *Pica pica*, *Parus atricapillus*, *Certhia familiaris*, and *Troglodytes troglodytes* occur partly in the taiga belt as well; thus their dispersal through the taiga was quite feasible. *Hirundo rustica* is classified as a woodland bird, but it is not dependent on the presence of forest. The only bird that in North America is largely dependent on the deciduous woods is *Asio otus*. In the old world, however, it is an inhabitant of woodlands and forest edges of all kind, being a nest parasite of the corvids. It occurs in coniferous stands as well, and it also could have spread over through coniferous, taiga types of parklands. Thus not a single temperate forest dweller is common to all parts of the Holarctic which could not have used the taiga as an ecological land-bridge between two otherwise separate temperate forest areas.

In conclusion, no satisfactory explanation has been found for the fact that the temperate forest avifauna of North America shows no specific connections with that of Eurasia. This circumstance, contrasted with the great similarities in the vegetation of the biome, and with its known history, means that either there was a barrier that was easily crossed by plants (Chaney, 1947) and mammals (Simpson, 1947) but which was insuperable for birds, or that the evolution of forest avifauna on the generic and species level happened mainly during relatively recent, Quaternary times, when the existence of a climato-ecological barrier was probable.

SCRUB

There is some difficulty in separating the avifauna related to the mediterranean type of coherent scrub from that of open woodland on the one hand and of desert scrub on the other. Therefore the numbers and percentages (tables 2 and 4) should be taken as tentative; fortunately this situation does not seem to alter the general conclusion which is the same for desert scrub and for the less arid, and more coherent type of scrub. No North American species out of the 22 scrub types occurs in the Palearctic avifauna, and only three out of 19 genera are shared by the two continents—*Falco*, *Corvus*, and, if we are to rely on Mayr's (1946) view, *Chamaea*. About half of the scrub birds belong to genera which primarily, or mainly, are forest inhabitants; there are only seven genera monotypic in North America which seem to be exclusive inhabitants of scrub.

DESERT SCRUB

The avifauna of the sagebrush and desert scrub shows no relations to the xerophil avifauna of the Palearctic, neither at the specific nor at the generic levels. The 29 species belong to 24 genera; of these, 22 are monotypic genera. Eleven genera are essentially

confined to the desert scrub habitat whereas 10 have related species in the woodland, and one has relatives in the mediterranean scrub habitat.

According to the paleobotanical evidence and its evaluation by Axelrod (1950, 1952), the chaparral scrub is of middle Tertiary origin, which then occurred under arid local conditions within the madrotertiary flora and its northern ecotone. The desert vegetation is much more recent, beginning to differentiate at the end of the Cenozoic.

These facts would suggest that the avifaunal specializations of the mediterranean scrub should be older and consequently richer in forms than that of the desert avifauna. This is not the case, as the tabulated data show. It seems, however, that the environmental conditions of the scrub do not necessitate a high degree of specialization. The chaparral is often heavily mixed with different kinds of woodlands and combined utilization of the two is also possible by many bird species (Miller, 1951). Hence there is a small number of scrub endemics.

In the desert avifaunal group the number of genera that are "desert specialists" is not higher than the number of scrub genera. The grouse, dove, cuckoo, owl, nighthawk, flycatcher, tit, wren, and thrasher genera are mostly thicket dwellers or ground feeders for which nest-sites are provided by the desert scrub. The genus *Toxostoma*, which has been intensively studied by Engels (1940) with respect to structural adaptations, seems to show that desert birds are late or recent adaptations of forest genera. There are species within this genus, woodland birds, that progress predominantly by flight and feed on the ground. The desert species progress mainly by running instead of flying and they scratch and dig after food. The species intermediate in their structural and habit adaptations live in intermediate habitats.

Because of the relatively young age of the deserts in North America, we could not expect greater adaptations or larger numbers of the desert-adapted birds. It is interesting to note that environmental physiological experiments on desert birds point also in the same direction, since the members of the desert avifauna studied are not specially adapted to extremely arid conditions (Bartholomew and Cade, 1956).

Although this preliminary survey of the avifauna of arid habitats is far from being complete without considering the birds of the Mexican and South American desert and scrub habitats, this much seems clear, that desert, and even scrub adaptations, are relatively few, and they represent recent departures from forest (woodland) dwelling types of New World origin. I abstain from a comparison with the old world desert scrub fauna, because I am not familiar with this habitat in the Palearctic.

GRASSLAND AND OPEN HABITATS AND THEIR BIRDS

If we consider the recent extent and uniformity of the North American grassland, its avifauna is surprisingly poor. I could only group here 32 species (table 1), some of them very recently evolved species pairs (*Tympanuchus*, *Sturnella*, some fringillids).

Two species are in common with the Palearctic, *Asio flammeus* and *Eremophila alpestris*. Since both are members of the circumpolar Arctic fauna, the assumption of their recent arrival on this continent and their spreading here via the Pliocene-Pleistocene tundra is beyond doubt (Mayr, 1946). Of the 26 genera another four non-passerine genera occur in common: *Buteo*, *Falco*, *Charadrius* and *Numenius*. All these are distributed in the Arctic and in arctic ecotones as well. The grassland species might be convergent adaptations. A fifth genus in common is the mainly tundra-inhabiting passerine genus *Calcarius*.

The North American endemic grassland birds consist of three grouse, a diurnal and a nocturnal bird of prey, two icterids, and a small number of emberizine sparrows.

If we compare the grassland birds with those of the western Palearctic (table 2)

the numerical and percentage ratio is not unfavorable for the New World. There are, however, three circumstances that indicate the much greater age of the Eurasian open country adaptations: (a) In the western Palearctic (table 2), besides the 25 grassland specialists, there is a substantial group of 15 bird species that live in the open desert habitat (sandy, stony, and alkali deserts). (b) Both these open-country bird groups are still more richly represented in the central part of the Palearctic, which is not analyzed here, where the grassland and desert belts are most developed. (c) There are amongst the grassland-desert birds of the Old World seven groups (some of them distributed in several zoogeographical regions, others restricted to the Palearctic) that are members of families that are as a whole adapted to open country. Their existence implies that bird evolution under open and xeric conditions has a much older history in Eurasia than in the New World, provided extinction in North America of most open country forms has not been the case, which is very unlikely. The Otidae, Burhinidae, Glareolidae, Pteroclididae, and Meropidae are the nonpasserine families concerned, whereas the Alaudidae and Motacillidae are the two passerine groups. Each of the latter two has an arboreal species as well, and it is outside the scope of this paper to decide whether these are primitive or reverting forms.

The open-desert avifaunal group is entirely lacking in North America, and this circumstance has to be kept in mind in further biogeographical work of the arid habitats of this continent.

LIMNIC BIRDS

This fauna is dominated by non-passerine birds. The 78 non-passerine species show a high degree of affinity to the limnic bird fauna of the Palearctic. Nearly 30 per cent of the species (23 species) are shared by the two regions. Seventy per cent of the genera in North America have representatives in the Palearctic as well. Finally, there is only one out of the 17 families that does not occur in Eurasia. Many zoogeographers omit the treatment of water bird families as unanalyzable elements because of their high degree of cosmopolitanism. At the present moment I have nothing more to suggest concerning their distributional history. If, however, we contrast them with the passerine inhabitants of the same environment, we find it remarkable that the 12 passerine species of North America have no relations whatsoever to the 12 passerines of the limnic habitat series of the western Palearctic. The two marsh wrens (*Telmatodytes* and *Cistothorus*) are members of this group. The Yellow-throat (*Geothlypis trichas*) is the only warbler which is probably justified for inclusion here (Mayr, 1946). Three icterids use the marshes for feeding and nesting as well, and finally there are six limnic buntings and sparrows.

The European group consists of a tit, a thrush, a wagtail, a sparrow, and a series of eight sylviid warblers. Still more of this latter group occur in the eastern part of the Palearctic, which has not yet been analysed.

I was not able to locate a comprehensive literature that deals adequately with the vegetational history of the marshes such as there is for forests, scrub and desert. The paleobotanical data available show that the characteristic genera of the marsh vegetation (*Typha*, *Scirpus*, *Phragmites*) had already evolved in the late Mesozoic and early Tertiary (Lamotte, 1952; Gothan and Weyland, 1954). Thus we might assume that the marsh habitat as such is at least as old as the angiosperm forest habitat on both continents.

Therefore the circumstance that the small passerine group utilizing marshes has no species in common between the New and the Old World poses a problem similar to that encountered in analyzing the two temperate avifaunas. The absence of every group on the other continent suggests an empty niche. Thus in North America there is an opening

for specialized small insectivores feeding on sedge and reed; in the Old World there is a niche vacant for the icterid type of marsh nester and feeder and for the swamp sparrows. It is also notable, that these limnic passerines are all very recent adaptations to the habitat. In many instances the genus is still dendrophilic, and only the species concerned is occupying the emergent, weedy or grassy vegetation.

UNANALYZED GROUP

Since some members of this group are shared by the Palearctic region and North America, we should see whether their distributional and ecological features might add something to what we have learned from the groups already discussed. The unanalyzed group in common contains, tentatively, the exclusively riparian forms, a few birds specialized for rocky habitat, and the true cosmopolitans and ubiquitous birds within the temperate and cold regions. Eleven out of 20 species are shared by the two geographic areas considered.

Forms of wide ecological tolerance that presently also inhabit the arctic are *Haliaeetus albicilla*, *Falco peregrinus*, *Corvus corax*, *Oenanthe oenanthe*, and two species of *Motacilla*. Presence in the Palearctic taiga belt explains the intercontinental distribution of *Histrionicus histrionicus*, *Aquila chrysaetos*, *Pandion haliaetus*, and *Riparia riparia*. Thus only one common element of the group remains, *Tyto alba*, which is cosmopolitan in its distribution but avoids the arctic and subarctic habitats.

CONCLUSIONS AND SUMMARY

An ecological analysis of the North American and European avifaunas and a comparison of the former with the whole of the Palearctic avifauna has led to the following conclusions.

The passerines of the two continents are much less related on the species and genus level than the birds of nonpasserine orders. This might be true for one or all of the following reasons: (a) The primarily arboreal passerines of the two continents were separated by some substantial barrier, whereas nonpasserines crossed easily. (b) The evolution of the passerines is much more recent than the evolution of nonpasserine orders. (c) Speciation in passerines probably occurred at a much faster rate than that in the nonpasserine orders.

Ten ecological groups were established within both faunas, and eight of the groups show similar structure of the avifaunas in similar habitats in the two continents.

The Palearctic montane fauna consists of numerous species (21 in Europe alone), has a disjunct type of range over the high mountain chains, and centers in the highlands of central Asia. It has no counterpart in North America. The six species thus classified show different familial affinities.

The avifauna of the Eurasian open desert is also without counterpart in North America. Its specialized passerine genera and nonpasserine genera and families suggest an older history of the desert habitat in the Old World than in North America.

The affinities in the avifaunas of subboreal and temperate forests are more in accord with the Recent and Pleistocene distribution of these habitats than with their earlier history which is reflected by botanical and mammalian evidence. The subboreal coniferous forest belt (taiga) has a great proportion of species and genera that are distributed evenly across both North America and Eurasia. The ranges of the peculiarly North American elements suggest that they are recently penetrating this habitat. The temperate forests and woodlands have very few elements common to the two continents. Many of these could have filtered through the coniferous forest belt.

We may for speculative purposes discard the possibilities of a sharp climatic barrier

between the arctotertiary forests of Asia and America, of distance and time as combined retarding factors in crossing the connecting land bridge, of an ecological barrier formed by mutually competitive, balanced avifaunas on both sides of the bridge, and of mass extinction of passerine species after their crossing the barrier. But if this is done, we have no explanation for the dissimilar avifaunas in the highly similar European-Chinese and North American temperate forests that exist now and were present in the latter part of the Tertiary.

The limnic, grassland, desert, desert scrub, and even scrub-type passerines of North America are mostly only imperfectly or partly adapted to these habitats and are best regarded as recent offshoots of typical arboreal families and genera.

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