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THE ROLE OF COMPETITION IN THE EVOLUTION OF MIGRATION

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One of the major objectives of modern ecology is analysis of the role of ecological processes in the evolutionary origin of adaptations. The problem of the origin of migration, however, has received little attention from this standpoint. Even for birds, in which the phenomenon of migration has been a major focus of research, most attention has been directed to the study of proximate factors important in initiating migration and the physiological processes and orientation mechanisms involved in the actual movements. Few studies have concentrated on the ultimate factors responsible for the origin of these complex mechanisms.

General theories of the evolutionary origin of bird migration have been in existence for a long time. Thomson (1926) and Lincoln (1939) have summarized early theories, which tend to fall into two main groups: (1) northern ancestral home theories, and (2) southern ancestral home theories. Northern ancestral home theories assume that most presently migratory forms were permanent residents in preglacial northern areas corresponding approximately to their present breeding ranges. With advance of continental glaciers and attendant climatic changes these birds were forced southward, from where they either attempted to return yearly to breed as close to their ancestral home as possible, or in some way retained a racial memory of the ancestral home, to which they were able to return seasonally following glacial retreat. It is often suggested that the stimulus for these return movements is the crowded conditions created in tropical and subtropical areas due to the northern birds being forced south. Southern ancestral home theories assume that most present migrants were originally permanent residents in southern

areas, possibly corresponding to their present winter ranges. Following glacial retreat these species began to invade seasonally favorable northern areas for breeding as a result of competition for food or breeding sites in southern areas. Some authors (Berlioz, 1950; Dorst, 1961) have suggested the operation of both of the above patterns. Although these ideas have received extensive criticism (Mayr and Meise, 1930; Wolfson, 1948; Moreau, 1951) they have found their way in almost unmodified form into some recent textbooks of ornithology (Wallace, 1955; Welty, 1963).

Mayr and Meise (1930) have suggested that the existence of areas with seasonally favorable and unfavorable conditions, rather than the occurrence of glaciation, is the condition required for the evolution of migration. They suggest that the normal reproductive excess, primarily through competition for food, is the factor favoring development of mechanisms allowing seasonal occupation of such areas. Although recognizing that migration must thus have existed in preglacial times, they conclude that, due to the great restriction of migration routes which must have occurred during glacial maxima, modern migration route patterns are almost entirely post-glacial in origin. They show that extreme crowding of birds in tropical and subtropical areas during glacial maxima is unlikely, and hypothesize that changes in distribution patterns and migration routes during glacial advances and retreats are the results of extinction of local populations and dispersal resulting from normal reproductive excess. Intraspecific competition and intensification of migratory drive are suggested as factors important in the elongation of migration routes and the origin of "leapfrog" patterns in which races breeding farthest north winter

farthest south. Migration between discontinuous ranges is postulated to be the result of environmental change, acclimatization to high latitudinal conditions (existing in the alternate season in the opposite hemisphere), and intensified migratory drive.

Wolfson (1948) hypothesized that continental drift was the stimulus for the origin of long range disjunct migration patterns, through physical separation of breeding and wintering ranges of short distance migrants which happened to straddle continental rifts. According to this view, migration does not represent an adaptive response to a basic ecological problem, but a best answer to a geologically embarrassing occurrence. Amadon (1948) and others, in refutation of this argument, have shown that if continental drift occurred, it did so much too early in the evolutionary history of birds to account for modern migration patterns.

Williams (1958) has recently suggested that latitudinal bird migration is primarily the result of seasonal change combined with the distribution pattern of land areas in the northern and southern hemispheres. Although admitting pre-Pleistocene occurrence of migration, he contends that seasonal release of large areas of the northern hemisphere from winter conditions since the retreat of Pleistocene glaciers has selectively favored northward spring migration at all latitudes through reduction in population pressure gained by migration into released areas or into areas from which other wintering species have departed. He further suggests that the winter range represents the evolutionary point of departure, to which the species returns as a result of a firmly based "locality-fixation," and that the breeding range represents merely an adventitious expansion of activity during the relatively brief breeding season. Mayr (1953), as well as Mayr and Meise (1930), has shown that many migrants represent clearly foreign zoogeographical elements in their winter ranges, thus making the idea of wintering ranges always representing the ancestral range very unlikely.

Over a period of years, students of S. C.

Kendeigh (Siebert, 1949; West, 1960; Cox, 1961; Zimmerman, 1965) have investigated energy balance as a factor through which advantage could be gained by both northward and southward migration. Siebert (1949) showed that metabolic requirements at the northern edge of the winter range corresponded closely to the maximum metabolic capacities of the Slate-colored Junco, *Junco hyemalis*, and the White-throated Sparrow, *Zonotrichia albicollis*, thus indicating that southward migration was a metabolic necessity. West (1960) also showed southward fall migration to be a metabolic necessity for the Tree Sparrow, *Spizella arborea*. Northward migration in the spring, however, did not appear to provide an improved energy balance. Cox (1961) found that resident tropical finches stood to gain little if any advantage in energy balance through northward migration to summer breeding areas with longer photoperiods. In contrast, Zimmerman (1965) concluded that the Dickcissel, *Spiza americana*, gains an improved energy balance through both spring and fall migrations. These studies emphasize the importance of considering bioenergetics in an analysis of the adaptive significance of migration, but deal only marginally with the selective forces involved in the origin of these adaptive systems.

As indicated by the preceding review, most theories of the evolutionary origin of migration are incomplete, highly speculative, or even contrary to much of the available evidence regarding the evolutionary history and present distribution of birds. These theories tend to emphasize catastrophic geological events such as glaciation and continental drift. Primary emphasis is placed on relations between the organism and the regional climatic regime, with the roles of intraspecific and interspecific competition poorly defined or even ignored.

For a phenomenon such as migration, which occurs not only in birds, but also in mammals, fish, and even invertebrates, a general evolutionary theory is desirable. Such a theory should, if possible, not be dependent on the occurrence of unusual

geological events, such as glaciation or continental drift, and should have a firm basis in ecological theory. This paper presents and tests the hypothesis that migration is a normal evolutionary consequence, for highly mobile animals, of intraspecific and interspecific competition operating in a seasonal environment.

STATEMENT OF HYPOTHESIS

The evolutionary sequence of stages in the evolution of migration in most land birds logically involves the initial change from a permanent resident condition to that of a partial migrant, having both permanent resident populations and populations migrating into seasonally favorable adjacent areas. Partial migrants may then evolve further, through elimination of resident populations and expansion of migrant populations, into forms with separate or disjunct seasonal ranges. This series of changes may occur as a result of the differential influences of intraspecific and interspecific competition.

Intraspecific and interspecific competition tend to modify the fundamental and realized niches (Hutchinson, 1965) of a species in opposite ways. Intense intraspecific competition relative to interspecific competition tends to enlarge the niche, i.e., broaden the range of environmental resources and habitats utilized. Crowell (1962), in the Bermuda Islands, found that reduced interspecific competition resulting from the existence of an impoverished North American bird fauna allowed existing species to maintain greater population densities. This was apparently accomplished through utilization of a wider range of food resources and occupation of habitat types made available through the absence of competitors. Another striking example of the influence of low interspecific relative to intraspecific competition is furnished by the chaffinches of the Canary Islands (Lack, 1947). On the islands of Gran Canaria and Tenerife the European Chaffinch, *Fringilla coelebs*, occupies lower elevation chestnut and laurel forest habitats,

while the Blue Chaffinch, *F. teydea*, is restricted to higher elevation pine forest areas. On the island of Palma, as well as on the European mainland, the Blue Chaffinch is absent, and the European Chaffinch occupies the entire range of forest habitats. Van Valen (1965) has shown, through an analysis of intraspecific variation in beak measurements of island and mainland populations of several species, that greater variation exists in island populations, which as a rule face reduced interspecific competition. This increased variation would seem to reflect selection favoring the utilization of a wider range of food types by island populations. Other studies demonstrating the expansion of the niche under conditions of low or reduced interspecific competition include those of Lack (1947) and Amadon (1947).

Intense interspecific competition, relative to intraspecific competition, tends, on the other hand, to restrict or displace the niche. This effect is shown in the habitat partitioning by the two chaffinch species on the islands of Gran Canaria and Tenerife (Lack, 1947). In the Hawaiian Islands the honeycreeper *Loxops virens* on Kauai possesses a heavier, more strongly curved beak and a more restricted type of foraging behavior than on other major islands, apparently due to competition from the similar *L. parva*, which is restricted to Kauai (Amadon, 1947). Examples of character displacement summarized by Hutchinson (1959) further demonstrate the role of interspecific competition in restriction or displacement of the fundamental niches of various species.

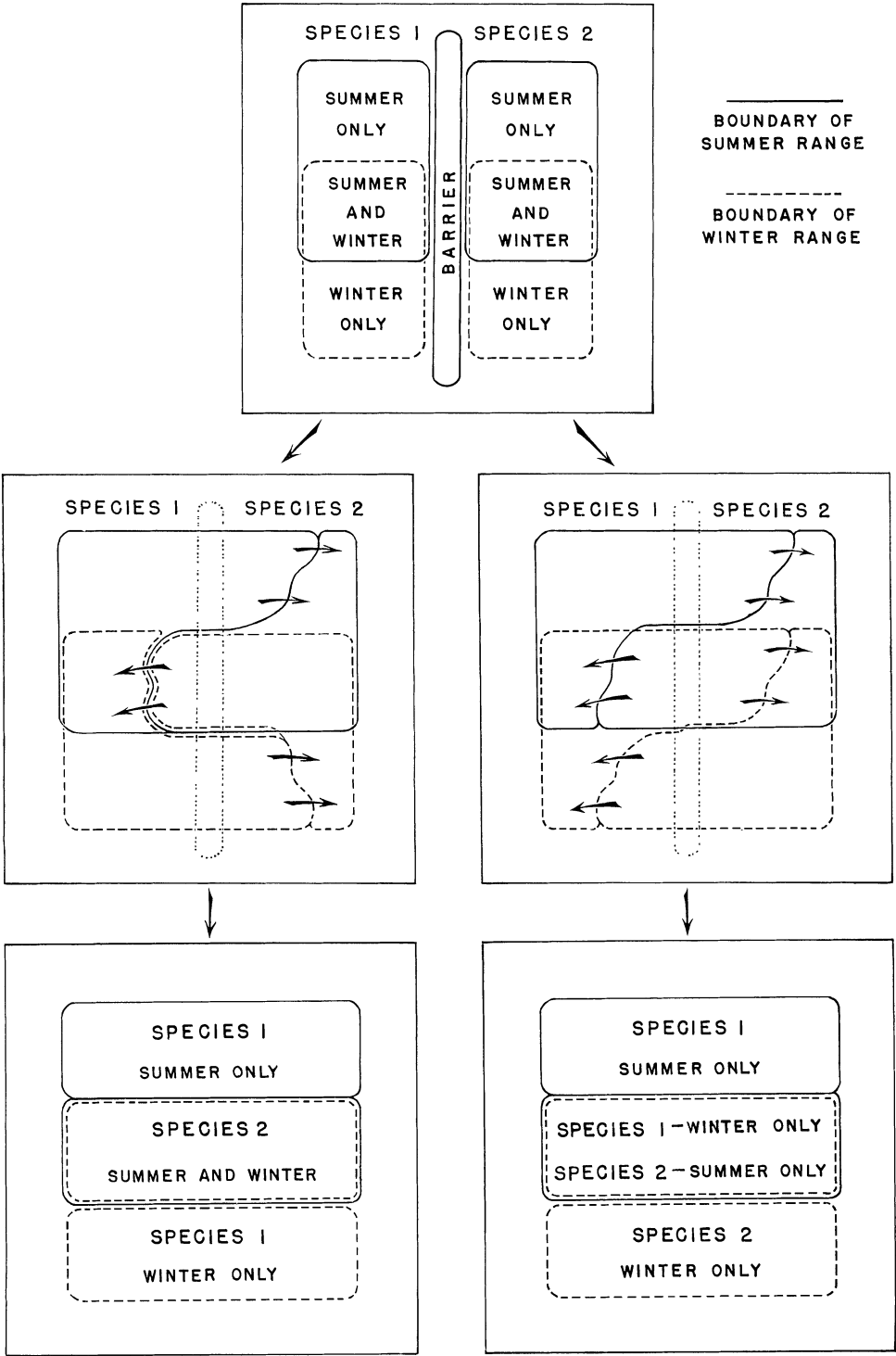
Both intraspecific and interspecific competition, under certain conditions, can potentially select for incipient migratory behavior in a resident species. Intraspecific competition may be more important at this stage, however, since it can operate for extended periods of time with no danger of extinction resulting from competitive exclusion processes. The conditions under which selection should favor genetically based incipient migratory movements are: (1) existence of seasonally favorable areas

adjacent to the boundary of the resident species range, and (2) existence of a reduced competitive regime in these areas. In order for favorable areas to occur adjacent to the range of a resident species during a particular season, the existing range boundary must be set by conditions in some other season. For example, in order for permissive summer conditions to exist north of the range of a north temperate resident form, the northern range boundary must be determined by winter conditions. Likewise, a temperate zone resident species limited northward by winter conditions and southward by summer conditions may have access to seasonally favorable adjacent areas during both summer and winter. Although such a general pattern of range limitation in a seasonal environment seems inherently likely, especially for temperate zone birds, there is little evidence available in this regard. Siebert (1949) and Cox (1961) have shown, however, that certain temperate and tropical resident species may be limited poleward by existence energy requirements during the winter period.

Given permissive conditions, selection should favor any genetically based variation leading to incipient migratory movements into adjacent areas if the reduction in total competition (intraspecific and interspecific) allows greater survival or reproduction (the cost of migration being taken into consideration) than in the original range. The raw material on which selection can act may be variation in genetically based mechanisms of dispersal, homing, or seasonal change in habitat preference. Selection for migratory behavior in this fashion can continue only until the competitive regime in the adjacent areas becomes as severe as that in the original range. This selection, if based primarily on intraspecific competition, represents essentially an expansion of the habitat parameters of the niche to include seasonally favorable habitats. Such selection may therefore lead to the production of a partial migrant, but cannot bring about the elimination of the resident population to produce a complete migrant.

Migration patterns involving separate or disjunct seasonal ranges may arise through the occurrence or intensification of interspecific competition or as a consequence of certain patterns of climatic change. Intense interspecific competition, resulting from recent breakdown of geographic barriers between closely related species of partial migrants, will lead to strong selection for ecological isolation. Such problems must be solved through some type of niche specialization if competitive extinction of one species is to be prevented. Often this specialization involves the partitioning of environmental resources, usually food resources. In the case of birds, this type of specialization may be achieved through differentiation of morphology of the feeding apparatus, as in the case of many of the Galapagos finches (Lack, 1947), or through differentiation of behavioral mechanisms of resource exploitation, as in the case of the five species of *Dendroica* warblers studied by MacArthur (1958). Specialization may also be spatial, leading to habitat isolation or allopatry. Temporal isolation, while theoretically possible, is apparently not widely used as a solution to the problem of interspecific competition by birds (Ricklefs, 1966). It should be noted that the number of possible avenues of specialization is greatest for an organism of high mobility. In the face of interspecific competition such a form may specialize through modification of feeding behavior or morphology, partitioning of available habitats, or even occupation of different habitats or geographical areas at different seasons.

Two of the possible ways in which intense interspecific competition between two partial migrants may be resolved with one or both forms becoming migrant between separate or disjunct ranges are illustrated in Figure 1. In the first case, one species may prove better adapted as a permanent resident and competitively eliminate the other from areas with favorable year-round conditions. The second species may prove better adapted in regions occupied through migration, and competitively eliminate the first in these areas, thus becoming a dis-



junct migrant. The second illustrated solution to this competitive situation is for both species to become fully migrant, one breeding in the seasonally occupied breeding areas of the former partial migrants and wintering in the former permanent resident zone, the other breeding in the former permanent resident zone and wintering in the seasonally occupied wintering areas of the former partial migrants. Still other solutions are possible, based on lack of complete competitive exclusion by the two species at certain seasons. Once a migration pattern involving separate or disjunct seasonal ranges has arisen, the different seasonal ranges may evolve independently, in response to different environmental regimes affecting survival or reproduction.

Separate or disjunct migration patterns may arise in quite a different manner, through gradual climatic change leading to increased seasonal differentiation in environmental conditions. In the case of a partial migrant (Fig. 2) increased seasonal differentiation may cause the boundaries (e.g., northern and southern) of the permanent resident zone to approach each other. As this change occurs, selection may favor an increased migratory segment in the species population. Continued change may eliminate the region of year-round favorable conditions completely, thus creating a complete migrant. Such a pattern of climatic change has characterized temperate zone areas through the Cenozoic Era (Axelrod, 1950), and has doubtless contributed to the evolution of many of the more extensive temperate zone migration patterns.

PROCEDURE FOR TESTING HYPOTHESIS

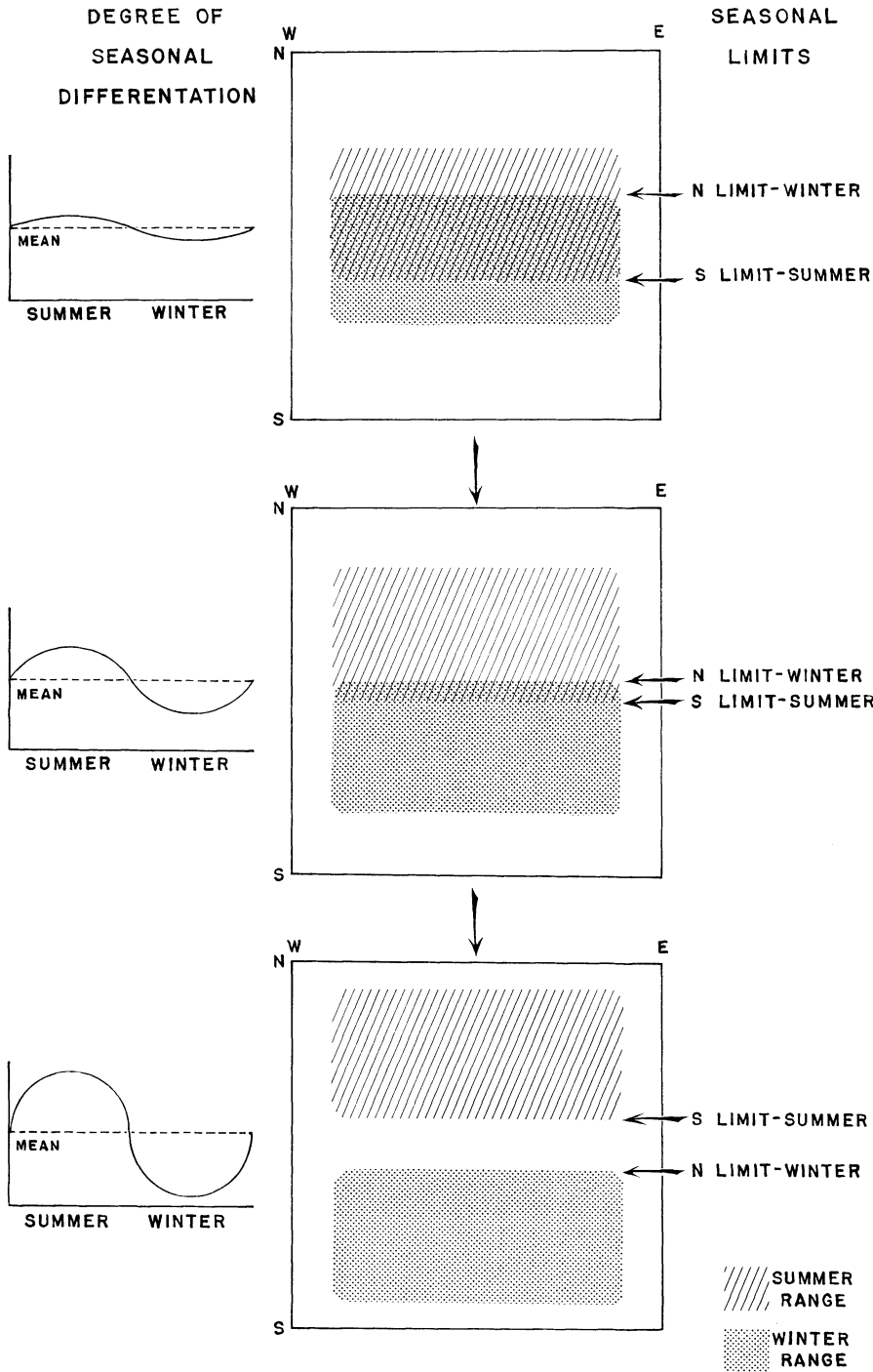
One of the more easily testable aspects of this hypothesis is that of the relative importance of interspecific competition in the evolution of the more extensive migration patterns. This factor may be evaluated

through a comparison of ecological isolating mechanisms utilized by tropical resident bird groups with those utilized by the same groups in temperate and arctic areas, where migratory behavior is shown in different degrees. If interspecific competition is unimportant in the evolution of migration, the extent to which differentiation of beak morphology furnishes the basis for ecological isolation should be the same for migrant and resident birds. If, on the other hand, migration represents one alternative solution to problems of interspecific competition for species less able to achieve ecological isolation through differentiation of the feeding apparatus, then one would expect migrants to show significantly less variation in beak morphology than do residents.

To test this specific hypothesis, data on culmen length and migrational status were summarized for representatives of 20 orders, families, and subfamilies of birds occurring both in North America (United States and Canada) and in Costa Rica. The analysis was limited to non-raptorial land birds, and included only groups having four or more representatives in each area. Migratory species breeding in North America but wintering in the Old World were excluded. Family was used as the basis for summarizing data for members of the Order Passeriformes, except for the Family Fringillidae, for which subfamily was used. Family was also used for members of the Order Apodiformes, which contains two suborders of quite different ecology and of questionable affinity (Jean W. Cohn, pers. comm.). Order was used for other groups. Data on the occurrence and migratory status of North American species were obtained from the Check-list of North American Birds (American Ornithologists' Union, 1957). Information on the occurrence of species in Costa Rica was obtained from Eisenmann (1955). Measurements of culmen length were obtained for males of all

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FIG. 1. Diagrammatic representation of two possible sequences by which interspecific competition between closely related partial migrants may bring about conversion of one or both species into complete or disjunct migrants. See text for further explanation.



species given in Ridgway and Friedmann (1901-1950). Data were taken for the species (monotypic forms), nominal subspecies, or the subspecies most widely distributed in the area under consideration, in that order of preference.

Data on migrational status of North American forms were summarized by subspecies. For each species the number and percentage of subspecies which are resident or migrant was determined. These values were averaged for all members of the group.

For culmen length values the mean and a coefficient of variation were calculated for the group as a whole. The coefficient of variation was obtained by the formula:

$$\text{Coefficient of Variation} = \frac{s}{\bar{x}}$$

Where: s = Standard deviation of individual culmen length values from group mean
 \bar{x} = Group mean.

This value may be directly compared for various groups, since the absolute size differences between groups have been removed. It reflects directly the degree of variation among culmen lengths of species in the particular group.

Relationships were sought between per cent migration and a number of other variables, including number of species in the group, coefficient of culmen variation, mean culmen length, and ratios of species number and culmen variation coefficients for North American and Costa Rican group representatives. Possible relationships were explored through plotting procedures and through a multiple regression screening procedure developed by Fritts (1962) for use in dendroclimatic analyses. In this procedure a multiple regression equation is developed one variable at a time, with the variable added at each step being that having the greatest significant effect in reduction of the unexplained variance of the dependent variable

(per cent migration). The equation so obtained is the best single equation possible with the independent variables utilized.

RESULTS

Basic data obtained for the 20 North American and Costa Rican orders, families, and subfamilies are summarized in Table 1. Per cent migration values for the North American groups varied from a low of 2.3 in the Corvidae to highs of 100.0 in the Apodidae, Hirundinidae, and Thraupidae. Averages of group values for number of species, coefficient of culmen length variation, and mean culmen length were similar for the North American and Costa Rican series, with Costa Rican values being slightly, but not significantly, higher.

Single regression analyses carried out in connection with the multiple regression screening procedure showed significant relationships between per cent migration and three of the independent variables tested. These were the mean culmen length and coefficient of culmen length variation for North American group representatives, and the ratio of coefficient of culmen length variation for North American representatives (numerator) to that for Costa Rican representatives (denominator). These relationships were in all cases negative, with decrease in values being associated with increased frequency of migration. Significance tests (t -test) of deviation of the regression slope, b , from a value of zero, and F tests for significance of reduction in variance associated with the per cent migration values showed each of these variables to be significant beyond the 0.01 probability level. Scatter diagrams and regression formulae illustrating these relationships are given in Figure 3.

The multiple regression analysis revealed no other significant independent variables, but combined the above three into the following single equation:

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FIG. 2. Diagrammatic representation of the manner in which gradually increased seasonal differentiation may convert a partial migrant species into a form migrating between separate summer and winter ranges. See text for further explanation.

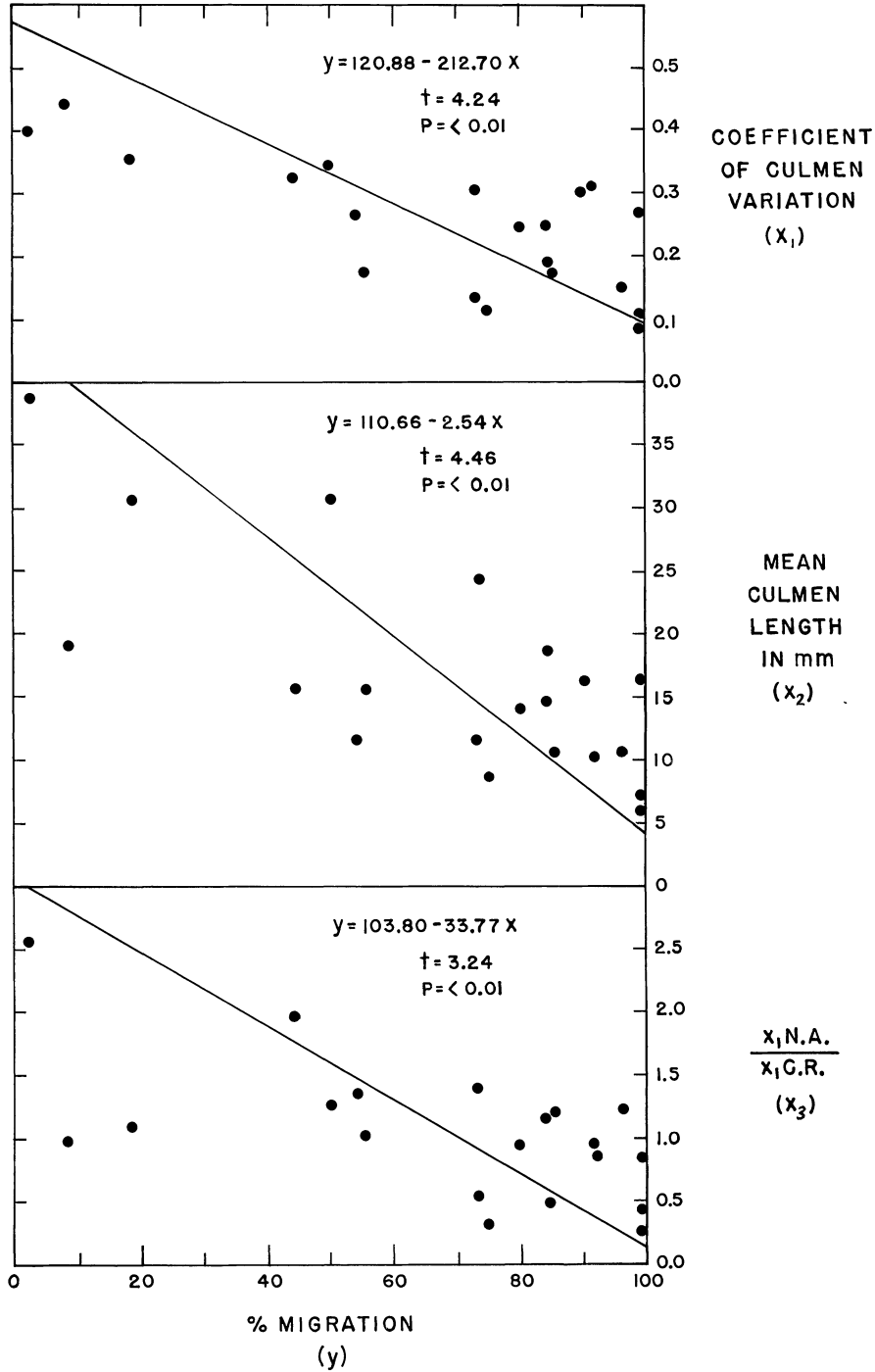


TABLE 1. Summary of numbers of species, per cent migration values, and coefficients of culmen length variation for groups of non-raptorial land birds represented in North America (United States and Canada) and Costa Rica. Numbers in parentheses indicate number of species for which culmen data was obtained, where that number differs from the total number of species in the group.

	United States and Canada				Costa Rica			Ratios	
	Number of Species	Total % Migration	Mean Culmen Length (mm)	Coef. of Culmen Variation	Number of Species	Mean Culmen Length (mm)	Coef. of Culmen Variation	Species N.A./C.R.	Coef. of Cul. Var. N.A./C.R.
1) Galliformes	18	8.2	19.10	0.440	11	25.04	0.446	1.636	0.986
2) Columbiformes	9	55.6	15.47	0.173	22	14.72	0.171	0.409	1.012
3) Cuculiformes	6	50.0	31.67	0.342	8	28.75	0.267	0.750	1.281
4) Caprimulgiformes	6	91.7	10.37	0.312	5	15.28	0.328	1.200	0.951
5) Apodidae	4	100.0	5.92	0.107	8	6.10	0.243	0.500	0.440
6) Trochilidae	13	84.6	18.71	0.190	52	20.22	0.383	0.250	0.496
7) Piciformes	22	18.6	30.59	0.355	15	25.39	0.324	1.467	1.096
8) Tyrannidae	30	90.0	16.22	0.304	59(57)	13.77	0.348	0.509	0.874
9) Hirundinidae	8	100.0	7.20	0.271	4	7.52	0.320	2.000	0.847
10) Corvidae	15	2.3	38.93	0.400	5	26.36	0.156	3.000	2.564
11) Troglodytidae	10	44.3	15.81	0.323	21	17.27	0.163	0.476	1.982
12) Turdidae	11	84.1	14.81	0.247	11	17.29	0.210	1.000	1.176
13) Sylviidae	4	75.0	8.78	0.114	4	16.38	0.361	1.000	0.316
14) Parulidae	54(53)	96.3	10.58	0.151	12	10.74	0.123	4.500	1.228
15) Icteridae	19	73.4	24.30	0.302	13	33.39	0.546	1.462	0.553
16) Vireonidae	11	85.4	10.62	0.171	6	11.75	0.141	1.833	1.213
17) Thraupidae	4	100.0	16.30	0.085	42(41)	12.28	0.306	0.095	0.278
18) Fringillinae	17	54.0	11.82	0.266	10	10.49	0.192	1.700	1.385
19) Richmondininae	10	80.0	14.15	0.244	12	17.69	0.261	0.833	0.935
20) Emberizinae	50(49)	73.2	11.55	0.137	17	14.24	0.098	2.941	1.398
Average	16.0	68.3	16.64	0.247	16.8	17.23	0.269	1.378	1.050

$$y = 130.71 - 99.00 x_1 - 1.40 x_2 - 13.88 x_3$$

Where: y = Per cent migration

x_1 = Coefficient of culmen length variation

x_2 = Mean culmen length (mm)

x_3 = Culmen length coefficient ratio (N.A./C.R.).

Tests for significance of reduction of unexplained variance in per cent migration values by each variable in the above equation showed variables x_1 and x_2 to be significant beyond the 0.01 probability level and variable x_3 to be significant at the 0.05 level. The coefficient of multiple correla-

tion for the equation as a whole was 0.823, indicating that about 67.8% of the total variation in per cent migration values was accounted for through the combined use of the three independent variables. These analyses indicate that increase in frequency of migration in a group is significantly related to decreased degree of culmen length variation, decreased mean culmen length, and decreased culmen length variation relative to that shown by resident tropical group representatives.

DISCUSSION

These results indicate that migrant and resident forms differ significantly in the ex-

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FIG. 3. Relationship of per cent migration in various North American land bird groups to the coefficient of culmen variation and mean culmen length of North American group members, and to the culmen variation coefficient ratio for North American (N.A.) and Costa Rican (C.R.) group members.

tent to which morphological differentiation of the feeding apparatus furnishes the basis for ecological isolation. The low coefficients of culmen length variation exhibited by highly migratory groups of both large (Parulidae, 54 species, and Emberizinae, 50 species) and small (Apodidae and Thraupidae, 4 species each) size indicate that migration tends to occur in groups less able to achieve complete ecological isolation through such variation. The relationship of increase in frequency of migration with decrease in the ratio of culmen length variation in North American representatives to that in Costa Rican representatives indicates that migration is best developed in portions of orders, families, or subfamilies most severely limited in this respect.

It should be noted that while some Costa Rican resident groups exhibit low coefficients of culmen length variation, such values are not shown by the groups of greatest diversity (e.g., over 40 species). Occurrence of a low degree of culmen length variability in a group, either tropical or extratropical, means simply that the group must use other mechanisms to achieve ecological isolation. In such groups, problems of interspecific competition must be solved primarily through behavioral mechanisms or through isolation in space or time. In the case of groups occurring in regions not possessing significant seasonal variation, seasonally favorable areas adjacent to range boundaries will be absent, and the evolution of migration is therefore unlikely. To achieve a relatively high degree of regional diversity these groups must employ highly refined mechanisms of feeding behavior differences, habitat partitioning, or allopatry. For groups occurring in regions with significant seasonal variation, on the other hand, selection may favor the development of migration as an efficient behavioral-spatial solution to problems of interspecific competition.

The relation of small culmen length to high frequency of migration also supports the hypothesis of the importance of interspecific competition in the evolution of migration. Mean culmen length in part simply

reflects the degree of culmen variation in a group. For most bird groups, increased variability must be achieved through development of larger-billed forms, since opportunities in the other direction are severely limited by a practical minimum beak size. Addition of larger-billed forms will obviously increase the mean value for the group as well as the degree of interspecific variability.

Schoener (1965) has shown, however, that large differences in beak size among sympatric, non-insular species tend to occur either in species with large body size relative to food abundance (e.g., hawks) or in species utilizing foods of restricted type or from restricted food environments (e.g., woodpeckers). With small bodied birds, feeding on abundant, widely distributed foods such as foliage insects, seeds, or fruit, the available food biomass may often be adequate to support more species populations than can be effectively isolated through beak specialization for particular food particle sizes. With increased interspecific competition a practical limit to the degree of beak specialization is quickly approached and selection tends to favor other mechanisms of ecological isolation, such as habitat partitioning (Schoener, 1965). Under such conditions selection for migration as a behavioral-spatial solution to interspecific competition problems seems quite likely.

Inability of bird groups to utilize morphological differentiation as the primary basis for ecological isolation may also be due to factors other than the practical limitation of degree of beak specialization discussed above. In some cases it may be possible that appropriate genetic variation on which selection can act is lacking. However, the frequency with which differentiation of beak morphology is utilized by island species (Amadon, 1947; Lack, 1947; Schoener, 1965), the populations of which are most subject to genetic processes tending to reduce variability, suggests that this is not often true.

It is likely, in many cases, that differentiation of beak structure is prevented by

the existence of other species already well adapted in feeding morphology to most potential feeding niches. Among land birds, migration is best developed in various families of the Passeriformes, such as the Hirundinidae, Turdidae, Vireonidae, Parulidae, Icteridae, and Fringillidae. The passerine birds represent the most recently evolved and behaviorally most advanced land birds. Within this group elaborate systems of territoriality, courtship, and mating are well developed. In addition, some passerine groups utilize almost purely behavioral mechanisms of ecological isolation, such as those shown by the *Dendroica* warblers studied by MacArthur (1958). The evolutionary premium placed on behavior in the passerines is very likely related to the fact that their evolutionary origin did not occur until after a moderately diverse fauna of non-passerines had occupied most of the morphologically characterizable feeding niches. Evolutionary emphasis was therefore directed along other lines, leading, among other things, to complex modern patterns of migration, through which the species involved are able to exploit resources in different geographical areas at different seasons more efficiently than are resident forms.

In this connection it should also be pointed out that the perfection of migratory behavior in a group may facilitate its extension of range into large areas from which it was formerly excluded. In such areas the competitive regime may be quite different from that of the original area, and morphological specialization may become possible due to the absence of critical competitors. This may be exemplified to some extent by the Parulidae, with 54 species in North America and 12 in Costa Rica. The North American forms are not only highly migratory, but also show a culmen variation greater than that of the Costa Rican representatives of the family.

SUMMARY

Intraspecific and interspecific competition are suggested as primary selective agents in the evolution of migration. Selec-

tion should favor genetic mechanisms leading to incipient migratory movements by individuals of normally resident species into seasonally favorable adjacent areas if gains in survival or reproduction due to reduced competition exceed the migration cost. Evolution of partial migration patterns may thus result from high overall competition or high intraspecific competition alone. Disjunct migration may evolve through elimination of resident, and selection for migrant, populations by intense interspecific competition, thus representing a complex behavioral-spatial mechanism of ecological isolation. An analysis of ecological isolating mechanisms utilized by migrant and resident American land birds supports this hypothesis. Migration occurs most frequently in groups apparently less able to solve problems of ecological isolation by morphological differentiation of the feeding apparatus, and which are characterized by small beak size, low actual beak variability, and low beak variability relative to that of tropical resident species of the same group. The high frequency of migration in passerine birds is interpreted as a consequence of their having evolved in competition with an already existing, diverse fauna of non-passerines occupying many of the potential morphologically characterizable feeding niches.

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