

Det Kongelige Danske Videnskabernes Selskab

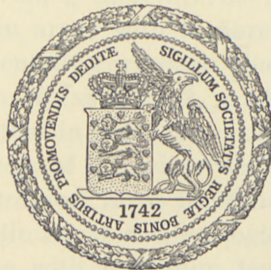
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THE EVOLUTIONARY
SIGNIFICANCE OF BIRD-MIGRATION

BY

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i kommission hos Ejnar Munksgaard

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Adaptive Variation and Migration.

The geographical variation in homoiothermous organisms is not fortuitous, but follows certain ecological rules, of which the most important ones are Bergmann's rule, Allen's rule and Gloger's rule (cf. HUXLEY 1942, p. 211, MAYR 1942, p. 90, DOBZHANSKY 1951, p. 152, RENSCH 1929, p. 131; 1936, p. 317; 1938, p. 364; 1947, p. 40; 1952, p. 137). These rules express correlations between geographical variation and environmental factors. Populations of different species respond to the selective forces of the environment in a parallel way and develop a number of morphological (and physiological) adaptive characters. In species with extensive continuous ranges the variation usually takes place as character gradients (clines), in which the correlation between the geographical differentiation and the gradually changing environment is often very accurate. The ecological rules are apparently of minor importance in the tropics, where the selection pressure of the environment is smaller and the mutation pressure is the main evolutionary factor. In tropical species random fixation of variants, therefore, is much more frequent than in species living in areas with a more severe climate, and consequently environmentally correlated characters are generally of much less significance (RENSCH 1952, p. 141). This corresponds very well with the fact that in birds the ecological rules generally reflect the selective effects of the winter-environment. The character-gradients in non-tropical birds must be regarded primarily as adaptations to the climatical and ecological conditions in the most severe winter-time with minimum temperatures and lack of food as the critical factors; cf. RENSCH 1939, p. 103; 1947, p. 42; 1952, p. 148. HEMMINGSEN (1951, p. 204) in a comprehensive paper on the birds of N. China has stressed similar

points, stating that "if the validity of Bergman's rule for migrants is to be tested—not only in this connection, but on a broad scale—with reference to latitudes, it should be to their winter ranges rather than to their breeding ranges (where also many spend so relatively little of their time)", a conclusion completely in agreement with the view-points which will be advanced in this paper.

The situation, extension and environmental conditions of the wintering grounds of a species is, therefore, of the outmost importance when analysing the evolutionary trends and processes of the species concerned. In migratory species the wintering grounds are completely or partially separated from the breeding area. The evolutionary consequences of this separation form the subject of the following discussion.

Subspeciation in Resident and Migratory Birds.

It is a well-known fact that the geographical variation is distinctly smaller in migratory than in resident birds. Among the palæartic Passeres the migratory polytypic species possess on an average 3.2 subspecies, while the sedentary ones have 7.2 subspecies (RENSCH 1933, p. 19).

The fact that the migratory populations leave the breeding areas and therefore are not subject to the influence of the winter conditions is of importance when discussing the evolution of different species breeding in the same climatical zone. When comparing, as an example, sedentary species of parids and picids, which are distributed over the greater part of the palæartic region and which are split up in a large number of subspecies, with migratory species like *Jynx torquilla* and *Phylloscopus trochilus* with a breeding range as extensive as that of the former groups but with a very slight geographical variation, it appears that the sedentary species in winter time are exposed to extremely varying life-conditions, ranging from the mild Atlantic climate of Portugal and Ireland to the icy cold of Kamchatka, while the said migratory species spend the winter in the uniform climate of tropical Africa.

Still more important is no doubt the fact that the scattering

of the migrants in the winter-quarter is much greater than that which takes place in strictly sedentary birds. Almost all results of ringing have demonstrated that the individual scattering in the winter-quarter of migratory birds originating from a circumscribed breeding area is much greater than that of the sedentary birds inhabiting the same area. As an example can be mentioned that sedentary birds inhabiting the Danish island Zealand rarely leave this island (7000 km²) in winter, while specimens of the migratory Song-Thrush (*Turdus philomelos*), ringed as nestlings in Zealand, have been recovered in the winter-time (Dec.—Feb.) in entire France, Spain and Portugal, and Linnets (*Carduelis cannabina*), breeding in Zealand, have been recovered in winter in an area extending from Belgium to Algeria, just to quote a few examples. The same extensive area is in winter inhabited by a number of other populations of the said species. This shows that the "synhiemic unit", *i.e.* the populations which mix freely in winter, is much greater in migratory than in resident birds, and consequently the populations of migratory birds are not in winter subject to the great differences in the selective influences due to local environmental factors as are the sedentary birds.

The difference in the extent of geographical variation between sedentary and migratory species is usually given another explanation. "It indicates", to quote MAYR (1942, p. 246), "that migration produces greater dispersal and hence decreased subspeciation." When the dispersal, *i.e.* the interchange of individuals in local breeding-populations, is increased, the gene-flow may outweigh the selection-pressure and in this way impede or completely prevent adaptive differentiation. It has, however, not been demonstrated with certainty that the dispersal is particularly greater in migratory than in resident species, although it appears that the area of the effective breeding units¹ is slightly smaller in the latter. The dispersal of the resident species is a result mainly of the individual movements in the off-season, while that of the migratory species depends on their capacity of homing. The adult birds are known generally to return to their nest or its immediate surroundings in spring, but the young birds scatter more or less in the breeding area and in this way give rise to

¹ The "panmictic unit" of DOBZHANSKY & WRIGHT (1943, p. 335).

a certain diffusion of genes in the population. BOYD & LANDSBOROUGH THOMSON (1937, p. 278) in a study on the recoveries of ringed Swallows (*Hirundo rustica*), an extreme long-distance migrant, found that 72 % of the one-year old birds bred within a radius of 25 km from the nest in which they were hatched, the greater part (38 %) within a radius of 3 km. The remaining young birds scattered in a larger area, but only exceptionally settled beyond 100 km from their place of hatching. In a partly sedentary population of the Song-Sparrow (*Melospiza melodia*) the dispersal of the yearlings was distinctly smaller, the young birds settling usually less than 1.4 km from the nest, the greater part within a radius of 500 m (MILLER 1947, p. 188). A similar result was recently achieved by KLUIJVER (1951, p. 13) as far as the Great Tit (*Parus major*) was concerned, in a population which was strictly resident. He found that the majority of the young birds settled to breed within 2 km of their place of hatching, but a few were recovered in the breeding-season as far as 25 km from the area in which they were hatched. Compared with the dispersal of the Swallow there is a pronounced difference. VON HAARTMAN (1949, p. 52) in a comprehensive paper on homing in the Pied Flycatcher (*Muscicapa hypoleuca*) gives the percentage of vernal returns of young birds in a number of species in which the movements have been thoroughly studied by means of ringing (usually with coloured rings). There is a considerable variation, but the difference between resident and migratory species is negligible. In migratory species returns of young birds in spring to a limited check area amount to 3 % (*Sturnus vulgaris*, Letland), 8 % (*Fringilla coelebs*, Finland), 1 % (*Muscicapa hypoleuca*, Finland), 6 % (*Phoenicurus phoenicurus*, Holland), 10 % (*Iridoprogne bicolor*, Connecticut), etc., while the corresponding figures in resident birds are 12 % (*Melospiza melodia*), 1 % (*Parus inornatus*, California), 10 % (*Erithacus rubecula*, England). I agree with HAARTMAN when he says that the percentage of returns is scarcely higher in the resident than in the migratory species. Nevertheless, there may possibly be a somewhat greater percentage of returns in the sedentary species studied, but a number of grave sources of error, enumerated by HAARTMAN p. 54, obscure the comparison.

Although far from conclusive the results of the investigations on ringed birds, so far carried out, show a tendency in sedentary populations to smaller dispersal and hence greater probabilities for adaptive differentiation. The tendency, however, is too slight to explain the pronounced difference in geographical variation between migratory and sedentary birds. This difference is probably mainly due to the much larger size of the "synhiemic units" in the migratory than in the sedentary species. In addition, it is of importance that the migratory populations evade the pessimum conditions of the winter season by moving to areas with a milder climate, where the selection-pressure is much smaller, and where life-conditions are more uniform. The comparative size of the synhiemic unit is a more essential evolutionary factor than the environmental differences. This is demonstrated in species belonging to migration-type VI, discussed on p. 28, below.

The Rôle of Competition.

The evolutionary significance of interspecific competition has been emphasized particularly by LACK (*e.g.* 1944, 1949, 1951). Subsequent to geographical isolation and development of full specific diversity the next step in speciation, when the two hitherto isolated species come into contact, will be—and necessarily must be—development of differences in ecology, usually in habitat selection. This theory appears to give a satisfactory explanation of the ecological diversification of closely related sympatric species. The selective effect of inter-specific competition must consequently be considerable, a view-point which is not shared by all students, however. UDVARDY (1951, p. 113) sharply criticises the competition concept, concluding that "it has not been possible to prove in one single case that the competition between species has any important influence upon the distribution ecology of European bird life". It must be admitted that it is difficult to demonstrate competition in action, "because its importance becomes obvious only when it is either lacking or reduced to a minimum" (MAYR 1942, p. 272). The reason for this is no doubt

that competition is not a "proximate" but an "ultimate" factor¹, which in a stable environment has produced a balanced equilibrium among the synecological species. Every change would therefore be a disadvantage and would result in a reversion to the original condition.

An analogous phenomenon is the appearance in wild populations of mutations; these are usually deleterious and the mutants are eliminated. This fact in former days gave rise to one of the main objections against the acceptance of mutations as being of any significance for evolution. The critics against the competition concept has a similar background.

The importance of competition appears when a change takes place between the competing species. Changes of this kind can be found when a species is followed to other geographical areas, just as the principles of speciation can be studied by following the geographical variation. Very little is gained in this respect by studying a local fauna, neither concerning speciation nor competition. It is necessary to compare the local conditions with those which are present in other localities. It can be demonstrated in a number of cases that in areas where a competitor is present a shift in ecology takes place in the species concerned. LACK (1944) has enumerated a number of the known cases and particularly draws attention to the geospizids, species of *Zosterops*, *Acanthiza*, *Dicrurus* and *Lalage* and the well-known case of *Fringilla coelebs* and *F. teydea*. I have added a number of cases of competition among arctic birds (*Somateria mollissima* and *S. spectabilis*, *Phalaropus lobatus* and *Ph. fulicarius*, *Falco peregrinus* and *F. rusticolus*, *Rissa tridactyla* and *Sterna paradisaea*, the *Stercorarius* species, and others (SALOMONSEN 1951). Finally, VAURIE (1951, p. 163) has presented a very fine example, viz. the two Nuthatches *Sitta tephronota* and *S. neumayer*. Cf. also MAYR (1948, p. 212—218), who recently has discussed the problem of competition.

It is most likely to assume that the ecological differences be-

¹ These handy terms were coined by BAKER (1938, p. 161) for a special situation, but used in a wider sense by LACK (1950, p. 307) and others. The ultimate factors denote the biological expediency or aim (the survival value), the proximate factors the releasing mechanisms. However, the number of causalities in biological phenomena are not exhausted by the distinction between proximate and ultimate factors.

tween two sympatric species are preceded by a certain degree of pre-adaptation. This took place while the two species were geographically isolated and was an unavoidable result of intra-specific competition. It is highly improbable that the ecological development should be exactly similar in two completely isolated species.

LACK (1944, p. 276) has drawn attention to the important point that related species, which in the breeding season are separated from each other by habitat differences in the wintering grounds are isolated geographically. On the basis of this evidence he draws the conclusion "that such closely related species are potential food competitors in winter and so have evolved geographical isolation at this season as a result of differential adaptation". Independently of LACK I have arrived at the same result. I want to quote this paragraph here in full as it contains certain statements which will be further dealt with below.

"It appears as if the extensive bird-migrations involve an unnecessary waste of time and energy. The irresistible urge of migration no doubt carries the birds further than it seems necessary when the question is to find an adequate climate and sufficient food. Why continue to S. Africa when the subtropical N. Africa offers just as good life-conditions? However, the migration of a species should not be singled out, but must be viewed in comparison with that of its relatives. With an even distribution of the different allied species over extensive continents the food resources can be utilized in much larger areas than if all migratory species were crowding in a smaller but not so distant region. The segregation of the migratory species is not arranged in conformity with the taxonomic units, in the sense that each family or genus has its own wintering area. On the contrary. The different species within a genus are generally the closest competitors for food, and hence they segregate in winter over as large areas as possible, each species occupying a separate part of the area. Typical examples are found in the genera *Anas*, *Larus*, *Calidris*, *Anthus*, *Phylloscopus*, *Lanius*, *Emberiza*, etc., the members of which often vary from being residents in arctic or temperate regions to long-distance migrants which move to the tropics or even further. In many instances the greatest differences in the migration pattern is found between the most closely related species, e. g. *Larus fuscus* and *L. argentatus*." (SALOMONSEN 1950, p. 311; translated from Danish).

It can safely be assumed that the spatial segregation in the wintering grounds in some way or other has influenced the

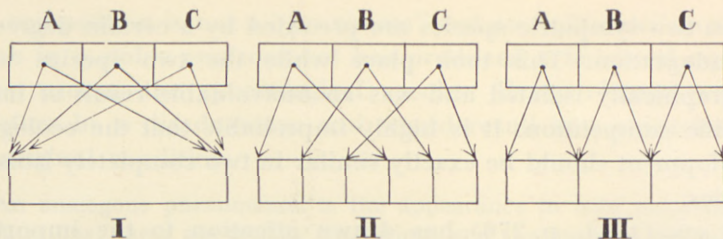


Fig. 1. Migration of three neighbouring populations (A, B, and C), left (I) showing synhiemy, right (III) allohiemy, centre (II) being intermediate. The upper rectangles symbolize the breeding areas, the lower ones the winter-quarters. The scattering in winter of the individuals belonging to the different populations is shown by the arrows.

evolution of the species in question, *i.e.* has contributed to change the genotype. In order to further elucidate this problem it is necessary to study the phenomenon at a more elementary stage and turn the attention to the intraspecific competition in wintering populations.

Spatial Segregation of Wintering Populations.

It would be very inconvenient if all populations of a given migratory species spent the winter in a restricted area. This would result in a devastating competition for the limited resources of the wintering ground and give rise to other deleterious effects of overcrowding. Most species avoid this development by scattering over so wide an area as possible. The limits of the winter range are conditioned mainly by competition with other species (cf. above, p. 9), geographical barriers and various extrinsic (*e.g.* climatical) factors.

Competition for food is probably the primary reason for the wide dispersal in the off-season. In a number of species breeding in the Arctic, scarcity of food in the breeding-places in summer keeps the population size within narrow limits, and hence their winter-quarters are often of a modest extension (many diving ducks and geese)¹. This is, however, not the normal situation.

In many species the different populations mix freely in the

¹ STRESEMANN (1934, p. 668) gives some other instances of a restricted winter-quarter.

entire wintering ground. Populations which in this way are united in a common winter-quarter (are components of a "synhiemic unit") I propose to call *synhiemic*. Ordinarily the dispersal in winter has been achieved by a spatial division of the available wintering grounds among the different populations. Such populations, which have separate winter-quarters, are here called *allohiemic*. In some species the populations hold an intermediate position between the state of synhiemy and allohiemy, in other species some populations are synhiemic while others are allohiemic. To make the difference between these concepts clear a case of synhiemy, a case of allohiemy and an intermediate stage in three neighbouring populations (A, B, and C) are shown in fig. 1¹.

The distinction between synhiemic and allohiemic populations is important when discussing the evolutionary significance of migration. Both synhiemy and allohiemy have certain advantages, as will be shown below. In most species a certain degree of allohiemy will no doubt gradually be established. Selection will produce various hereditary differences between individuals belonging to different allohiemic populations, in direction and choice of migration route, in time and speed of migration, *i.e.* in the strength of the urge or instinct of migration, and finally in the adaptation to local climatic and other environmental factors in the winter ground. Ringing of American Passeres (*e. g.* *Zonotrichia albicollis*) has shown that the same individuals return year after year to a restricted winter-quarter (BALDWIN 1921, p. 236, and others). Similarly, recent experiments with transported birds have demonstrated that a number of species (gulls, Coot, etc.) possess a homing faculty also in the wintering grounds, just as in the breeding grounds (RÜPPELL & SCHIFFERLI 1939, p. 224; PETERSEN 1953, p. 153). It is important, however, that the homing capacity in winter was much greater in adult birds than in young birds in their first winter (PETERSEN, *l. c.*). Consequently, the immature birds to a considerable extent scatter in the wintering grounds and in this way strongly reduces the effects of allohiemy. This phenomenon can be compared

¹ When nothing else is stated the figures are original. I am indebted to Mr. ERIK PETERSEN for his careful drawing of the diagrams and maps. My thanks are also due to EJNAR MUNKSGAARD, Publishers, for the loan of the block to fig. 8.

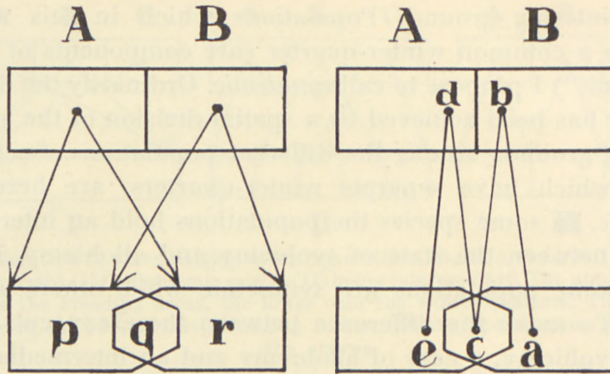


Fig. 2. Migration of two partly allohiemic populations (A and B). For further explanation cf. text p. 12—13.

with the dispersal of young birds in the breeding area, as discussed above (p. 6).

ISAKOV (1949, p. 54), on the evidence of ringing results, is of the opinion that most species of birds form minute fixed, so-called elementary populations. The members of these populations not only breed in the same limited area but follow the same migration route and winter in the same area. They have a synchronous biological rhythm just as is the case in various micropopulations of certain migratory fish. However, in birds such conditions are developed only in rare instances. What concerns us here is the fact that only in species which are divided into so small units the populations display virtual allohiemy in the strictest sense of the word (without scattering). It should be borne in mind that the difference between allohiemy and synhiemy is one of degree. No doubt the greater part of migratory birds display a partial allohiemy, holding an intermediate position, as shown in fig. 1, II. Allohiemy does not need to be complete in order to affect evolution. In winter (which here means the non-breeding season) selection is the only genetic factor involved, and the influence of the selection-pressure cannot be hampered or impeded by disturbing mutations or by gene-flow.

Let us now consider two populations, A and B, which are partially allohiemic, *i. e.* of the intermediate type shown in fig. 1, II. In fig. 2, left, is shown the scattering in the winter grounds of the individuals coming from a locality in the breeding area of

A and from one in the breeding area of B, respectively. It appears that the two populations overlap considerably in the winter grounds. This is one of the most common distributional types among migratory birds. If adaptive differences have developed between A and B owing to selection in the winter-quarters, the populations of p and r will never reach a stage of stability under the circumstances presented in fig. 2. Dispersal from the zone of overlap (q) will steadily tend to counteract the work of selection by mixing the populations A and B. If the differences in selection-pressure are sufficiently great such stragglers will be eliminated owing to the minor survival value of their genotype. Before this, however, they may very well have contributed to gene-flow between A and B. This situation is shown in fig. 2, right. A specimen belonging to population B, having wintered at "a" breeds at "b". Owing to the normal scattering of the immature birds the offspring of the said individual winters at "c", which locality is situated in the zone of overlap, where the survival value of the B-genotype is not virtually reduced. Next spring the bird migrates from "c" to "d", which is situated in the breeding area of A. This is a normal procedure, due to the usual dispersal of first year birds. The locality "d" is the breeding place of our bird, which originally was a member of the population B. In this way the individual in question contributes to furnish the gene-pool of A with genes of B. Some of the offspring, carriers of B-genes, may winter at "e", where their genotype will be inferior if the difference in selection-pressure between A and B is strong. The steady mixing of A- and B-genes will in a case like that shown in fig. 2 prevent subspeciation, at least in the sense in which it is usually applied in ornithology. However, the selection in the winter-quarters will nevertheless leave its mark and produce a cline, but with a broad overlap of its characters. Under the circumstances discussed above a subspeciation will be possible only when the zone of overlap (q in fig. 2) is sufficiently narrow or in any other way the interchange of individuals between A and B is limited, *i. e.* if the differences in selection-pressure between the population of p and r, respectively, outweigh the effects of dispersal.

The evolutionary effects, described above, have been due to the influence of selective forces in winter only. Naturally this

does not imply that conditions in summer (*i. e.* the breeding time) are without importance. The discussion has shown, however, that notwithstanding the evolutionary activity in the breeding population, alone the spatial segregation of the populations in the winter-quarter may have important evolutionary consequences and suffices to change the genotype, provided that the degree of allohiemy is tolerably great.

When discussing the variation in migratory birds it is necessary to consider the conditions both in the breeding area and in the wintering grounds. In accordance with this view we can conclude that the evolutionary processes in a migratory bird is influenced by the following factors:

1. Rate of mutations (mutation-pressure).
2. Selective processes (selection-pressure).
3. Degree of dispersal, causing gene-exchange (being nil in completely isolated populations).
4. Numerical size of the breeding unit (Sewall Wright effect).
5. Limitation of the synhiemic unit, *i. e.* the degree of allohiemy.

Granted that the mutation-pressure is negligible, that the numerical size of the population is fairly large, that allohiemy is present and that random dispersal in the breeding area is slight, the following four possibilities exist for the development of adaptive diversity between two populations (A and B) of a migratory species:

I. The difference in selection-pressure (by environment) between A and B is great in the breeding area but slight in the wintering ground. In this case the adaptive variation will be a result mainly of the conditions in the breeding area.

II. The difference in selection-pressure by environment between A and B is great in the wintering grounds but slight in the breeding area. In this case the adaptive variation will be a result mainly of the conditions in the wintering ground.

III. The difference in selection-pressure (by environment) between A and B is great both in the breeding area and in the wintering ground. In cases like this the adaptive variation will reflect the conditions in both areas, sometimes with both in-

fluences equally manifested, sometimes one more prominently than the other.

IV. The difference in selection-pressure (by environment) between A and B is slight both in the breeding area and in the wintering ground. In this case the adaptive variation will be slight and the possibility for fixation of random variants is considerable.

Of these four theoretical possibilities, present in "ideal" populations, the second is the one which is most often realized in nature, thus demonstrating that the selective forces in the winter grounds are among the most potent agencies in the evolution of migratory birds.

Synhiemic populations follow the first possibility (evolutionary type I). They are subject to the influences of the same environment in winter and, consequently, the natural selection by environment must be much reduced. Any differences in the adaptive variation of A and B must be due to differences between the selective influences in the respective breeding areas.

Synhiemic Populations.

When individuals belonging to different populations do not show any morphological differences the only way to decide whether they are allohiemic or synhiemic is by means of recoveries of ringed birds. The results of ringing have demonstrated that the populations in a number of sea-birds are synhiemic. As a good example of this the European populations of the Sandwich Tern (*Sterna s. sandvicensis*) can be mentioned. In fig. 3 the recoveries of birds ringed in Denmark, N. Germany, Holland and England are plotted, and it appears distinctly that all these populations winter in the Benguella Current along tropical W. Africa and S.W. Africa, where they mix freely. So far as can be judged on the evidence of the ringing records the populations in question are completely synhiemic. This is no doubt the case also in many other terns, in which, however, ringing has not yielded equally conclusive results. It is worth

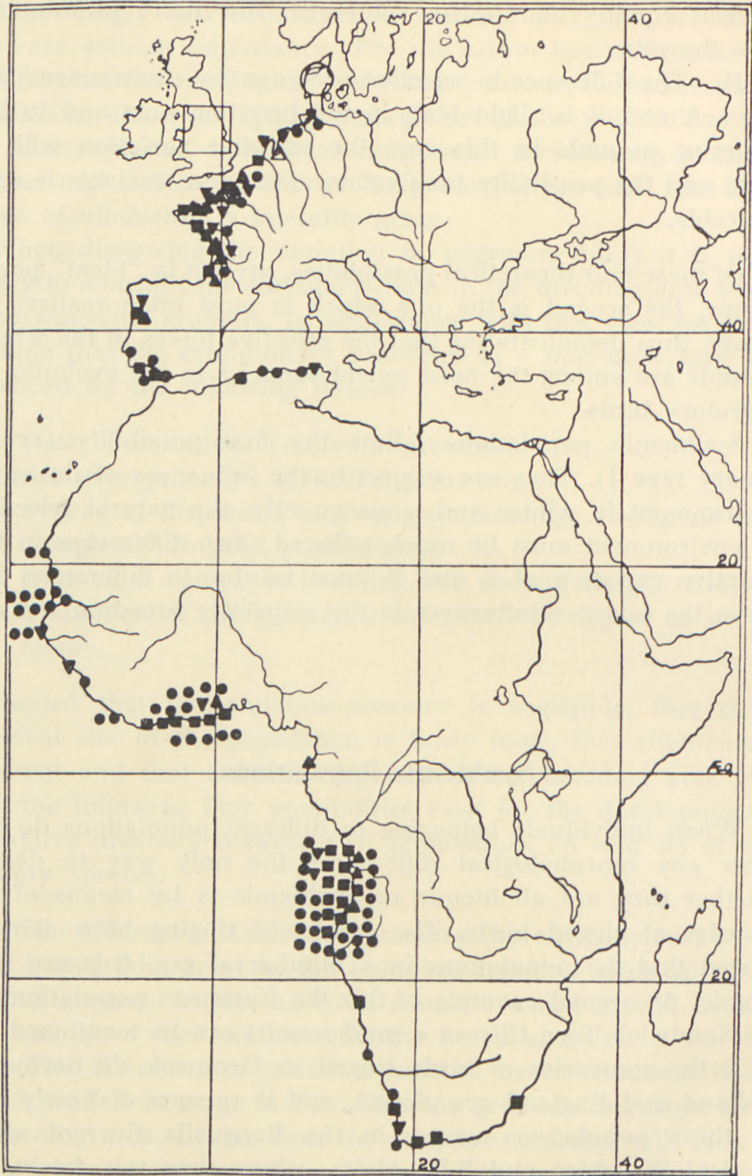


Fig. 3. Recoveries abroad of Danish, German, Dutch and English Sandwich Terns (*Sterna sandvicensis*). Open signatures indicate areas of ringing, solid signatures corresponding recoveries. (After F. SALOMONSEN 1953.)

mentioning that all Scandinavian populations of the Common Tern (*Sterna hirundo*) appear to winter in the coastal waters of S. Africa. In the Cape Province there are winter recoveries (Oct.–April) of 1 Danish, 1 Norwegian, 4 Swedish and 7 Finnish specimens. Of the closely allied Arctic Tern (*Sterna paradisaea*) there are winter recoveries in S. African waters not only of birds originating from European breeding-places but also from N. America and Greenland. Probably all Atlantic populations of this species are synhiemic, wintering in S. African and antarctic waters. The American populations of the Common Tern differ in their migration pattern considerably from the species mentioned. AUSTIN (1951, p. 1), on the basis of very extensive ringing, concludes that the Common Tern of the Western Hemisphere displays a certain amount of “group-adherence” which persists even in the winter-quarter. Presumably this phenomenon will gradually lead to allohiemy. AUSTIN in another paper (1953, p. 39) demonstrated that this development has actually taken place. The birds from the colonies on the Atlantic coast winter in the W. Indies going southwards to Brazil, those from the interior breeding-places winter at the Gulf coast westwards to Florida, while a certain number continue to Central America where some individuals even cross the isthmus of Panama to winter at the Pacific coast south to Peru. The allohiemy of the two populations is partial; there is some overlapping. “Even when the bulk of the recoveries from any group has been made in one restricted area, some of the others are frequently scattered in faraway places” (AUSTIN 1953, p. 44).

The populations of a number of N. Atlantic sea-birds show a pronounced synhiemy. Ringing has shown that this is the case in *Rissa tridactyla*, *Uria lomvia*, *Fulmarus glacialis*, *Gavia stellata* and others. European specimens cross readily the ocean and have been recovered along the N. American coasts.

The type of synhiemy developed among the populations of terns and other sea-birds mentioned above is outlined in fig. 4, I. It shows that neighbouring populations (or rookeries) intermingle in a common extensive winter-quarter, where the individuals mix freely. There is no spatial segregation of the different populations, but the adequate utilization of the available food-resources is secured by an even dispersal of the individuals over

wide areas, in this way preventing large concentrations in any one locality¹.

The most important consequence of synhiemy is the fact that the populations involved share the same habitat in winter and hence are subject to similar environmental influences. Consequently, selection cannot give rise to any adaptive differentiation. The result will be that species with synhiemic populations are monotypic or, at most, show only a slight geographical variation.

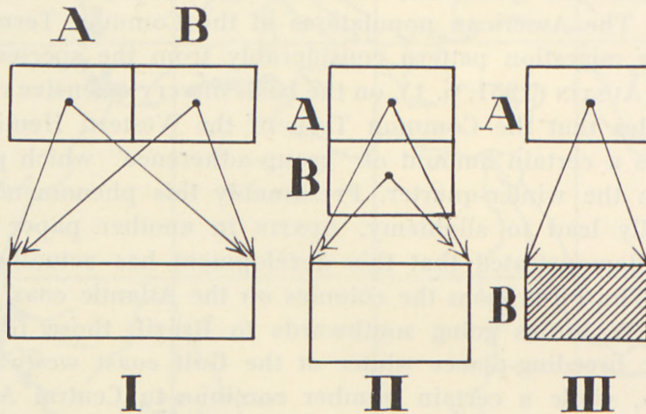


Fig. 4. Three types (I—III) of migration in synhiemic populations. Hatching indicate a resident population. For further explanation cf. text to fig. 1, p. 10.

The adaptive differentiation in these species is due exclusively to selective forces working in the breeding-area (cf. below, p. 21, on *Fulmarus*).

It is possible that the dispersal of the individuals in the breeding area is greater in synhiemic than in allohiemic populations, but the evidence available does not favour this view. As far as we know the homing faculty is equally finely developed in both groups. Ringing of a large number of *Rissa tridactyla* in Greenland has shown that the immature birds wander far and wide on the Atlantic and do not return to the breeding place in the first summer. However, in spite of the long absence and the extensive movements on the ocean, when they are two years old they return regularly to the area in which they hatched (BER-

¹ This is of course dependent on the distribution of the food. In areas rich in food (like the Newfoundland waters) large concentrations of birds may occur.

TELSEN 1932, p. 37); the places of recovery were all situated within 50 km of the place of hatching. It appears, however, that the adherence to the breeding-place is rather unstable in many colonially breeding sea-birds, *e. g.* the Sandwich Tern. In this species the dispersal is rather wide. There are two instances of a specimen ringed in northern Jutland, Denmark, in subsequent years being recovered as breeding in N. W. Germany (Mellum). Species, in which this phenomenon is common, have few possibilities of development of geographical races. Only few instances of long-distance dispersal in the breeding area are known. A very pronounced example offered a Ruff (*Philomachus pugnax*) ringed as nestling in Denmark, recorded in the breeding-time at Archangelsk in N. Russia¹. This case may be indicative. The Ruff has an enormous breeding area and yet does not show any geographical variation. However, we do not know whether its populations are allohiemic or synhiemic.

Strict synhiemy is developed in the populations of the herbivorous birds which like the Waxwing (*Bombycilla garrulus*), the Crossbill (*Loxia curvirostra*) and a number of finches, tits, etc., undertake irregular irruptions over wide areas in correlation with fluctuations in the crop of their food-plants. Ringing has revealed some facts about the movements of such species. In the case of the Waxwing a specimen ringed in winter in Poland was recovered the subsequent winter at Chita in eastern Siberia, 5700 km distant. This implies synhiemy among widely scattered populations. In the Crossbill a case of long-distance dispersal is known, *viz* a specimen ringed as nestling in Denmark, recovered two years later breeding in Czechoslovakia. A similar case is known in the Coal-Tit (*Parus ater*), of which species a Czechoslovakian specimen was found breeding in Switzerland after an irruption. The nomadic populations of these species are characterized by absolute synhiemy and excessive dispersal, hence they do not show any subspeciation².

A sort of synhiemy is found in the populations of most ducks, this holding good of both surface-feeding and diving ducks. The populations are often allohiemic, but the dispersal (of the males)

¹ STRESEMANN (1934, p. 686) mentions a few other examples of long-distance dispersal.

² Many of these species possess a number of resident or normally migratory populations, which may form distinct subspecies.

in the breeding areas is extraordinarily great, and this results in a subsequent mixture of the populations in the winter-quarters, which makes the allohiemy illusory. The extensive dispersal is due to a peculiar migration pattern in these birds for which LANDSBOROUGH THOMSON (1931, p. 382) has proposed the term "abmigration". The chance for adaptive differentiation in species with abmigration is practically nil. In most ducks the populations of the New and Old World keep separate and often form distinct subspecies. In some few species, however, the abmigration covers all populations, which implies that the panmictic unit ranges through the entire holarctic region. The Long-tailed Duck (*Clangula hiemalis*) exhibits probably the most extreme case of this development. This is evidenced by some interesting recoveries of ringed birds. A number of nestlings were ringed at Disko Bay, West Greenland in 1947. Of these birds one was recovered in 1950 as a breeding-bird in N.W. Canada, not far from the Alaskan border, where the local populations move to the Pacific in winter. Another specimen was recovered in Jan. 1951, wintering in the southern Baltic Sea, where the winter-visitants of this species usually originate from N. Russia, as evidenced by ringing (cf. SALOMONSEN 1952, p. 113; & 1953, p. 134). Russian birds will easily mix with Siberian birds wintering in the Pacific. This shows that the Long-tailed Duck in a few years' time obviously is capable of undertaking a circumpolar "migration".

A pronounced synhiemy appears to be present among the populations of a number of waders, just as in most sea-birds, but the ringing results are usually not conclusive. Owing to extensive ringing of the Dunlin (*Calidris alpina*) it is possible to say that the populations passing Denmark, Sweden and Norway, respectively, on migration, mainly are synhiemic, although the Norwegian birds differ slightly from the Swedish-Danish ones (SALOMONSEN 1953, p. 156).

Lack of recoveries in the tropics makes it difficult to form any idea of the type of wintering in the African winter-visitants. Ringing has yielded good results only in a few cases. The populations of the Stork (*Ciconia c. ciconia*) are synhiemic, while those of the Swallow (*Hirundo rustica*) display a distinct allohiemy (maps and description by SCHÜZ 1952, p. 53).

Allohiemy is present in the greater part of the polytypic species with more than one subspecies wintering in tropical Africa, sometimes, as in the case of *Phylloscopus trochilus* and its races (*trochilus*, *acredula* and *yakutensis*) with a broad zone of overlap (q in fig. 2) between the winter-ranges of the races (cf. TICEHURST 1938, p. 33—38). The subspecies of its near ally *Ph. borealis* (*viz: borealis*, *examinandus*, *xanthodryas* and *kennicotti*), which all winter in Malaysia and the Philippines, appear to be synhiemic, but the winter-range is not properly worked out. A pronounced synhiemy is displayed also by the members of the variable group *Motacilla flava*. In Kenya Colony in British East Africa no less than 5 forms are known to winter (*flava*, *thunbergi*, *beema* (rare), *lutea* and *feldegg*). The synhiemy is not absolute, but two forms at least appear to share the same winter-quarter in most districts of Africa and India. The evolutionary history of *Motacilla flava* is very complicated. The capricious combination of clear-cut colour patterns is apparently due to random fixation of mutants, but the plumage design can of course form the exterior manifestation of the presence of genes with certain pleiotropic effects on adaptation. At any rate, the geographical differentiation in this puzzling group of birds has a historical background and is due to factors which have worked in several isolated breeding areas. It is hardly possible that influences originating from conditions in the winter habitat have played any part in this development.

When synhiemic populations display morphological differences and these are not the result of a former isolation of the populations, they must be due to adaptive variation in the present breeding areas. A subspecific differentiation often takes place when the breeding areas of the two populations are situated in widely differing life-zones. An example of this type is shown in fig. 4, II. The breeding areas of the two synhiemic populations A and B are situated in different latitudes and therefore, presumably, must be subject to considerable differences in temperature conditions, etc.

A development along these lines has taken place in a number of palæarctic and nearctic birds. The two Atlantic populations of the Fulmar (*Fulmarus glacialis*), *viz: F. g. glacialis* and *F. g. minor*, are synhiemic in the off-shore and pelagic zones of Labrador and Newfoundland. The short-billed *F. g. minor* (which follows Allen's rule) breeds in the high-arctic region, the nominate form in low-arctic and boreal environments. The races of *Phylloscopus borealis* form another example. The populations breeding

in various Pacific areas (Japan, Kamtshatka, Alaska) differ from those breeding in Siberia¹.

In some species the synhiemic subspecies follow Bergmann's rule. This rule denotes that in a species the body-size (in birds usually measured by the wing-length) increases with decreasing air-temperature of the habitat. In populations inhabiting more northern regions the body-size is therefore often larger than in those living further south. An example of synhiemic populations which follow Bergmann's rule is offered by the Cuckoo (*Cuculus canorus*). The larger northern subspecies (*C. c. canorus*) and the smaller Mediterranean one (*C. c. bangsi*) are apparently synhiemic, both wintering in tropical Africa.

A special case of synhiemy is developed in species in which a northern migratory population winters in the area of a southern sedentary form (cf. fig. 4, III). In the following examples the synhiemic populations follow Bergmann's rule:

	Northern migratory form:	Southern sedentary form:
<i>Acrocephalus orientalis</i>	<i>orientalis</i>	<i>harterti</i>
<i>Pyrrhula pyrrhula</i>	<i>pyrrhula</i>	<i>minor</i>
<i>Anthus richardi</i>	<i>richardi</i>	<i>rufulus</i>
<i>Dicurus leucophaeus</i>	<i>leucogenis</i>	<i>bondi</i>
<i>Ninox scutulata</i>	<i>scutulata</i>	<i>borneensis</i>
<i>Butorides striatus</i>	<i>amurensis</i>	<i>javanicus</i>
<i>Egretta alba</i>	<i>alba</i>	<i>modesta</i>
<i>Ixobrychus minutus</i>	<i>minutus</i>	<i>payesii</i>

A number of other instances might be cited, but they are not all as typical as those mentioned above. In some cases the morphological differences among the synhiemic populations are very great, as *e. g.* in the forms of the Paradise Flycatcher (*Terpsiphone paradisi*), in which the distinct *T. p. incei* and *T. p. atrocaudata*² winter in Malaysia among the sedentary *T. p. affinis*. In other cases the synhiemic populations do not differ at all, as *e. g.* in a number of species of which the Scandinavian migratory populations winter in Great Britain among the in-

¹ I want again to emphasize that this is not a good example since the winter distribution of the populations of *Phylloscopus borealis* is not properly worked out; some of them may be allohiemic.

² *Terpsiphone paradisi incei* and *T. p. atrocaudata* are allopatric, but the latter is usually considered a full species.

digenous resident birds; in the Starling (*Sturnus v. vulgaris*), however, the two populations display important differences in physiology (cf. BULLOUGH 1946, p. 165).

When comparing the status of allohiemic and synhiemic populations it is obvious that the greatest amount of evolutionary potentiality is available to allohiemic populations. In synhiemic populations, on the other hand, the intrapopulation variability in winter is much greater (best to be seen, of course, when the populations are subspecifically different), because the variability is not reduced by local differences in the selection pressure in winter-time (cf. p. 15). The main advantage of synhiemy is consequently to be sought in the fact that a larger number of gene-combinations, with a greater variation in adaptive value, will be preserved than under the rigid system of allohiemy. This is of particular importance in case of environmental changes.

Longitudinal Migration of Allohiemic Populations.

The arrangement of allohiemic populations in the winter grounds is much more varied and more complicated than in the case of the synhiemic populations¹. The forms of migration which lead to allohiemy can be divided into four groups: 1. Longitudinal Migration, 2. Parallel Migration, 3. "Leap-frog" Migration, and 4. Crosswise Migration. These terms are rather inappropriate and have been chosen only for the sake of brevity. The longitudinal and parallel types of migration occur much more frequently than the two other types.

The term "Longitudinal Migration" is just a brief designation for the type of migration in which the migratory populations move along the same degree of longitude. Actually, this category comprises the cases in which one of the two populations concerned breeds under more unfavourable life-conditions, primarily at lower air-temperatures, than does the other population. Such conditions are generally found further north, but the term "longitudinal" should not be applied too literally. The lower

¹ "Allopatric diversity has one more dimension than the sympatric one"; DOBZHANSKY 1951, p. 136.

temperatures may prevail to N.E., as is very often the case in Europe.

In the following discussion the adaptive variation will be tested in its accordance with Bergmann's rule. This rule, working with quantitative measurements, is the most suitable for a comparison of populations, and the size differences are obviously of adaptive significance.

Types of longitudinal migration are shown in fig. 5. In migration type IV the population (A) which has the northernmost

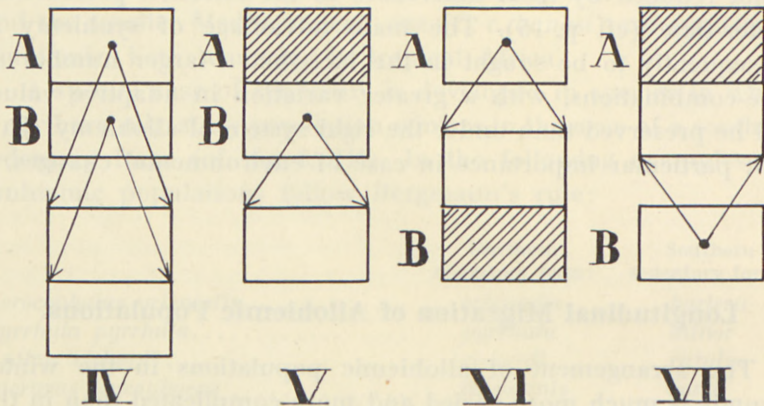


Fig. 5. Four types (IV—VII) of longitudinal migration in allohiemic populations. Hatching indicates a resident population. For further explanation cf. text to fig. 1, p. 10.

breeding area has also the northernmost wintering ground, *i. e.* the winter-quarters of the two populations A and B are situated in the same latitudinal sequence as are the breeding areas. In this migration type the selective forces in the breeding area and in the winter-quarter, respectively, affect the populations in a parallel way and hence sum up their influences. Good examples of species which follow this type of migration are found among American fringillids, as *e. g.* *Carduelis hornemanni* (*hornemanni* and *exilipes*)¹, *Carduelis flammea* (*rostrata* and *flammea*) and *Aimophila aestivalis* (*bachmanni* and *aestivalis*). *Anser caerulescens* (*atlanticus* and *caerulescens*) could also be mentioned. Of Old World instances can be mentioned *Tringa totanus* (*robusta* and *totanus*), *Turdus musicus* (*coburni* and *musicus*), and *Muscicapa*

¹ The populations are given in brackets, "A" being the first mentioned.

parva (*albicilla* and *subrubra*). The variation in all these species are in agreement with Bergmann's rule.

This migration type (IV, in fig. 5) is not so commonly established as should be expected. The populations frequently have a tendency to synhiemy in such cases, as shown by ringing in the Scandinavian and Central European populations of *Fringilla doelebs*, *Turdus philomelos*, *Ardea cinerea*, *Anas platyrhynchos*, *Anas crecca*, *Columba palumbus*, *Vanellus vanellus* and many others. In other cases the southern population (B in fig. 5) is resident and is synhiemic with the northern one (A), which winters in the area of B. This gives the migration type III (cf. fig. 4). Of the numerous examples of this type can be mentioned the large number of species in which the Scandinavian populations winter among their sedentary congeners in the British Isles (cf. above, p. 22), and among American birds the Alaskan species wintering among the sedentary populations of California.

In another type of migration (V in fig. 5) the northern population (A) is resident, while the southern one (B) is migratory. In such cases the difference in selection-pressure (by environment) between A and B is greater in the wintering grounds than in the breeding areas, and consequently the adaptive variation will be a result mainly of the conditions in the wintering grounds (evolutionary type II; cf. p. 14). The following species can be mentioned as examples:

	Northern, resident form:	Southern, migratory form:
<i>Melospiza melodia</i>	<i>sanaka</i>	<i>melodia</i>
<i>Anthus spinoletta</i>	<i>kleinschmidti</i>	<i>littoralis</i>
<i>Sturnus vulgaris</i>	<i>faroensis</i>	<i>vulgaris</i>
<i>Anas platyrhynchos</i>	<i>conboscas</i>	<i>platyrhynchos</i>
<i>Mergus serrator</i>	<i>schioeleri</i>	<i>serrator</i>
<i>Phalacrocorax carbo</i>	<i>carbo</i>	<i>sinensis</i>
<i>Haematopus ostralegus</i>	<i>occidentalis</i>	<i>ostralegus</i>
<i>Fratercula arctica</i>	<i>naumanni</i>	<i>grabae</i>
<i>Uria aalge</i>	<i>hyperborea</i>	<i>aalge</i>
<i>Plotus alle</i>	<i>polaris</i>	<i>alle</i>

In all species in this list the populations have responded in conformity with Bergmann's rule, the northern form being the larger. In some of these species, however, the two populations are not quite comparable from an evolutionary point of view.

This holds good of the species with an endemic sedentary population in the Faeroes (*Sturnus vulgaris*, *Anthus spinoletta*) and the Aleutians (*Melospiza melodia*). These populations are completely isolated (*i. e.* dispersal from neighbouring populations is practically non-existent) and are numerically small and therefore subject to the Sewall Wright effect. In the large continental populations, with which they are compared, these factors are of no influence. A similar difference, although not so pronounced, exists between the Central European and the Iceland populations of *Tringa totanus* and *Turdus musicus*, dealt with above (p. 24). Most of the other "A"-populations are northern sea-birds in which the breeding-area usually is isolated from that of the southern migratory B-population. However, this does not necessarily need to be so. In the North American Herring-Gull (*Larus argentatus smithsonianus*) three groups can be distinguished, according to EATON (1934, p. 70). The populations breeding along the Atlantic coast from New Brunswick to Massachusetts undertake extensive first-year migrations southwards along the coast, often reaching the Gulf States. The populations breeding in the interior continent, around the Great Lakes, are characterized by a wide dispersal during the first winter throughout eastern North America, from James Bay south along the rivers to the Gulf Coast of Texas and Mexico. Finally, the northern populations, breeding in the St. Lawrence region, are resident, or at least have no true habit of migration. The three groups are typically allohiemic, their winter ranges only slightly overlapping. EATON is of the opinion that the three groups may show morphological differences.

In the Cormorant (*Phalacrocorax carbo*) there is a gradual increase in the distance of migration from north to south. The population of low-arctic W. Greenland is resident, in so far as it never leaves the country and in winter moves so far to the south only that it avoids the un-broken ice-cover. The population breeding at the northern shore of St. Lawrence is migratory, but the movements are short, the winter range covering the southern coast of Newfoundland, the southern and western coast of Nova Scotia and the northern coast of Maine (LEWIS 1937, p. 11). Finally, the boreal population breeding at the Danish waters and belonging to *P. c. sinensis* winters in the subtropic

environment of the Mediterranean countries (SALOMONSEN 1953, p. 142 and fig. 46).

The migration type VI (fig. 5) is the opposite of V. The northern population (A) is migratory, but does not reach the area of the southern form B, which is resident. The Linnet (*Carduelis cannabina*) can be given as an example. Ringing in Scandinavia has shown that the breeding population spends the winter in Belgium and France, rarely south to Algeria. South of the winter-quarter of the Scandinavian population (Spain, North Africa) the subtropical, sedentary *C. c. mediterranea* lives. The wing-length of the latter is 75–80 mm, compared with 78–82, rarely 85, in the Scandinavian population (HARTERT 1910–38, p. 2052). Still smaller forms (*nana*, *harterti*, etc.) inhabit the Canary Islands and Madeira. *C. c. cannabina* and *C. c. mediterranea* are usually allohiemic, although there is a slight overlap. The difference in environment between the ranges of *C. c. cannabina* and *C. c. mediterranea* is probably greater in summer than in winter, although generally not much. At any rate, the difference in body-size between the two subspecies is no doubt a response to the combined effect of the natural selection in the breeding area and the winter ground. The well-marked subspecies of the Canaries owe their racial characters not only to adaptive variation, but also to the complete isolation and the limited number of individuals (cf. the Faeroe races mentioned above, p. 26). The same holds good of the other insular forms (of the species *Falco tinnunculus*, *Turdus merula* and *Asio otus*) mentioned in the list below. Other examples of this type of migration, all in conformity with Bergmann's rule:

	Northern, migratory form:	Southern, resident form:
<i>Corvus corone</i>	<i>cornix</i>	<i>sardonius</i>
<i>Carduelis carduelis</i>	<i>carduelis</i>	<i>africana</i>
<i>Carduelis cannabina</i>	<i>cannabina</i>	<i>mediterranea</i>
<i>Turdus merula</i>	<i>merula</i>	<i>cabrerae</i>
<i>Falco tinnunculus</i>	<i>tinnunculus</i>	<i>canariensis</i>
<i>Asio otus</i>	<i>otus</i>	<i>canariensis</i>
<i>Pipilo erythrophthalmus</i>	<i>erythrophthalmus</i>	<i>alleni</i>
<i>Agelaius phoeniceus</i>	<i>phoeniceus</i>	<i>floridanus</i>
<i>Gallinula chloropus</i>	<i>chloropus</i>	<i>parvifrons</i>
<i>Phalacrocorax pelagicus</i>	<i>pelagicus</i>	<i>resplendens</i>

This type of migration grades into type III (fig. 4), in which the two populations in question are synhiemic. It was already stressed that in *Carduelis cannabina* a slight synhiemy is present between the two subspecies discussed (*cannabina* and *mediterranea*). A good example of the transition to type III is offered by *Agelaius phoeniceus*, in which the winter-quarter of the northern migratory forms (e. g. the nominate form of eastern North America) extends south into the area of the southern sedentary forms (e. g. *littoralis* at the Gulf Coast; cf. OBERHOLSER 1938, p. 584). In this wide-spread and very plastic species a northern partly migratory form (*A. p. phoeniceus*) is replaced in the south by a number of sedentary forms with small body-size and of restricted ranges in southern U.S. and in the West Indies. The coastal regions of Florida alone is inhabited by three forms. The environmental differences between the habitats of these forms are certainly much smaller than those present in the huge area inhabited by the nominate form, extending from southern Canada to the Gulf States. The reason for this phenomenon is no doubt that racial differentiation is favoured in the extreme sedentary populations in the south, while it is prevented or at least considerably inhibited in the northern populations which in winter scatter over extensive areas and are largely synhiemic. This demonstrates how adaptive variation is impeded by synhiemy.

Among the longitudinal types of migration should finally be mentioned type VII (fig. 5), which is a special case, established, as far as I know, in some alcids only. In birds following this migration type the northern population (A) is sedentary as in type V, but the southern population (B) moves northwards in winter, approaching the range of A. The environmental differences between the winter-quarters of the two populations are thus considerably reduced. This migration type is realised e. g. in *Uria aalge*, in which the southern population (*U. a. albionis*) of Heligoland and England undertakes a first-winter migration northwards to southern Norway. Here they mix with the indigenous population (*U. a. aalge*), which, however, partly moves southwards in winter. All these populations keep strictly off the wintering grounds of the large-sized northern resident *U. a. hyperborea*; the populations are completely allohiemic (cf. HOLGERSEN 1951, p. 53).

Parallel Migration of Allohiemic Populations.

In these types of migration the two populations A and B are neighbouring, living approximately in the same latitude, and migrate side by side in a parallel way, as outlined in the different types shown in fig. 6. The greater part of migratory species with allohiemic populations display this type of migration. In both the Old and the New World a great number of species inhabit the continent in its entire breadth and, moving south, segregate in winter in an area which has a huge extent in east-western direction. In many species the different populations have de-

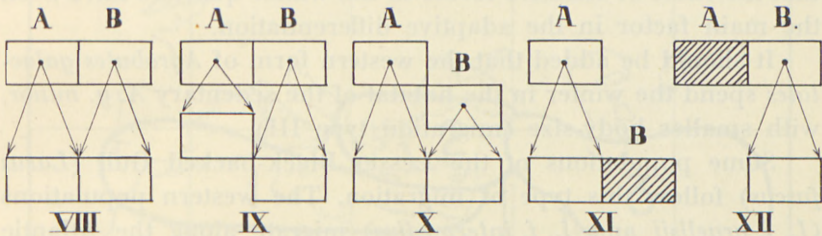


Fig. 6. Five types (VIII—XII) of parallel migration in allohiemic populations. Hatching indicates a resident population. For further explanation cf. text to fig. 1, p. 10.

veloped a high degree of allohiemy and hence are subject to the influence of widely different environmental factors in the winter-quarters. There is a considerable variation in this form of migration.

In type VIII (fig. 6) the two neighbouring populations undertake a migration of almost the same extent, that of "A" not being appreciably shorter or longer than that of "B". Among the numerous examples the superspecies *Lanius collurio*—*L. cristatus* forms one of the most beautiful cases. According to the map prepared by STRESEMANN (1927, tafel II) the Asiatic subspecies demonstrate a practically complete allohiemy. When combining this map with that prepared by GEYR (1926, p. 388), concerning the distribution of *L. c. collurio*, it appears that the populations wintering in Africa are allohiemic also. A zone of overlap is present only in N.E. Africa, where *L. c. phoenicuroides* (belonging to the *collurio* group) is partly synhiemic with *L. c. isabel-*

linus (belonging to the *cristatus* group). The superspecies *Luscinia luscinia*—*L. megarhyncha* offers another good example of almost absolute allohiemy of the two populations, according to the map issued by NIETHAMMER (1937, Vol. I, p. 415). A number of similar cases could be mentioned, but I shall restrict myself to that of *Agrobates galactotes*. The breeding areas and winter-quarters of the three migratory subspecies of *Agrobates galactotes* are shown in fig. 7. This example is particularly interesting because the breeding areas of the said races are contiguous while the winter-quarters are mutually isolated. Hence the populations are probably subject only to an insignificant interpopulational dispersal in winter. In such cases it is obvious, in my opinion, that the effect of selective forces in the winter-quarters have been the main factor in the adaptive differentiation.

It should be added that the western form of *Agrobates galactotes* spend the winter in the habitat of the sedentary *A. g. minor*, with smaller body-size (migration type III).

Some populations of the Lesser Black-backed Gull (*Larus fuscus*) follow this type of migration. The western populations (*L. f. graellsii* and *L. f. intermedius*) migrate along the Atlantic coasts, the East Danish *L. f. fuscus* through Central Europe to the eastern Mediterranean and tropical Africa, and the Swedish and Finnish *L. f. fuscus* via Russia to the Black Sea and sometimes to Africa. There is some overlapping in the winter-quarters of the populations of *L. f. fuscus*, but the allohiemy, nevertheless, is marked; cf. fig. 8, based on recoveries of ringed birds.

In a number of waders the subspecies are allohiemic, although in most cases there is some overlapping of the respective winter-quarters. Such cases are *Pluvialis dominica* (*dominica* and *fulva*, which are absolute allohiemic), *Numenius arquata* (*arquata* and *lineatus*), *N. phaeopus* (*phaeopus* and *variegatus*), *Haematopus ostralegus* (*ostralegus* and *osculans*), *Limosa limosa* (*limosa* and *melanuroides*) and so forth. In *Limosa l. lapponica* and *L. l. baueri*, which apparently are completely allohiemic, the morphological differences are greater than in the other waders mentioned. *Sterna hirundo* (*hirundo* and *longipennis*) forms a similar case.

The tendency to allohiemy is seen in smaller units too. Ringing in European populations of a number of species has demonstrated that the populations scatter in a fan-like manner, moving

to the nearest areas with a mild winter-climate, segregating into partly allohiemic units. A good example is the Starling (*Sturnus vulgaris*) as shown in a figure in SCHÜZ 1952, fig. 12, p. 46 (with winter-isotherms drawn). Another example is the Redshank (*Tringa totanus*), as shown in fig. 12 in this paper. The degree of allohiemy of the populations in this species is pronounced, but many other species are similar. In fig. 9 is shown the distribution of a number of populations of the Black-headed Gull

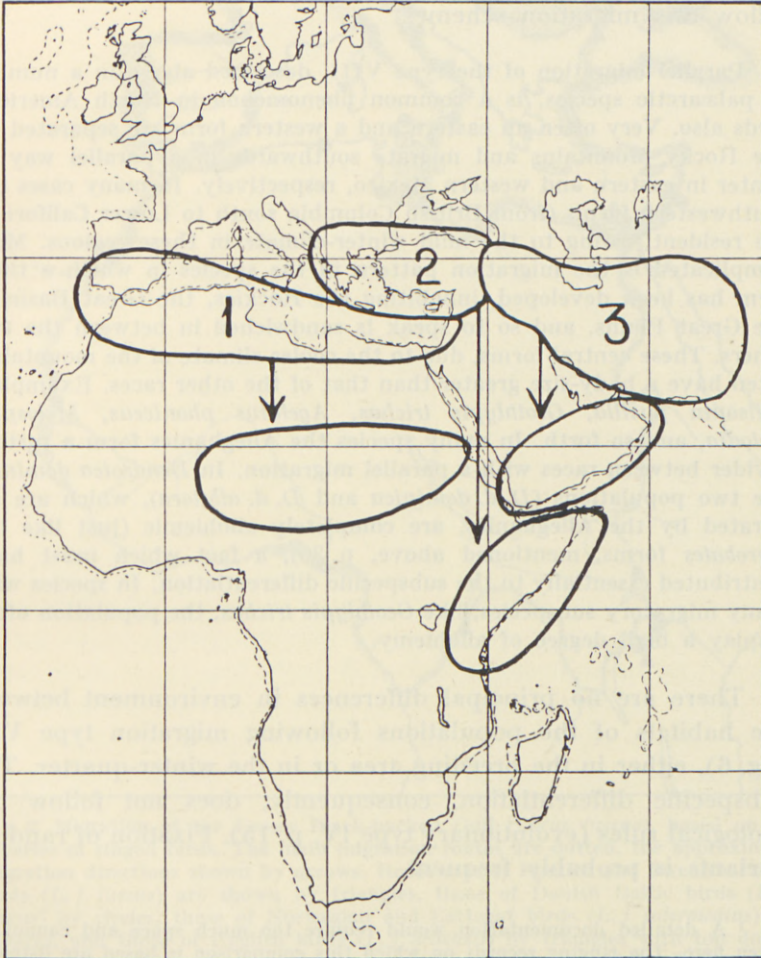


Fig. 7. Breeding areas and winter-quarters of the palaeartic forms of *Agrobates galactotes*. 1: *A. g. galactotes*, 2: *A. g. syriacus*, 3: *A. g. familiaris*.

(*Larus ridibundus*) in Europe, based on ringing records. The different populations demonstrate a marked allohiemy, although the overlapping is considerable.

A situation similar to that found in *Larus ridibundus* is widespread among Scandinavian birds. A comparison of Danish Swedish and Finnish populations of migratory birds reveals that a pronounced allohiemy is established in no less than 22 species, as demonstrated by recoveries of ringed birds¹. A greater number of recoveries would no doubt show that still many other species follow this migration scheme.

Parallel migration of the type VIII, described above in a number of palæarctic species, is a common phenomenon in North American birds also. Very often an eastern and a western form are separated by the Rocky Mountains and migrate southwards in a parallel way to winter in eastern and western Mexico, respectively. In many cases the southwestern forms (from British Columbia south to Lower California) are resident, owing to the mild winter-climate in these regions. More complicated is the migration pattern in the species in which a third form has been developed, inhabiting the Rockies, the Great Basin or the Great Plains, and so to speak is sandwiched in between the two others. These central forms, due to the cooler climate of the mountains, often have a body-size greater than that of the other races. Examples: *Wilsonia pusilla*, *Geothlypis trichas*, *Agelaius phoeniceus*, *Melospiza melodia*, and so forth. In many species the Alleghanies form a further divider between races with a parallel migration. In *Dendroica dominica* the two populations (*D. d. dominica* and *D. d. albilora*), which are separated by the Alleghanies, are completely allohiemic (just like the *Agrobates* forms, mentioned above, p. 30), a fact which must have contributed essentially to the subspecific differentiation. In species with many migratory subspecies, like *Geothlypis trichas*, the population often display a high degree of allohiemy.

There are no principal differences in environment between the habitats of the populations following migration type VIII (fig. 6), either in the breeding area or in the winter-quarter. The subspecific differentiation, consequently, does not follow the ecological rules (evolutionary type IV, p. 15). Fixation of random variants is probably frequent.

¹ A detailed documentation would require too much space and cannot be given here. The ringing records on which this comparison is based are listed in my book SALOMONSEN 1953.



Fig. 8. Migration of the Lesser Black-backed Gull (*Larus fuscus*), based on recoveries of ringed birds. The main migration routes are dotted, the approximate migration directions shown by arrows. Recoveries of Finnish and Swedish Baltic birds (*L. f. fuscus*) are shown by triangles, those of Danish Baltic birds (*L. f. fuscus*) by circles, those of Norwegian and Cattegat birds (*L. f. intermedius*) by squares, and those of English birds (*L. f. graellsii*) by triangles with top down. Figures give number of recoveries in the locality in question. (After F. SALOMONSEN 1953.)

A large number of migratory species with a wide distribution in the northern hemisphere are divided into populations which are completely separated in the breeding areas and show absolute allohiemy. Many of these species follow migration type VIII. When the environment is homogenous in both the breeding areas and in the wintering grounds of these populations, the evolutionary type IV (p. 15) will often be realized. When the populations in question have been separated for a sufficient lapse of time they may drift apart as species. This has happened in many species with a nearctic and a palæartic population, separated completely from each other. In fact, most of the examples enumerated below are generally treated as species-pairs, probably because the differences between them—which are often very distinctive—are non-adaptive. The following instances of species with an Old and a New World representative have no doubt originally been differentiated by fixation of random variants, in conformity with the evolutionary type IV:

- Anas crecca* (*crecca* and *carolinensis*)
- Anas penelope* (*penelope* and *americana*)
- Aythya fuligula* (*fuligula* and *collaris*)
- Circus cyaneus* (*cyaneus* and *hudsonius*)
- Haliaetus albicilla* (*albicilla* and *leucocephala*)
- Actitis hypoleucos* (*hypoleucos* and *macularia*)
- Himantopus himantopus* (*himantopus* and *mexicanus*)
- Recurvirostra avosetta* (*avosetta* and *americana*)
- Porzana porzana* (*porzana* and *carolina*)

These examples could be augmented with many more, while it would be difficult to make a list of species with a similar distribution which had followed the evolutionary types I—III. There are some few—but not very typical—instances, however.

The populations following the migration type IX (fig. 6) breed under similar environmental conditions, just like those following type VIII, but winter in a highly differing climate, *e. g.* population A in the subtropical region, B in the tropics. In such cases it must be taken for granted that the adaptive variation is due mainly to the effect of the selective forces in the winter-quarters (evolutionary type II, p. 14). The same is the fact in the populations following the migration type XII in fig. 6, in which one of the populations (A) is resident, while in type IX it carries out a short migration.

In the species dealt with below the adaptive variation follows Bergmann's rule, *i. e.* the population wintering more northerly (A) attains larger body-size than population B wintering further south.

The Kingfisher (*Alcedo atthis*) has a large European form (*A. a. ispida*), with wing-length 77—81 mm¹, which moves only slightly to the south in winter, at most to the Mediterranean countries. The East Asiatic form (*A. a. bengalensis*) is strictly migratory and leaves altogether eastern Siberia and Manchuria in the autumn, wintering in the area from North China to Malaysia and the Philippines. It is a small form with wing measuring 68—74 mm. In the White Stork (*Ciconia ciconia*) just the opposite takes place. A smallish European form (*C. c. ciconia*, with wing 560—620 mm) winters in subtropical South Africa, a small Turkestan form (*C. c. asiatica*, with wing 590—620) winters in India, while a large East Asiatic form (*C. c. boyciana*, with wing 620—670), breeding from S.E. Siberia to Japan, winters in North China and is almost resident. Other instances: The European Grasshopper Warbler (*Locustella n. naevia*; wing 63—66 mm) winters in subtropical N. Africa (Morocco, Algeria), while the smaller W. Siberian form (*L. n. straminea*; wing 57—60) winters in tropical India. In the superspecies *Phylloscopus occipitalis*—*Ph. coronatus*² the large form *Ph. occipitalis* (wing 64—70.5)³, breeding in Bokhara, Afghanistan and Kashmir, winters in northern India, the smaller *Ph. c. coronatus* (wing 60.5—66)³, breeding in S.E. Siberia, N. China and Japan, winters in Siam, Malay Peninsula, Sumatra and Java, and finally *Ph. c. ijimae* (wing 62—65)³, breeding on Seven Islands off Hondo, winters in the Philippines (cf. GILLIARD 1950, p. 496). The three forms have thus complete allohiemy.

To the same category belong the North European and North American populations of the Peregrine Falcon (*Falco peregrinus*). The North European form (*F. p. peregrinus*) moves only slightly south in winter, from Sweden to Germany-France, while the North American form (*F. p. anatum*) goes to the tropics, from where there are several recoveries of ringed birds. There is no difference in body-size between the two populations, but *F. p. anatum* is much darker than *F. p. peregrinus* in the juvenile

¹ According to HARTERT (1910—38, p. 881). When nothing else is stated the measurements given in this paper are based on the figures given by HARTERT (*l. c.*) concerning palæartic birds, and by RIDGWAY (1901—14), concerning nearctic birds.

² These two forms are usually regarded as conspecific, but TICEHURST (1938, p. 162) holds them to be closely allied allopatric species.

³ Measurements from TICEHURST (1938).

plumage (which is kept for a year). This is probably an adaptive character, the variation agreeing with Gloger's rule. This rule denotes that populations inhabiting areas with a higher temperature and a higher degree of moisture tend to be darker.

As an example of migration type XII some populations of

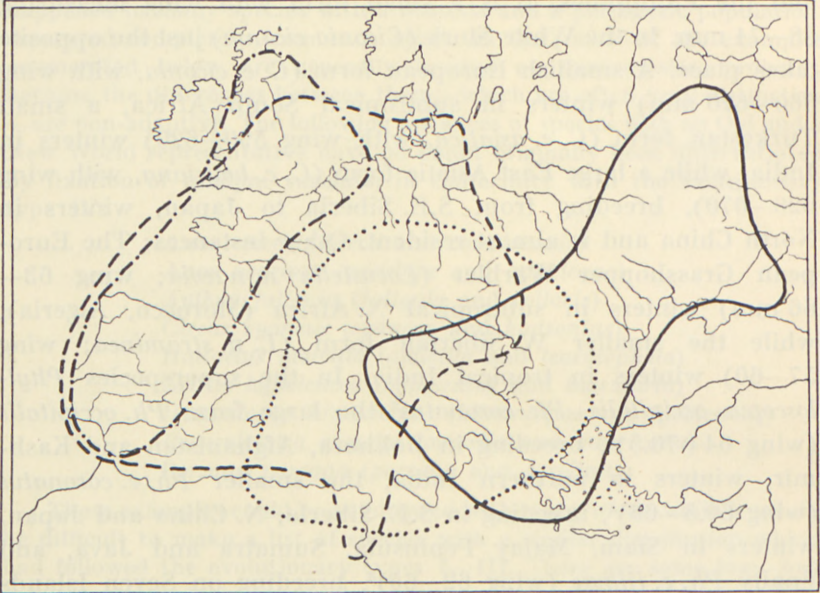


Fig. 9. Distribution of a number of European populations of the Black-headed Gull (*Larus ridibundus*), based on recoveries of ringed birds. Breeding areas: - · - · - · - : Cumberland, England, - - - - - : Oberlausitz, Germany, · · · · · : Ungarn, ————— : Moscow, Russia. (Redrawn after SCHÜZ & WEIGOLD 1931.)

the Redshank (*Tringa totanus*) can be mentioned. The British population (*T. t. britannica*) is mainly resident, while the Danish one (*T. t. totanus*) is strictly migratory, wintering in the subtropics. Another example is offered by the Herring-Gull (*Larus argentatus*). The European populations are usually resident, while a number of the North American ones are highly migratory (cf. above, p. 26).

The migration type X (fig. 6) is just contrary to type IX. Populations A and B have contiguous winter-quarters, situated in about the same latitude, while the breeding area of A is situated much farther north than that of B. Consequently, A makes a

longer migration than B. Migration type XI differs only in the fact that population B is resident. Adaptive variation in populations following types X—XI must be the result of the selection in the breeding area (evolutionary type I, p. 14).

The Lesser Black-backed Gull (*Larus fuscus*) offers a clear example of migration type X. The arctic form *L. f. taimyrensis*, breeding in North Russia, is slightly larger than the boreal Scandinavian *L. f. fuscus*. Both winter in the tropics, *taimyrensis* in Indian waters, *fuscus* from the Black Sea to Central Africa. The difference in body-size demonstrates that these gulls follow Bergmann's rule. Some other examples from the New World: *Pinicola enucleator* (*alascensis* and *flammula*) and *Passerella iliaca* (*iliaca* and *schistacea*). *P. e. flammula* and *P. i. schistacea* are the "B"-forms with smaller body-size than the "A"-forms, thus demonstrating that they follow Bergmann's rule.

Finally, I shall mention two species in which migration type XI is established. *Buteo r. rufinus*, breeding from southern Russia to Turkestan and W. Mongolia, winters in northern India and N.E. Africa from Egypt to Abyssinia. *B. r. cirtensis* breeds from Morocco to Tunisia and southern Algeria, where it is resident. Being much the smaller it follows Bergmann's rule. In addition, the largest form, *B. r. hemilasius*, can be mentioned. It breeds in Central Asia eastwards to S.E. Siberia and winters in N. China. This form and *B. r. rufinus* display migration type IX (p. 34), demonstrating a close resemblance to the migration of the forms of *Ciconia ciconia*, described above (p. 35). Another example of migration type XI is offered by the Little Ringed Plover (*Charadrius dubius*). The European form (*Ch. d. dubius*) winters mainly in tropical Africa and have larger proportions than the resident Indian and Malaysian form (*Ch. d. jerdoni*), thus following Bergmann's rule. There is a tendency to synhiemy, the winter ranges of the two forms overlapping in N.W. India.

"Leap-Frog" Migration.

In many migratory birds the northern populations winter south of the southern ones, *i. e.* the northern and southern popu-

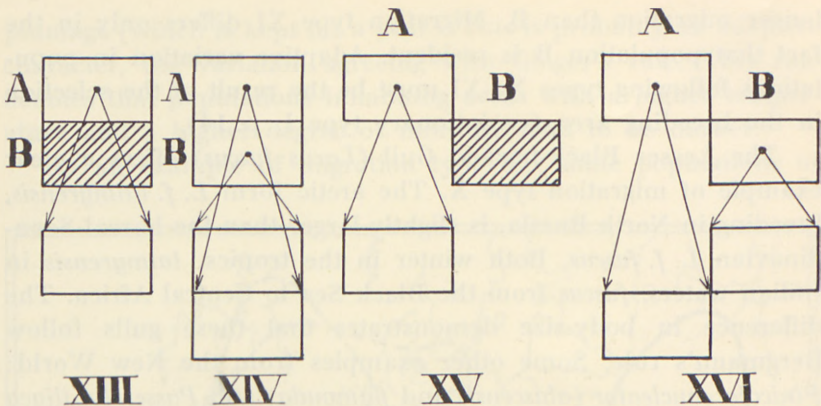


Fig. 10. Four types (XIII—XVI) of leap-frog migration in allohiemic populations. Hatching indicates a resident population. For further explanation cf. text to fig. 1, p. 10.

lations so to speak play at leap-frog with each other during migration. This is shown as migration type XIV in fig. 10. Type XIII is very similar, only is the southern population (B) resident. Leap-frog migration has been developed as well in species with "longitudinal" migration as in those with parallel migration. Type XIII and XIV in fig. 10 show leap-frog migration of the "longitudinal" type, and type XV and XIV the corresponding "parallel" types.

Type XIII and XIV can be combined, as can type XV and XVI. This is demonstrated in a species in which a population C is resident, a population B, breeding north of C, winters south of C, and finally a population A, breeding north of B, winters south of B. Cf. e. g. *Geothlypis trichas*, *Passerella iliaca*, *Charadrius hiaticula*, *Tringa totanus* and other species mentioned below.

There is a wide-spread tendency among migratory species to develop this form of migration. I have studied the recoveries of birds ringed in Scandinavia and found that among the comparatively few species in which ringing has given a fairly good idea of the migration, leap-frog movements are carried out, to a varying extent, in 12 species¹. The origin of this type of migration might be a development of a certain "prolongation" of the migration among the northern populations, as postulated by

¹ For documentation cf. footnote on p. 32.

some students, but in my opinion it is primarily a result of the intraspecific (intergroup) competition, which will necessarily lead to allohiemy. To give an example, which shows the initial stage of leap-frog migration: The Danish population of the Oyster-Catcher (*Haematopus ostralegus*) moves slightly to the S.W. along the Northsea coasts, some being resident. The main winter-quarter extends from Denmark proper along the German and Dutch coasts to North France; only one recovery was made in Vendée, W. France, while 50 % of the recoveries were made in Holland. The Norwegian and Swedish Oyster-Catchers winter in the same area and, consequently, the density of individuals may reach the point of crowding. Owing to this population pressure the individuals arriving later continue slightly longer and settle just south of the others, where the wintering population is more scattered. There are several recoveries of Norwegian birds in Vendée and one of a Swedish bird even in Gironde. In cases like the Oyster-Catcher, where the leap-frog migration is still in its being, the phenomenon may be purely phenotypical and the guiding influence may still be the intraspecific competition. In species with a well-marked leap-frog migration the populations differ genetically in their migration habits, the releasing factors (the proximate causes)¹ no longer being competition (which now is relegated to an "ultimate cause"), but a fixed and stabilized system of inherent mechanisms built up by means of selection.

The first to draw attention to this form of migration was SWARTH (1920, p. 75) in his study of the Fox-Sparrow (*Passerella iliaca*) in western North America. His results have been quoted and commented on in most handbooks on migration (e. g. STRESEMANN 1934, SCHÜZ 1952, SALOMONSEN 1953, etc.). STRESEMANN (1934, p. 666) adds some characteristic examples, viz: *Hirundo rustica (savignyi)* resident in Egypt, *transitiva* breeding in Palestine, wintering in N.E. Africa, *rustica* breeding in Europe, wintering in tropical and southern Africa), *Motacilla flava (pygmaea)* resident in Egypt, *feldegg* breeding in S.E. Europe, wintering in N.E. Africa south to Kenya and Uganda, *flava* breeding in Central Europe, wintering in entire tropical E. Africa and South Africa) and a few others.

¹ Cf. footnote p. 8.

When discussing the adaptive variation in a species with leap-frog migration, following *e. g.* type XIV in fig. 10, it is important to draw attention to the fact that selection by environment in the winter-quarters influences the populations in just the opposite way of that in the breeding areas. According to Bergmann's rule the population A when under the conditions of the breeding area will tend to attain larger proportions than B, but in the winter-quarter it will, on the contrary, tend to be smaller. Populations with leap-frog migration will generally follow the evolutionary type III (p. 14), *i. e.* the adaptive variation will be the result of the influences of the selective forces in both the breeding area and the winter-quarter. However, in species with leap-frog migration these two influences counteract each other. In some species the summer-influences, in other species the winter-influences are the superior ones and stamp the morphology of the populations, while in other instances a certain balance between the two influences is reached. The result of the fight between the counterworking influences is dependent upon the degree of difference in the selection pressure in the breeding areas and in the winter-quarters, respectively. The selection pressure is the result of various influences. Significant in this respect is the degree of difference in climate and other environmental factors between the habitats of the populations (both in summer and winter) and the extension of the period spent in the breeding area and winter-quarter, respectively. It is obvious that the winter-influences will be the more important when the populations in question spend a long time in the winter-quarter, while the stay in the breeding area is short and ephemeral, like in many waders. If, on the other hand, the environmental differences between the breeding habitats of the populations in question are considerable, while those between the respective wintering grounds are slight, the adaptive variation will mainly be due to influences of the selective forces in the breeding area.

The adaptive variation in species with leap-frog migration has usually evolved in accordance with the above considerations, which therefore probably express something essential.

SWARTH's classic study of the Fox-Sparrow, mentioned above, deals with the migratory subspecies inhabiting the coastal areas of western North America. In the table below the variation in

this species is compared with that in its near ally, the Song-Sparrow (*Melospiza melodia*), which is as "plastic" as the Fox-Sparrow, *i. e.* just as readily respond to the comparatively small differences in environment in the extreme maritime climate of N.W. America. The figures in the table give the average wing-lengths of adult males.

	<i>Passerella iliaca</i>		<i>Melospiza melodia</i>
Shumagin Islands	<i>unalaschkensis</i> ¹	84	<i>sanaka</i> 85
Kodiak Island	<i>insularis</i> ¹	84	<i>insignis</i> 82
Kenai Peninsula	<i>sinuosa</i> ¹	82	<i>kenaiensis</i> 78
S.E. Alaska (islands)	<i>townsendi</i> ¹	81	<i>rufina</i> 72
S.E. Alaska (coast)	<i>annectens</i> ¹	82	<i>caurina</i> ³ 69
Brit. Columbia-Oregon	<i>fuliginosa</i> ²	82	<i>morphna</i> 68
N.W. California	} Various forms ¹ 80—84 {		<i>cleonensis</i> 62
Middle California			<i>samuelis</i> 61
Santa Barbara Islands			<i>graminea</i> 60

¹ Migratory, wintering in California, lowland.

² Mainly resident.

³ Migratory, wintering south to North California.

The Fox-Sparrow forms dealt with breed from the islands and coasts of S. Alaska south to the mountains of eastern California, where it inhabits the Canadian zone. Most populations winter in the Californian lowland, where the local differences in climate are small, much smaller indeed than those present between the respective summer habitats extending from Alaska to California (although these differences are not particularly pronounced either). The populations inhabiting the region from Alaska to Oregon make a pronounced leap-frog migration. It appears from the table that the subspecies breeding in the northern areas are slightly larger than the southern ones (wing-length 84 mm, as compared with 81—82). According to Bergmann's rule (other ecological rules are not considered here) this shows a slight preponderance of the influences due to the selective forces in the summer habitats, while the "winter-influences"¹ are negligible. In the resident *Melospiza melodia* the northern populations, likewise, are the larger, but the adaptive variation is enormous compared with that in the Fox-Sparrow. From Oregon

¹ A brief term to signify the adaptive influences due to selection by environment in the winter-quarters.

to South Alaska the average wing-length increases from 68 to 85 mm, forming a gradual cline¹. This is due to the combined effects of the summer- and winter-influences and demonstrates that the "winter-influences"—which the migratory Fox-Sparrow avoids—are much the stronger of the two.

A similar difference in the variation between resident forms and migratory populations which evade the cold season, has recently been demonstrated in the Drongo *Dicrurus leucophaeus* by MAYR and VAURIE (1948, p. 238). In the resident subspecies there is a gradual cline for increasing size from Malaysia to southern China, viz:

<i>D. l. stigmatops</i> (Borneo),	wing-length	127—134	(129.4)	mm
— <i>bondi</i> (Siam),	—	128—138	(132.9)	—
— <i>salangensis</i> (S. China),	—	139—145	(143.0)	—

The North China form, *D. l. leucogenis*, is migratory, and its proportions are similar to those of the South China form *salangensis* (wing-length of *leucogenis*: 138—148 (average 142.8) mm), i. e. the size-gradient is not continued into the N. China population, which is probably due to the fact "that the northern populations are migratory and spend the cold season in the subtropical and tropical parts of eastern Asia" (quotation from MAYR and VAURIE, l. c.).

The counteracting influences of the selective forces in the breeding areas and winter-quarters, respectively, in species with leap-frog migration make the pattern of adaptive variation extremely complicated. In some species the "summer-influences", in others the "winter-influences" predominate. Populations belonging to the same species may differ in their response to the environmental influences. When the northern population (A in fig. 10, XIV) has attained larger body-size than the southern one (B), it will be explained, below, as a reaction on the "summer influences", in accordance with Bergmann's rule. If, on the contrary, population A, which winters south of B, is smaller than B, it will be interpreted as a response to the "winter-influences".

¹ The Californian forms of the two species are not comparable since in this state the Fox-Sparrow is a mountain bird, the Song-Sparrow a lowland bird. The Californian populations of the Song-Sparrow have very small proportions; the smallest body-size is attained in *M. m. pusillula* of the San Francisco salt-marches, with an average wing-length of 58.4 mm. The southern forms, including a number of Mexican populations, have again somewhat greater proportions.

I. Positive reaction to "summer-influences" ($A > B$):

Muscicapa s. sibirica, breeding S.E. Siberia, wintering Malaysia, wing 76—82 mm; *M. s. fuliginosa*, resident on southern slopes of Himalaya, wing 70—75 mm. (Migration type XIII).

Motacilla f. flava, breeding Central Europe, wintering tropical Africa, wing 80—85; *M. f. pygmaea*, resident in Egypt, wing 72—79. (Type XIII).

Jynx t. torquilla, breeding Europe, wintering tropical Africa, wing 86—92; *J. t. mauretanicus*, resident in Algeria, wing 76—82. (Type XIII).

Turdus m. migratorius, breeding from tree-limit in Alaska to northern U.S.A., wintering in southern U.S.A. and northern Mexico, wing (average of ♂♂) 134; *T. m. achrusterus*, resident in middle U.S.A., wing 122; greatly synhiemic with *T. m. migratorius*. (Type XIII).

Hylocichla ustulata swainsoni, breeding from N.W. Alaska to Pennsylvania, wintering from southern Mexico to Argentine, wing 101; *H. u. ustulata*, breeding west-coast of N. America south to California, wintering from Mexico to Ecuador and British Guiana, wing 98. (Type XVI, but the two subspecies are largely synhiemic and the difference in wing-length is slight).

Geothlypis trichas brachyactyla, breeding N.E. America from southern Labrador to Pennsylvania, wintering Bahamas, West Indies and entire eastern Mexico, wing 55; *G. t. trichas*, breeding from Pennsylvania to Texas, wintering from North Carolina to Bahamas and Haiti, wing 53; *G. t. ignota*, resident from South Carolina to Florida. (Type XIII and XIV combined, but geographical variation slight).

Geothlypis trichas occidentalis, breeding S.E. Alaska to California, wintering from Lower California to S.W. Mexico, wing 58; *G. t. sinuosa*, resident in California, wing 53, darker plumage. (Type XIII).

A number of birds have developed in the same way as the western *Geothlypis*, e. g. *Falco columbarius*: *F. c. bendirei*, breeding from N. Alaska to N.E. California, wintering from California to North Mexico, wing 191; *F. c. suckleyi*, resident in W. British Columbia, wing 189, plumage darker. A similar example offers *Hylocichla guttata*: *H. g. guttata*, breeding from Alaska to British Columbia, wintering in California and northern Mexico, wing 88; *H. g. nana*, breeding British Columbia, wintering California, wing 87, darker plumage. The two subspecies are partly synhiemic and share their winter-quarter also with the still smaller Californian *H. g. slevini* (wing 84). There is a large number of similar instances.

II. Positive reaction to "winter-influences" ($A < B$):

Motacilla f. flava, breeding Central Europe, wintering tropical Africa, wing 80—85; *M. f. feldegg*, breeding in Balcan, wintering in N.E. Africa, mainly Sudan and Abyssinia, wing 84—90. (Type XIV; the two subspecies overlap largely in the winter-quarters).

Otus s. scops, breeding in Mediterranean region, wintering in Africa

south to Uganda, wing 144—162; *O. s. cyprius*, resident in Cyprus, wing 153—167. (Type XIII).

Ceryle a. aleyon, breeding eastern North America (north to tree-limit), wintering in southern U.S.A., Central America to Columbia and British Guiana, wing 156; *C. a. caurina*, breeding from Alaska to California, wintering from California to North Mexico, wing 163. There is apparently absolute allohiemy. (Type XVI).

Piranga r. rubra, breeding in eastern U.S.A., wintering from Central Mexico to Ecuador, Peru and Guiana, wing 95; *P. r. cooperi*, breeding in southwestern U.S.A. and northern Mexico, wintering in central Mexico, wing 100. Almost full allohiemy. (Type XVI).

Guiraca c. caerulea, breeding eastern U.S.A., wintering from southern Mexico to Costa Rica, wing 86, darker plumage; *G. c. interfusa* and *G. c. salicaria*, breeding in southwestern U.S.A., wintering in northern Mexico, wing 90, paler plumage. (Type XVI).

Vireo s. solitarius, breeding Canada and northeastern U.S.A., wintering from the Gulf States to Nicaragua, wing 74; *V. s. alticola*, breeding in the Alleghanies, wintering from South Carolina to Florida, wing 80. (Type XIV). There is a pronounced allohiemy among all the 5 subspecies of this species.

Passerculus sandwichensis alaudinus, breeding Alaska and N.W. Canada, wintering from California to Guatemala, wing 72; *P. s. sandwichensis*, breeding Unalaska, wintering southwards to Central California, wing 76. (Type XIV).

Passerculus sandwichensis princeps, breeding on Sable Island, Nova Scotia, wintering at the Atlantic coast to Georgia, wing 76, paler plumage; *P. s. savanna*, breeding boreal zone of eastern Canada and north-eastern U.S.A., wintering from southeastern U.S.A. to north-eastern Mexico and the West Indies, wing 69, darker plumage. (Type XIV).

Falco c. columbarius, breeding in eastern Canada, wintering from Gulf States to Ecuador and northern Venezuela, wing 189; *F. c. richardsoni*, breeding in the Great Plains, wintering from Colorado to north-western Mexico, wing 198. (Type XVI).

The interpretation of the facts set forth above is somewhat schematical, it is true. A much closer analysis of each species is required in order to explain the correlation between migration and geographical variation. There are many sources of error. Island forms of restricted distribution and small population size (like those mentioned of *Passerculus sandwichensis*) are not well suited to be compared with continental forms with a wide range, owing to their different evolutionary history. When comparing mountain forms, like those breeding in the Great Basin of N.W. America, with lowland populations it must be kept in mind that microclimatical, edaphic and other factors are very different in

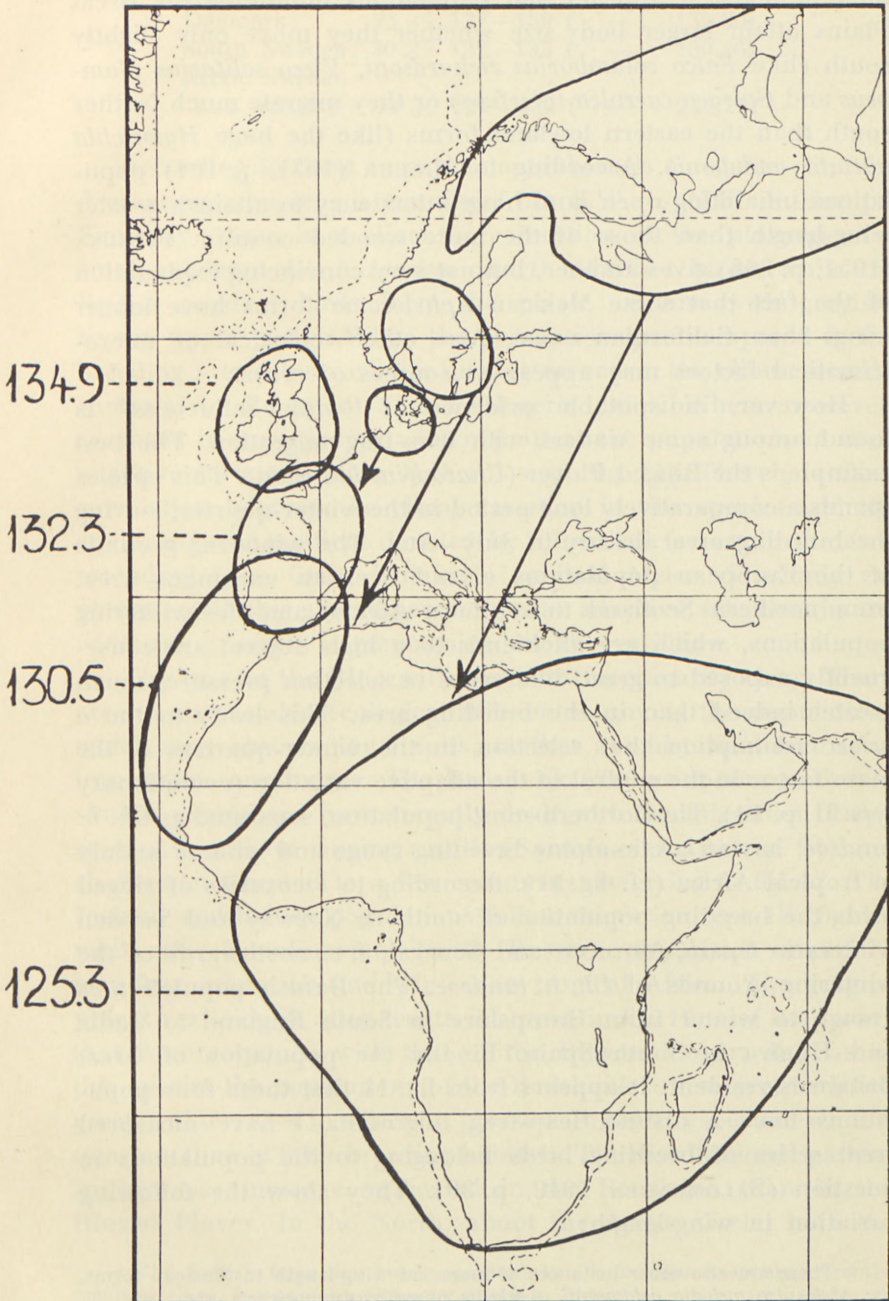


Fig. 11. Breeding-areas and winter-quarters of a number of populations of the Ringed Plover (*Charadrius hiaticula*), partly based on recoveries of ringed birds. Breeding-areas and corresponding winter-quarters are connected by arrows; the British population is resident. Figures inserted a left give average wing-length of the population wintering in the area in question.

their habitats. It appears that populations inhabiting the Great Plains attain larger body size whether they move only slightly south (like *Falco columbarius richardsoni*, *Vireo solitarius plumbeus* and *Guiraca caerulea interfusa*) or they migrate much further south than the eastern lowland forms (like the huge *Hylocichla guttata auduboni*). According to MILLER (1931, p. 104) populations inhabiting open land have a tendency to attain a greater wing-length than those of the more wooded country. PITELKA (1951, p. 366) gives another, but not very convincing explanation of the fact that some Mexican *Aphelocoma* forms have longer wings than Californian ones¹. Also other ecological or micro-climatical factors may appear as sources of error.

However, indisputable evidence of "winter-influences" is found among some waders with leap-frog migration. The best example is the Ringed Plover (*Charadrius hiaticula*). This species spends a comparatively long period in the winter-quarter, leaving the breeding area already in July—Aug. The wintering grounds of the European populations extend over an enormous area, from northern Scotland to southern Africa, and the wintering populations, which are allohiemic to a high degree, are consequently exposed to great differences in selection pressure, much greater indeed than in the breeding area. This leads to the *a priori* assumption that selection in the winter-quarters is the main factor in the control of the adaptive variation (evolutionary type II, p. 14). The northern-most population, separated as *Ch. h. tundrae*, has an arctic-alpine breeding range and winters mainly in tropical Africa (cf. fig. 11). According to recoveries of ringed birds the breeding population of southern Norway and Sweden winters in Spain, Morocco and Senegal, *i. e.* northwards of the wintering grounds of *Ch. h. tundrae*. The Danish population is known to winter from Hampshire in South England to Cadiz and Huelva in South Spain. Finally the population of Great Britain is resident. It appears from fig. 11 that these four populations have a distinct leap-frog migration. I have measured great series of breeding birds belonging to the populations in question (SALOMONSEN 1949, p. 30). They show the following variation in wing-length:

¹ There are also other instances of increased wing-length in Mexican forms, viz: *Melospiza melodia goldmanni*, *Agelaius phoeniceus sonoriensis*, etc.

England:	36 ♂♀	130—140	(average 134.89)	mm
Denmark:	73 ♂♀	127—139	(— 132.30)	—
South Sweden:	30 ♂♀	127—135	(— 130.46)	—
Arctic Sweden and Russia:	44 ♂♀	121—132	(— 125.21)	—

According to these measurements there is a regular cline for decreasing wing-length running from S.W. to N.E. in Europe. Similarly, there is a cline for coloration of the plumage; the small northern *Ch. h. tundrae* are the darkest birds, while the British resident birds form the palest extreme with greyish-brown upper-parts¹. When the populations are compared in the breeding areas this variation makes no sense, the clines running contrary to Bergmann's and Gloger's rules. When, however, arranged in their proper winter-quarters the populations in their adaptive variation follow both rules (cf. fig. 11). There is a close correlation between the clinal variation in this species and the environmental gradient dictated by climatical factors in the area extending from Great Britain to tropical Africa. The only explanation of this phenomenon is that adaptive selection in the wintering grounds is responsible for the variation.

The case of the Ringed Plover is extraordinarily clear. There are no appreciable ecological differences among the populations which may obscure the results; neither are historical factors of importance any longer. The Redshank (*Tringa totanus*) offers a similar example. I have recently dealt with the migration of this species, based on ringing results (SALOMONSEN 1954, p. 94) and shall restrict myself to a few comments, referring to fig. 12. The Iceland and British populations follow migration type IV (fig. 5), while the Scandinavian—North Russian population makes a leap-frog migration and winters in tropical Africa. The geographical variation in wing-length is shown in fig. 12, and it appears that it corresponds with that of the Ringed Plover. Just as in this species the populations of the Redshank are subject to much greater differences in selection pressure in their respective winter-quarters than in their breeding habitats. The distributional pattern is, however, more complicated in the Redshank than in the Ringed Plover. In the North, about the Arctic Circle, both the

¹ The British form has been separated as *Ch. h. major* Seebohm, recently renamed *Ch. h. harrisoni* by CLANCEY (1949, p. 319).

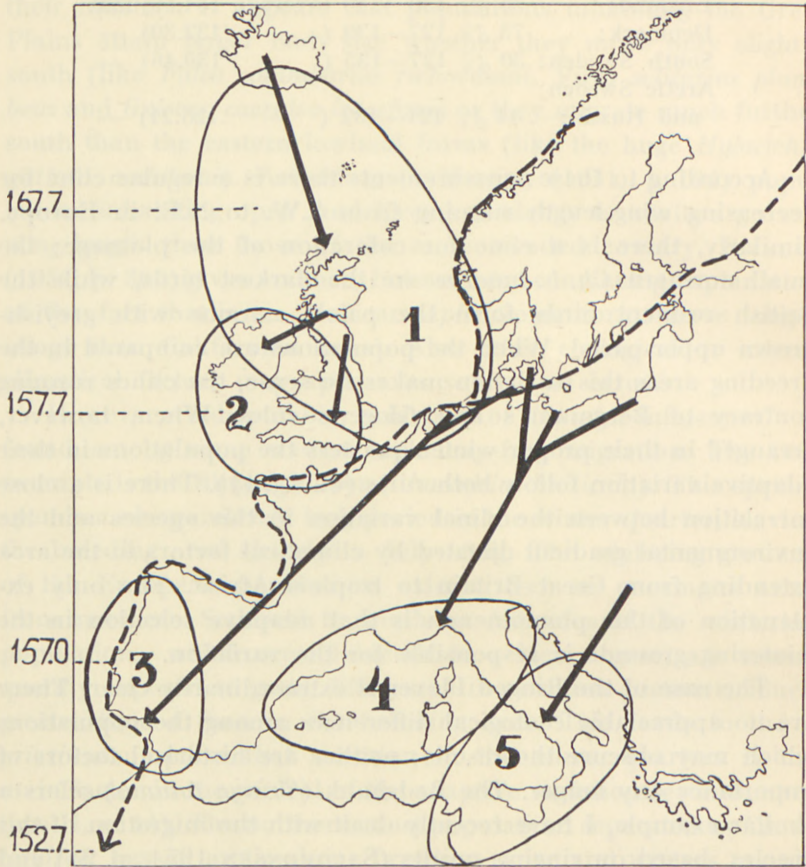


Fig. 12. Main winter-quarters of various European populations of Redshank (*Tringa totanus*). 1: Iceland, 2: British, 3: Belgian-Dutch-W. German, 4: Danish-E. German, 5: Hungarian population. Broken line: Migration route of Swedish and Norwegian (and ?Russian) populations to tropical Africa. Figures inserted at left give average wing-length of the population wintering in the area in question. (After F. SALOMONSEN 1954.)

Redshank population with the biggest proportions (in Iceland) and that with the smallest proportions (in Norway) breed, which indicates that any "summer-influence" cannot be involved in the adaptive variation. In winter, however, the smallest form inhabits the tropics, the largest one the Northsea countries, which gives a satisfactory explanation of the variation in body-size.

Finally, the case of the Common Buzzard (*Buteo buteo*) should be mentioned. The northeastern form (*B. b. intermedius*) is small

(wing-length ♂♂ 340—380) and has a dark, reddish-brown plumage. It migrates from northern Scandinavia and from Russia to tropical Africa. The southwestern form (*B. b. buteo*) is larger (wing-length ♂♂ 370—395) and paler. It remains within the boundary of Europe in winter. The Danish *B. b. buteo* are partly resident, partly migrants which winter in N.W. Germany, the Netherlands and N. France, according to recoveries of ringed birds. The population of Central Sweden, which is intermediate between the two races, winters in France and Spain. Finally, *B. b. intermedius* from northern Sweden early in the autumn pass on the migration southern Europe (from where there is a number of recoveries) and winter in Africa (one recovery in Morocco). The case is quite similar to that of *Charadrius hiaticula*, the smallest and darkest forms breeding farthest north and wintering in the tropics¹.

Apparently a number of geese follows this scheme. Owing to their strict family adherence and their tendency to winter colonially in isolated restricted areas the geese are subject to the selective influence of widely differing environments during their hibernation. When the species are sufficiently "plastic" as is the case in the Canada Goose (*Branta canadensis*) this will give rise to adaptive variation. In this and other species (*Anser albifrons*, *A. fabalis*) size-mutations occur at a considerable rate and give rise to a remarkable individual variation in proportions. In my opinion selection in the winter-quarters forms the main control and regulation of this variation. The populations of the Canada Goose form a wide continuum in the breeding-time, but have often isolated winter ranges. The smallest forms breed highest to the north and, making a leap-frog migration, winter farthest south. According to the newest hand-list (HELLMAYR and CONOVER 1948, p. 297) the small and dark *B. c. minima* (wing-length 350—390 mm)—which is now usually given full specific rank—from its Alaskan breeding range migrates south to California, where it mainly winters in San Joaquin and Sacramento Valleys. Of the two forms of the *leucopareia* group *B. c. leucopareia* is the smaller (wing 378—410); it breeds from N. Alaska to the Aleutians and winters from Washington to northern Mexico. The

¹ The case of the Ringed Plover and that of the Common Buzzard have previously been described by me (SALOMONSEN 1951, p. 184).

larger *B. c. occidentalis* (wing 451—485) breeds from S. Alaska to British Columbia, where it is mainly resident. Of the eastern forms the smallest one, *B. c. hutchinsii* (wing 370—405), breeds in the Eastern Arctic and winters in Texas and Mexico. The intermediate *B. c. parvipes* (wing 420—430) breeds in the interior of northern Canada and winters in the southern U.S.A. from California to Louisiana. The regions south of the breeding area of *B. c. parvipes* are inhabited by the largest forms (*moffitti*, *interior* and *canadensis*) with wing measuring 465—495. They are partly resident, but the greater part move southwards along the Atlantic States, sometimes to the Gulf Coast westwards to Louisiana. Recent ringing of *B. c. interior* on the breeding places at the southeastern coast of Hudson Bay has shown that this population winters along the Atlantic coast from Chesapeake Bay to the Lake Mattamuskeet area in North Carolina (HANSON and GRIFFITH 1952, p. 1—22).

In the Bean-Geese (*Anser fabalis*) the northern "Tundra-Geese" are slightly smaller than the southern "Taiga-Geese". The latter winter from Turkestan westwards to Central and South Europe, while the Tundra-Geese mainly winter in S.E. China and Japan (cf. also JOHANSEN 1945, p. 119). The smallest form, *A. f. brachyrhynchus*, is partly high-arctic and winters in temperate Europe.

Above such cases only have been discussed in which the populations differed in body-size. There are of course many other instances of leap-frog migration, and in some of them the populations involved do not differ in proportions. As an example can be mentioned *Phylloscopus inornatus*, in which the nominate form breeds in Siberia and winters in the area from Burma and South China to Malaya, while *P. i. mandelli* breeds in Kansu and Szechwan and winters in Sikkim and North Burma. The two races are identical as regards body-size.

In most species more than one migratorial trend can be distinguished. In the Mallard (*Anas platyrhynchos*), the migration of which has been thoroughly studied by means of ringing, the Greenland and the boreal population show a clear example of migration type V (cf. the table, p. 25), and the European population demonstrates both synhiemy (based on abmigration) and local allohiemy, and, in addition, some populations have a tendency to leap-frog migration.

Crosswise Migration.

In a small number of birds the migration routes of neighbouring populations cross each other, as shown as migration type XVII in fig. 13. This is a rare form of migration; I know of a few cases only. There is no particular evolutionary interest attached to the crosswise migration, only it symbolizes an urgent need for allohiemy; the populations attempt, so to speak, with all means to keep clear of each other in the wintering grounds,

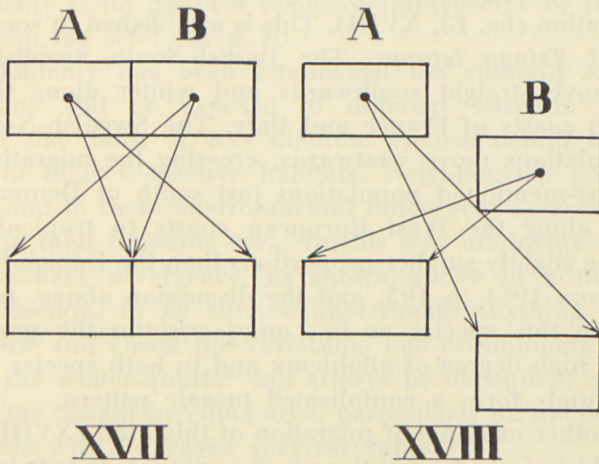


Fig. 13. Two types (XVII—XVIII) of Crosswise migration in allohiemic populations. For further explanation cf. text to fig. 1, p. 10.

and this sometimes results in complicated arrangements. This is most clearly seen in the East Astatic forms of *Lanius (collurio) cristatus*, as demonstrated by STRESEMANN (1927, map tafel II). The East Siberian *L. c. cristatus* winters in India, western Burma and the Malayan Peninsula, the Japanese *L. c. superciliosus* in Indochina, Sumatra, Java and the Lesser Sunda Islands. In order to reach to Sumatra from Indochina *L. c. superciliosus* crosses Malaya, which is inhabited in winter by *cristatus*. The Chinese *L. c. lucionensis* has two isolated wintering grounds. The first one, which is much the larger, is situated on the Philippines, northern Borneo and northern Celebes. In order to get there it has to cross the migration route of *superciliosus* in southern China. The other wintering ground of *lucionensis* is the Andaman and Nicobar Islands, which are reached by an overcrossing in Burma

of the winter-ground of *cristatus*. The information about this restricted and isolated winter-quarter rests on HUME's and RICHMOND's notes, according to STRESEMANN (1927, p. 72). It appears that *lucionensis* is very common in winter on the Andamans and Nicobars. It can be added that the Zoological Museum in Copenhagen possesses 8 skins of this form collected on the Andamans by F. A. DE ROEPSTORFF. The only clear-cut examples of crosswise migration so far known in American birds is found in *Dendroica p. palmarum* and *D. p. hypochrysea*.

In a few cases crosswise migration is combined with leap-frog migration (fig. 13, XVIII). This is established in some populations of *Tringa totanus*. The Danish-South Swedish populations move straight southwards and winter along the Mediterranean coasts of France and Italy. The Swedish-North Russian populations move westwards, crossing the migration route of the first-mentioned populations just south of Denmark, and continue along the West European coasts to tropical Africa. They have slightly smaller proportions than the Danish birds (cf. SALOMONSEN 1954, p. 105, and the discussion above, p. 47 and fig. 12). In this species as in *Lanius cristatus* the populations display a high degree of allohiemy and in both species the wintering-grounds form a complicated mosaic pattern.

As another example of migration of this kind (XVIII, fig. 13) *Turdus sibiricus* can be mentioned. *T. s. sibiricus* breeds in Siberia and winters in the region from South China and Burma south to Java and Borneo. *T. s. davisoni* breeds in Japan and winters in Burma; it is slightly larger than the nominate form.

Discussion and Conclusion.

I have endeavoured to demonstrate the evolutionary significance of natural selection by environment in the winter-quarters of migratory birds. The extrinsic factors of importance for evolution operate in a similar way in the breeding area and in the winter-quarter. It is now a well-established fact that the spatial replacement of populations tends to modify the members of the panmictic units and may lead to morphological differen-

tiation. A similar spatial segregation in the winter-quarter is achieved in species with allohiemic populations. A development of allohiemy, consequently, is a necessary requirement if the environmental factors in the winter-quarter have to contribute to the development of diversity. Although in many species the populations are synhiemic a certain degree of allohiemy has been established in the greater part of migratory species, as has been shown in this paper. In a number of species the allohiemy is complete or almost complete. This widespread development of allohiemy is no doubt a result of intraspecific or intergroup competition, as set forth p. 10.

If allohiemy has been established the spatially segregated populations will be exposed to different selection pressures owing to the more or less different environmental conditions present in their respective habitats. Neighbouring populations will respond to these environmental differences as accurately as they do in their breeding area. In this way allohiemy may lead to evolutionary divergence, as shown above in a number of cases. Selection, to be sure, cannot create anything new, but only adjust and check the variation. The evolutionary development in the winter-quarter will always be dependent on phenomena in the distant breeding area, particularly on the occurrence of mutants with increased survival value.

The absence of gene-flow between populations will accelerate adaptive differentiation. A similar effect will be achieved by absence of dispersal in the winter-quarters of allohiemic populations. In this respect it is possible to distinguish between four situations:

1. The populations in question form a continuum both in the breeding area and in the winter-quarter (*e. g. Haematopus ostralegus ostralegus* and *H. o. osculans*).

2. The populations have separated breeding areas but form a continuum in the winter-quarters (*e. g. Tringa t. totanus*, *T. t. britannica* and *T. t. robusta*).

3. The populations form a continuum in the breeding area but have separated winter-quarters (*e. g. Sterna h. hirundo* and *S. h. longipennis*).

4. The populations are separated both in the breeding area

and in the winter-quarter (e. g. *Ciconia c. ciconia* and *C. c. boyciana*).

Only in the latter case is gene-flow completely prevented and selection is allowed full scope. This does not necessarily mean that the adaptive variation is greater than in other cases, also other factors being involved (the time factor, differences in selection pressure, mutation rate).

The selection in the breeding area and that in the winter-quarter may cooperate or may counteract each other. Significant for the evolutionary trend in a migratory bird is mainly the degree of difference in selection pressure to which the populations are exposed in their breeding area and winter-quarter, respectively. This leads to the establishment of the four evolutionary types, described on p. 14-15.

Allohiemy does not need to be complete in order to be of evolutionary significance. In populations with partial synhiemy, as outlined in fig. 1, II, an isolation by distance is present between the individuals inhabiting the extreme areas of the wintering ground. If the environmental differences between the extreme areas are sufficiently great, selection will tend to shift the gene frequencies in the populations inhabiting these areas. Even when selection is of a weak order it will be capable of adjusting the populations somewhat to local conditions. In this way random dispersal will be checked, because it would result in maladaptation in the individuals which strayed too far away. Consequently, the degree of allohiemy will be stabilized or may even be increased until a certain equilibrium has been established.

The state of synhiemy have certain evolutionary advantages also, which have been mentioned on p. 23.

It may be objected that too much emphasis has been laid on the evolutionary significance of allohiemy, while other factors have been neglected. It is of course well-known that influence of environmental conditions in earlier geological periods, operating for instance in isolated refugia during the glacial epoch, have been of immense importance for the evolution in holarctic birds. RAND (1948, p. 315) has drawn attention to these factors in regard of the evolution in the Canada Geese, JOHANSEN (1945, p. 122) similarly in regard to the variation in the Bean-Geese.

I do not wish to underestimate the historical factors and am well aware that the differences between various populations in body-size which in this paper have been ascribed to selection by the present day environment in many cases may be due to isolation in previous epochs in refugia with a different climate. However, evolution was not brought to a stand still in the periods subsequent to the isolation, and in many cases adaptive diversities due to selection in recent periods have been superimposed on the more fundamental morphological characters achieved during an isolation in a distant past. The variation in a species will usually not remain unchanged when it has been exposed to the selective forces of the environment for thousands of generations.

May allohiemy in its extreme form, when the populations in question are completely isolated in their respective winter-quarters, lead to speciation? I do not think so. Speciation requires an establishment of discontinuity in the breeding area in order to perform a complete reproductive isolation of the populations; cf. discussion by MAYR 1947, p. 263 on ecology and speciation. It is thinkable, but highly improbable, that in certain species, like geese, with strongly social wintering habits, populations isolated in the wintering grounds subsequently choose separate breeding grounds and in this way secondarily attain a reproductive isolation. I have the Canada Geese in mind particularly. In recent treatises (ALDRICH 1946, p. 94; HELLMAYR and CONOVER 1948, p. 297) these geese are split up into a number of separate species (*Branta minima*, *canadensis*, *leucopareia* and *hutchinsii*) on somewhat slender grounds. They are partly sympatric, to be sure, but hybrids are common and there is a gradual transition between some of the species; alleged ecological differences are indistinct or uncertain.

However, the importance of the principles set forth in this paper is evidenced by the fact that they hold good also in units on the species level. There is an interspecific allohiemy almost as pronounced as the intraspecific one, dealt with above, and, further, the allohiemic species follow the same rules as do the populations within the same species.

The presence of allohiemy among closely related species has been stressed by LACK and myself, as mentioned above, p. 9,

where a number of genera in which the species displayed a particular high degree of allohiemy, were enumerated. Interspecific competition was given as the cause of this development. In the Scandinavian members of the genus *Larus*, for instance, *L. fuscus* migrates to the tropics (and the subspecies are allohiemic; cf. p. 30), *L. ridibundus* to S.W. Europe, *L. canus* to the Northsea coasts, while *L. argentatus* is resident (and *Rissa tridactyla* moves to the pelagic zone of the Atlantic). In North America, where *L. argentatus* is exempted from competition with the closely allied *L. fuscus*, it moves far to the south, just as *L. fuscus* in the Old World.

The spatial segregation of related species in the winter-quarters has been emphasized also by STRESEMANN (1934, p. 666), who draws attention particularly to the fact that the northernmost species often choose the southernmost wintering grounds, *i. e.* he describes leap-frog migration carried out by a number of species (within the genera *Sylvia*, *Phylloscopus*, *Hippolais* and *Acrocephalus*), just as it was described above (p. 39) to take place in intraspecific units.

The significance of selection by environment in the winter-quarters is evident also when comparing units with specific rank, as will be demonstrated by a few examples. The Ringed Plover (*Charadrius hiaticula*), which was dealt with above (p. 46), is closely related to two other species, *Ch. semipalmatus* and *Ch. placidus*, both being monotypic. As a matter of fact, they are so nearly allied that I formerly considered them members of the same superspecies (SALOMONSEN 1930, p. 71), a view which is now known to be incorrect. The separation of the different forms of Ringed Plovers is due to historical factors, no doubt to isolation in different refugia during the glacial epoch, *Ch. hiaticula* in Europe¹, *placidus* in China and *semipalmatus* in America. *Ch. semipalmatus* breeds in the arctic of the New World, and winters in the tropics, from Louisiana to Patagonia and Chile. From a migratorial point of view it is a counterpart to *Ch. h. tundrae* of the Old World. It is even smaller than this form, the wing measuring less than 125 mm. *Ch. placidus* breeds from south-eastern Siberia far down in China, where it is partly resident, wintering from Central China to northern Burma and Tonkin, only rarely

¹ *Ch. h. tundrae* possibly in Central Siberia.

passing beyond these areas. It is very similar to *Ch. hiaticula*, but is even larger than the British population, the wing measuring 139—146 mm. When comparing all these forms it appears that they fit in with the same pattern. The smallest forms (*Ch. h. tundrae* and *Ch. semipalmatus*) spend the winter in areas in which the mean-temperature of the coldest winter month is not lower than 20° C. and where night-frost does not occur, while the biggest forms (*Ch. h. hiaticula* and *Ch. placidus*) winter in areas in which the monthly mean-temperature varies in winter between zero and 20° C. and in which night-frost may occur more or less frequently, at least in the northern part of the areas. It is noteworthy that the interspecific differences are greater than those present between the populations of *Ch. hiaticula*, i. e. *Ch. semipalmatus* and *Ch. placidus* have drifted farthest apart both genetically and morphologically.

In the sympatric species *Larus argentatus* and *L. fuscus* the former, resident in a temperate climate, is distinctly larger than the latter, which winters in the tropics.

A final example: In the closely allied species of North American Tanagers (*Piranga*), which has developed a considerable degree of allohiemy, the winter-quarters are distributed as follows:

	Average Wing-length:
<i>P. flava hepatica</i> : Sonora to State of Mexico	103
<i>P. rubra cooperi</i> : Sonora to Colima-Morelos	100
<i>P. ludoviciana</i> : Central Mexico to Costa Rica	96
<i>P. rubra rubra</i> : Central Mexico to Ecuador-Guiana . .	96
<i>P. erythromelas</i> : Colombia to Bolivia-Peru	96

The three latter forms winter in a slightly hotter climate (mean winter-temperature higher than 25° C.) than the two former ones, which do not on the migration surpass Central Mexico, where the mean winter-temperature is 20°—25° C. These forms are of slightly larger body-size than the three others which winter further south.

Examples like these are not common, because even closely allied species are physiologically different units and morphologically have drifted so far apart that their adaptive differentiation is usually not comparable. The tendency is clear, however. In

many species-pairs which now differ considerably it is obvious that the adaptive differentiation is due to the influence of selection in allohiemic populations. The separation of the two species in such pairs is due to isolation in separated areas and is in itself not the result of allohiemy. However, allohiemy is responsible for some of the morphological characters of the present species, and this development thus forms the logical continuation of the phenomena described in this paper. In a recent paper HEMMINGSEN (1951, p. 138) draws attention to these facts, demonstrating that in a pair of closely allied species that one which winters in a warmer climate attains the smallest proportions. He gives a number of examples of such species-pairs, of which many carry out a leap-frog migration, *e. g.* *Sturnus (Spodiopsar) cineraceus* and *S. (Agriopsar) sturninus* (p. 148), *Erythrura rosea* and *E. erythrura* (p. 151), *Circus cyaneus* and *C. melanoleucus* (p. 153), *Ardea cinerea* and *A. purpurea* (p. 154), *Calidris tenuirostris* and *C. canutus* (p. 184), *Numenius arquata* and *N. phaeopus* (p. 184), and some more. HEMMINGSEN also draws attention to the fact that the smaller species of a pair, wintering furthest south, is the latest in spring to migrate to the north, *i. e.* it is exposed to a higher temperature also during migration. After a collective treatment of a large number of migratory East Asiatic species HEMMINGSEN (p. 204) arrives at the conclusion that "there is thus apparently in the majority of the species an association between, on the one hand, early spring migration, great body size, and relatively northern (colder) winter quarters, and, on the other hand, late spring migration, small body size and relatively southern (warmer) winter quarters«.

In order to get a closer knowledge of the evolutionary significance of bird migration it is necessary to make a detailed analysis of single species, including a study of the adaptive variation, the ecological amplitude and the influence of the environmental factors. What has been given in this paper has been only an adumbration. Nevertheless, the theories set forth may open up new possibilities and add to the understanding of the mechanisms in avian evolution.

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