

Bird migration and natural selection^{1,2}

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Abstract

1. With the present interest in analysing and experimenting upon migration, it is important to keep in mind that it is a product of natural selection, but the danger of the evolutionary approach is that it is speculative.

2. It is probably advantageous for migrant birds to leave their breeding grounds because they could not find enough food there in winter (though they usually leave before food is short), and to return there because they can find more food for their young there than in crowded winter quarters.

3. Correspondingly, the size of the world population of a migrant species is probably determined by winter supplies and its breeding dispersion (range, habitat etc.) by where it can find most food for its young.

4. The critical factor is not the absolute quantity of food, but the amount available in relation to actual or potential competition. Indirect evidence for this is provided by the existence of competitive exclusion among related species on the wintering grounds.

5. The advantages of, respectively, migration and winter residence are roughly equal in partial migrants, but they differ in different places, different years in the same place, and different sexes and age-groups.

6. The historical factor in migration was formerly over-stressed, but it has had an influence on directions taken because it is hard to evolve a successful hereditary change in direction.

7. Movements into or out of England occur almost every day throughout the winter, hard-weather movements south or west because food becomes scarce, return movements in each mild spell presumably owing to intense competition in the crowded milder areas.

8. Irruptive movements, like migration, can have been evolved through natural selection.

Резюме

1. В настоящее время возрос интерес к экспериментальному исследованию перелетов птиц. При этом важно помнить, что перелеты продукт естественного отбора. Опасность эволюционных подходов к этой проблеме состоит в том, что они могут быть спекулятивны.

2. Приспособление птиц к сезонным перелетам дает им ряд преимуществ в связи с тем, что птицы покидают зимой места обитания, где они не могут достать пищу (хотя они улетают до того, как пища исчезает), и возвращаются обратно, т.к. здесь легче прокормить своих птенцов, чем в густо населенных местах зимовки.

3. Размеры мировых популяций перелетных птиц определяются их зимней численностью, а также характером распределения при перелетах (дальность перелета, выбор летней резиденции и т.п.).

4. Критическим фактором является не абсолютное количество имеющейся пищи, а доступная пища в соотношении с потенциальной или существующей конкуренцией. Косвенным доказательством этого является элиминация родственных видов птиц в местах зимовки в результате конкуренции.

5. Преимущества зимних и летних резиденций у мигрантов грубо равны, но они различаются в разных местах и в разные годы, а также в одних и тех же местах, но для птиц разного пола и возраста.

6. Исторический фактор перелетов птиц раньше переоценивался, но он имеет существенное значение в том отношении, что направление пролетного пути у птиц наследственно закрепляется.

7. Ежедневно в течение всей зимы регистрируются пролеты птиц на территорию Англии и обратно. Отмечены также пролеты на юг и на запад в поисках пищи при ухудшении погоды и обратные пролеты, очевидно в результате более сильной конкуренции в заселенных местах.

8. Местные непериодические перемещения птиц, как и перелеты, могут рассматриваться как результат естественного отбора.

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1. The concept of migration

With the present interest in quantitative analyses of migration seen or detected by radar, in plotting the recoveries of ringed birds, in determining the factors initiating departure or those involved in fat metabolism, and in experiments on orientation, it is important not to lose sight of the basic ecological and evolutionary background to migration.

In its most typical form, migration is a regular, seasonal, large-scale, long-distance movement of a population twice a year between a fixed breeding and a fixed non-breeding area. As such, it is found not only in birds, but in various mammals, fish, marine invertebrates and land insects, though in some of these animals the pattern is different. For instance various whales migrate to high latitudes in summer, where they put on much fat, which they utilise while breeding in winter in the tropics. Again, various fish migrate only twice in their lives, from the breeding grounds as young, returning several years later as adults. This is in marked contrast to various butterflies, which breed in both the summer and the winter quarters, and a different generation makes each journey.

2. Selective advantages

Migration is obviously advantageous and, though this is not proven, it presumably depends largely on hereditary factors, and so has been evolved through natural selection. In particular, it is often "anticipatory". For instance, while the advantage of the southward autumn migration of northern insectivorous birds is food shortage in winter, most of them leave while their food is still abundant, so that the proximate timing factor is not food shortage itself. This is particularly important in long-distance migrants which need big fat stores, as they can form these most easily when food is still abundant and the days are long. Moreover, the size of the fat stores is different in different species, correlated with

the length of journey to be undertaken (e.g. Odum et al. 1961).

At high northern latitudes, a southward autumn migration has presumably been evolved when the average mortality is greater among those individuals wintering on the breeding grounds than in those making two migratory journeys each year and wintering in a milder climate further south. The advantage of leaving the milder climate again in spring is presumably that the birds concerned can raise more offspring in the north than if they stay in more crowded winter quarters, and in this connection it may be recalled that most species have larger clutches and raise larger broods at high than low latitudes. The critical mortality factor in winter is probably starvation, while in summer it is probably the amount of food which can be brought to the young. But at both seasons it is not simply the total quantity of food in the environment, but the quantity in relation to the hours of daylight available for feeding and also, and especially, in relation to the other birds competing for it.

While long-distance migration involves complex adaptations in physiology and behaviour, there is no difficulty in seeing how it might have been evolved, because transitional or intermediate stages are found in living species. For instance, many species do not migrate at all, others travel only a short distance, and others a long way. Variations between a long journey and none are found even among different subspecies of the same species, e.g. the European Robin *Erithacus rubecula*, and in the intermediate populations, some individuals migrate while others do not (Lack 1943). Again, "hard-weather" or irruptive movements directly correlated with food shortage intergrade with true migratory movements in advance of food shortage (see Rudebeck 1950, Svårdson 1957, Ulfstrand 1963 for irruptions). Further, the main adaptations needed for long-distance migration, such as big fat reserves, physiological timing

mechanisms and the ability to orient, are found in rather different forms and with rather different functions in non-migratory birds, and also in other animals, so they may well have been evolved prior to the evolution of migration.

3. Partial migrants

Those populations are of special interest in which some individuals migrate while others stay for the winter on the breeding grounds, because in such cases the relative advantages of migration and permanent residence must be nearly equal (Lack 1944a, Snow 1966, Österlöv 1966). They need not be equal in different places and it is suggestive that in various European partial migrants, such as *E. rubecula* just mentioned, a higher proportion migrate from northern than southern parts of the breeding range. Nor need the chances of survival be equal in every year in the same place. Migrants presumably have a selective advantage in severe winters, when many residents are known to die, and residents presumably have an advantage in mild winters. But it has not yet been possible to demonstrate corresponding shifts in the proportion of different genotypes in such populations. Moreover it is probably not a simple question of two genotypes, one migrating and the other staying for the winter, but of a polytypic population in which different individuals have different hereditarily-based thresholds of migration, and the latter may also vary with the winter conditions and with age or sex.

In many partial migrants, a higher proportion of juveniles than adults, and of adult females than adult males, migrate. That it is advantageous for some but not all the individuals of a population to migrate suggests that there is competition for food on the breeding grounds in winter. In such competition, it is reasonable to suppose that inexperienced juveniles come off less well than experienced adults, particularly adults which hold individual territories in winter like *E. rubecula*. Further, in species in which there is direct competition for food items, females tend to be subordinate to males in the pecking order, so probably come off less well.

The proportion of a population which migrates may change if there is a change in the environment. For instance, prior to 1940 the British Lesser Blackbacked Gull *Larus fuscus graellsii* was mainly migratory, only a few individuals staying in Britain for the winter, whereas at the present day large numbers stay the winter, feeding on refuse dumps outside towns (Barnes 1961, Brown 1967). Two changes have occurred. First, man has provided a new source of food suitable for the gulls, and secondly the gulls have changed their habits sufficiently to discover and utilise it. The chances of survival of any migrant *L. fuscus* have presumably remained about the same as before, and since the number wintering in Britain has increased, one would expect an increase to have occurred in the British breeding population, and this is evidently so, at least on the west coast of England and Wales.

4. Historical factor and recent changes

Various writers formerly sought to explain the origin of migration, and the routes taken, through historical factors, notably the "Ice Age" or even Continental Drift, but I fully support the conclusion, reached long ago by Mayr and Meise (1930) and Grinnell (1931), that the historical factor has been greatly exaggerated. In particular, extensive migrations occur within the tropics (e.g. Moreau 1951 for Africa, see also the discussion by Mayr 1957). It is its survival value at the present time which determines whether or not a migration is undertaken, and the routes followed.

The historical factor has, however, had some influence on the directions taken. For instance, most passerine migrants breeding in northern Europe travel S.W. in autumn. But a few, such as the Greenish Warbler *Phylloscopus trochiloides viridanus*, go S.E., and Rudebeck (1956) is surely right in attributing this to the species concerned having spread into Europe in relatively recent times from breeding grounds to the east, with associated wintering grounds in Asia, and that the latter have been retained by the European populations. Similarly, many passerine birds

breeding in Greenland migrate along a comparatively easy route to North America, but the Wheatears *Oenanthe oenanthe leucorrhoa* travel S.E. across the stormy north Atlantic Ocean to western Europe and then on to Africa. The breeding range of *Oe. oenanthe* makes it clear that the Greenland race was derived from European birds, which winter in Africa, and the Greenland population has retained the same wintering area.

While, however, the directions taken by European *P. trochiloides* and Greenland *Oe. oenanthe* can be explained through the history of the spread of these species, their S.E. autumn movements could persist today only if, on balance, they are advantageous. Natural selection, as has often been stressed, is primarily a conservative force, due to the fact that nearly all changes in complex systems are likely to be disadvantageous. The hereditary orienting behaviour evolved by a bird to bring it to its normal winter quarters may be highly complex, so is likely to be modified successfully only with difficulty, and there is the further, and perhaps greater, difficulty that there may not be any new winter quarters where it could survive the competition for food with species already present there. Hence it is not so unlikely as it might at first seem that those individuals of *P. trochiloides viridanus* and *Oe. oenanthe leucorrhoa* which make a long and perhaps dangerous journey south-eastward should survive better than any which travel southwestward from the breeding grounds.

The complexity of the orienting behaviour in various long-distance migrants is only gradually becoming known. For instance, many passerine night migrants breeding in Britain leave S.S.E. in autumn, but later turn S.W. over France (Lack 1963), perhaps to take advantage of suitable resting and fattening areas in Iberia (Evans 1966), and these and other European night migrants change their direction again to east of south after leaving Iberia to reach their wintering grounds south of the Sahara (Moreau 1961). Various limicoline birds have likewise evolved routes which take them to transitory moulting and fattening areas, e.g. the Wood Sandpipers

Tringa glareola in the Camargue in autumn (Hoffmann 1957), and other species evidently change direction in the course of their flight, e.g. the Knots *Calidris canutus* travelling from Siberia to England (Lack 1963).

While, however, natural selection is primarily conservative, it is also responsible for evolutionary changes. The difficulty so far as migration routes are concerned is that ornithologists are much more plentiful and well informed now than formerly, so that most previously unrecorded migratory habits may be due to their having been overlooked in the past. However, there is good evidence for a change of migratory direction in the Shore Lark *Eremophila alpestris*, which is one of the species that has spread into northern Europe from the east and typically migrates S.E. in autumn. It has been claimed, though the evidence does not seem entirely satisfactory, that it reached Scandinavia as a breeding bird only in the first part of the 19th century. Whether this is so or not, the evidence is rather good that it evolved new wintering grounds on the shores of the North Sea in the second half of the 19th century (*cf.* Newton 1871–74, Gätke 1895). This change presumably started from one or more individuals with inefficient navigation which accidentally found themselves in a new area where they could survive satisfactorily for the winter. It is widely believed, though it needs proof, that the standard directions of migration of passerine birds are innate, and if this applies to *E. alpestris*, it would not be enough merely that one or more of them were blown off-course to the North Sea; there must have been some hereditary change in their orienting behaviour which could be passed on to their offspring.

5. The effect of tradition

The direction of migration can be changed much more easily in those species, probably a small minority, in which the young learn the direction of migration through travelling with adults of their kind, either because the young stay with their parents, or because a whole

population migrates together, as in various geese. For instance, Bewick's Swans *Cygnus columbianus bewickii* have enormously increased in winter in England during the last twenty years (Nisbet 1959, Scott 1965), but this new habit, which involves a shift of only a few hundred miles from the former Zuider Zee, could be quickly acquired, as the young migrate with their parents. Again, the British population of the Herring Gull *Larus argentatus* is resident, but when M. P. Harris transferred chicks of this species to nests of the closely related *L. fuscus*, at least some of them migrated to the wintering grounds of *L. fuscus* (ringing recoveries in Harris 1965, Britton 1966, also Harris D. phil. thesis, Oxford). The young of *L. argentatus* depend on their parents for food for several months after fledging (e.g. I saw them begging from their parents in the last week of October 1951 in Cornwall), so the transferred young of *L. argentatus* presumably migrated because they followed their *L. fuscus* foster-parents.

6. Winter food and competition in winter quarters

While actual proof is not yet available, I think it likely on theoretical grounds that the numbers of a migratory species are determined in a density-dependent way by the availability of food on the wintering grounds. This implies that there is a competition for food in winter, and this, in turn, that Gause's principle of interspecific competitive exclusion should hold on the wintering grounds, as the chance of two species being equally well adapted to the same food supply is negligible, so one will normally eliminate the other. If such elimination has occurred, however, the eliminated species, unless extinct, will normally have evolved behaviour bringing it to different wintering grounds. Hence such competition will rarely be seen at the present day, though for such segregation to be maintained today, any individuals which reach the wintering grounds of the other should continue to be eliminated. Gause's principle provides the most reasonable explanation of the frequency with which

similar congeneric species spend the winter in different areas. e.g. Chiffchaff and Willow Warbler *Phylloscopus collybita* and *P. trochilus*, Curlew and Whimbrel *Numenius arquata* and *N. phaeopus*, and others (Lack 1944b, Salomonsen 1955), and the existence of such segregation provides the best evidence so far available that there is competition for food among migrant species in winter.

Another example of Gause's principle was formerly provided by the winter distribution of the two British gulls, the resident *L. argentatus* and the migratory *L. fuscus*, and these species are so similar that it is hard to see how they could have evolved separate wintering areas except through competition for food. Nowadays, however, as already mentioned, though many *L. fuscus* still migrate for the winter, others then feed together with *L. argentatus* on rubbish tips in England (Brown 1967). But as both species have been increasing, this is evidently an unstable situation due to a temporarily superabundant food supply, and it will be interesting to see whether segregation is re-established when their numbers have once more reached the level set by winter food.

There are, of course, many other congeneric migrant species which spend the winter in the same area, e.g. ducks in the genus *Anas*. But this has presumably happened only where the species concerned have evolved different feeding adaptations, or different ecological niches, and so take mainly different foods. This, for instance, has been shown to hold in several North American species of *Dendroica* warblers on their wintering grounds (MacArthur 1958). Once again, foods supplied indirectly by man may obscure the natural situation. For instance, the 6 species of *Carduelis* and the 3 cardueline finches in other genera which spend the winter in Britain are much more clearly segregated in diet in natural habitats than in agricultural land (Newton 1967).

Apparently, competitive exclusion need not apply to different subspecies of the same species, which often mingle on the same wintering grounds. This is presumably because they are about equally well adapted to feeding

there, and not because they have evolved different feeding niches. Where two or more races winter together, as in the White-crowned Sparrow *Zonotrichia leucophrys* in California or the Yellow Wagtail *Motacilla flava* in tropical Africa, the members of each race differ from each other in the date in spring at which their gonads develop, or at which they depart, although they are subject to the same environmental influences. Hence hereditary differences are presumably involved, and these are clearly adapted to the time at which their respective summer habitats become suitable for breeding (Blanchard 1941, Curry-Lindahl 1963). In some migrant species, however, different subspecies occupy different wintering areas, presumably due to competitive exclusion, which may result in "leap-frog" migrations, and may also have various evolutionary consequences discussed by Salomonsen (1955).

Competition for food in winter may also affect a whole group of species. For instance, Moreau (1966) attributed the huge number of northern limicoline birds which winter on the shores of tropical African lakes to the paucity of resident African shorebirds which might be potential competitors for food (and their paucity might presumably be due to this huge annual invasion of efficient species from the north). In contrast, the migratory sylvine warblers from the palaearctic scarcely enter the African evergreen forest in winter, presumably because, though this would otherwise provide them with suitable ecological niches, the latter are already occupied by better adapted resident African warblers. Instead, the palaearctic warblers winter primarily in savanna, often in hot arid conditions very unlike the northern forests. The same does not apply in the New World, however, where many parulid warblers which breed in the forests of North America winter in tropical forest (cf. Slud 1960).

Yet again, various palaearctic and nearctic limicoline species travel an immense distance twice each year to winter on the beaches of New Zealand (Oliver 1955), and the only factor likely to make such journeys advantageous is competition on more crowded beaches nearer to their summer homes. It may be

suggested, likewise, that potential competition with related species in other areas is the factor which restricts the wintering grounds of the Alaskan Bristle-thighed Curlew *Numenius tahitiensis* to remote Pacific Islands and of Michigan's Kirtland Warbler *Dendroica kirtlandii* to the Bahamas (Amadon 1953); and the enforced restriction of these species to such small wintering areas may well be responsible for their scarcity on the breeding grounds.

In these and many other migratory species, the size of the world population is probably determined by the available food on the winter grounds, and ecological factors operating on the breeding grounds may have no influence. Nevertheless ecological segregation, presumably as a result of competitive exclusion, is also characteristic of many migrant species on their breeding grounds (e.g. many examples of migrants among those cited by Lack 1944b, and the *Dendroica* species in North America analysed by MacArthur 1958). Once again, segregation may be less clear-cut in habitats modified by man than in natural habitats. For instance, in planted broad-leaved woods in England, the breeding habitats of the Blackcap and Garden Warbler *Sylvia atricapilla* and *S. borin* apparently overlap extensively, though there are minor and rather indefinite differences, but in primeval broad-leaved forest in Poland they are separated by the height above the ground at which they feed (per I. Newton).

7. The effect of changes in wintering habits on the breeding population

The reason that competitive exclusion among migrant species holds also in summer is presumably because the breeding dispersion of each species, which determines the density of pairs in different places and different habitats, has been evolved in relation to the comparative success in raising young. For instance, there has since 1948 been a big decline in the number of White Storks *Ciconia ciconia* breeding in Baden-Württemberg, the reasons for which are not known (but they might perhaps be linked with factors operating in the African wintering grounds). The critical point here is

that, whatever its basic cause, this decline has not been uniform throughout the area studied, but has been much steeper, and started much earlier, in dry habitats less suitable for raising young than in wet habitats more suitable for raising young, owing to local movements of the birds (Zink 1963, cf. Lack 1966). Hence while the total world population of a migratory species is probably determined by its survival on the wintering grounds, the dispersion of the surviving pairs is probably determined by their success in raising young.

If winter food supplies regulate numbers, then we must expect drastic changes in the next decades in those European breeding species which winter in tropical Africa, owing to the rapid large-scale destruction of natural habitats which is taking place there at the present time. Some species may lose their main wintering areas, but others will find new ones. For instance, the Black-tailed Godwit *Limosa limosa* has recently become a pest in irrigated rice fields in western Africa (Morel and Roux 1966), and this may presumably lead to an increase in the European breeding population.

Similar big changes due to agriculture of course occurred in the migratory species that spend, or formerly spent, the winter in western Europe, but these changes happened in the period before ornithological records were kept, so we tend to overlook them. For instance, most of the common land birds coming from northern or central Europe to winter in England there feed primarily on cultivated land, including the Starling *Sturnus vulgaris*, Chaffinch *Fringilla coelebs*, Blackbird *Turdus merula*, Lapwing *Vanellus vanellus*, Golden Plover *Pluvialis apricarius* and geese in the genus *Anser*. The migratory habits and numbers of these species must have been very different a few thousand years ago, when nearly the whole of Britain was covered in forest. It may be wondered, incidentally, whether the unusually complicated changes in migratory direction of Norwegian *F. coelebs*, first S.E., then south down the east side of the North Sea, then gradually changing to S.W., west and eventually N.W. to reach England (Perdeck 1961), may be of comparatively recent origin.

8. "Hard-weather" movements

Radar studies have shown that between November and the end of February, i.e. during the winter months when migration was formerly thought not to occur, there are in fact movements into or out of England almost every day and night. "Hard-weather" movements of such birds as *V. vanellus* and *S. vulgaris*, both westward from the Continent into southern England and Ireland, and southward from England into Iberia, were of course known before the advent of radar, but the frequency with which they occur was not in the least appreciated, nor was it known that corresponding return movements are also frequent throughout the winter, eastward with westerly winds and northward with southerly winds (Lack 1963). The chief species concerned are probably those which cannot obtain food when the ground is frozen or covered by snow, so their retreat to milder areas in cold weather is obviously advantageous. The advantage of their almost immediate return with milder weather is less obvious, but it is in line with the viewpoint of this lecture to suggest that there is severe competition for food in wintering areas such as Ireland or Iberia, so that the birds concerned have a greater chance of survival if they return as soon as is feasible to the empty fields from which they were earlier driven by the cold, even though this may entail a flight of several hundred miles. I do not mean, of course, that the birds are directly driven out by competition; but that this is the ultimate factor concerned. The proximate factor could well be a change in the wind-direction or in temperature. Similarly the hard-weather movements themselves may be proximately initiated by the wind-direction or by temperature. In hard-weather movements, as in true migration, it is advantageous for the birds to leave before they are weakened by food shortage, and hence that their departure should be correlated with proximate factors.

9. Irruptive movements

Hard-weather movements differ from true migration in that they occur as a more or less

immediate response to adverse conditions, and not long beforehand, in anticipation of them. Further, they may not take place, or a much smaller number of individuals may take part, in mild than severe winters. Likewise a very variable number of individuals take part in irruptive movements, which also occur, at least in part, as a response to food shortage, though the situation is more complex, and the resemblance to true migration greater, than was formerly supposed (Rudebeck 1950, Svårdson 1957, Ulfstrand 1963). It has often been claimed that, contrary to true migratory movements, irruptive movements are of no advantage to the participating individuals, which are a "doomed surplus", and that, instead, they benefit the species, through relieving the pressure on food resources in the area from which the birds have come, thus allowing a remnant of the population to survive there (e.g. Wynne-Edwards 1962). However, the evidence which has gradually been accumulating in the last 15 years has strengthened, not weakened, my earlier view (Lack 1954) that it is advantageous for the irrupting individuals to move out because, if they stay, they will almost certainly starve, whereas some of those which move out find places where they survive the winter and from which they later return safely to the breeding grounds. Hence the irruptive habit can have

been evolved through natural selection. There are now a number of recoveries of birds ringed on irruptions which have survived to a following breeding season or winter, but more are needed before my interpretation can be considered fully established.

10. The evolutionary and ecological aspect

Similar arguments in terms of natural selection and competition for food could be set out to explain other features of migration, but I have said enough to illustrate the approach that I wish to stress. The danger of this approach is that it is speculative. Many of the ideas put forward cannot be tested quantitatively in the field, few if any can be checked by experiments, and some depend on what happened in the unobservable past. The results are therefore less satisfying, and in one sense less "scientific", than quantitative or experimental studies on particular aspects of migration. But studies of the latter type are either descriptive (e.g. radar studies, or the analysis of ringing recoveries) or concern proximate adaptations (e.g. timing factors, fat metabolism or orienting mechanisms), and for their full interpretation, proper appreciation of the evolutionary and ecological background is fundamental, so that in this sense the approach outlined here is at least as scientific as these others.

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