Bird Migration and the Concept of Continental Drift

Albert Wolfson
Northwestern University, Evanston, Illinois

THE ORIGIN AND EVOLUTION OF MIGRATION in birds has long been a favorite topic for theoretical discussion, but current theories, although numerous, fail to provide a satisfactory explanation for some of its fundamental features.

When a recent study of continental drift revealed some correlations with the routes of migration, the concept was studied still further in relation to the time of origin and distribution of birds and the evolution of migration.

This critical study and analysis have led to the conclusion that *continental drift was the stimulus for the evolution of the more highly developed forms of migration.* In essence, the hypothesis to be presented holds that the birds that responded to the movements of the continents as they drifted apart and moved northward, and/or followed the development of the new oceans created by drifting land masses, belong to those species which at the present time exhibit migration in its most highly developed form.

Since some knowledge of the problems of migration and the concept of drift are requisite for an evaluation of the arguments, a review of each is presented before elaborating the hypothesis.

THE PROBLEMS OF BIRD MIGRATION

The fundamental problems of bird migration, as formulated by Thomson (*8*), provide a convenient framework for a discussion of the present status of our knowledge. These problems are (1) the origin of migration, (2) the ends served by migration, (3) the annual stimuli for migration, and (4) the path and goal of flight.

The origin of migration. Current theories of the origin of migration are based on the assumption that migration as we know it today has resulted from the response of birds to a repetitive event in their racial history, with this induced response ultimately becoming hereditary.

With such a broad assumption, numerous theories can and have been postulated, differing in their selection of the factors responsible for initiating migration and in their speculation on the distribution of the stationary, ancestral stock. Two major patterns are evident in these theories.

According to one pattern, migratory birds originated in the Northern Hemisphere and were originally stationary. With the occurrence of a great climatic change as manifested, for example, by glaciation, they were forced southward. With the gradual retreat of the glaciers they returned northward to their ancestral home, only to be forced southward again with the approach of winter. Eventually the habit became inherent in the species.

The objections to such a theory are numerous and strong. It can be readily dismissed on the grounds that the birds that were forced southward were extinct long before the glaciers receded, if they had not been destroyed on their breeding grounds. Consequently, there would be no population with an urge to return to the ancestral "home."

A more refined form of this theory omits the idea of an urge to return to the ancestral breeding grounds, but postulates that as a result of glaciation there was a concentration of birds in tropical latitudes. Subsequently, the breeding range was extended northward as the ice receded.

According to the other pattern, birds originated in the Southern Hemisphere and spread into northern regions because of the competition for breeding places. At the close of the breeding season they returned to their ancestral home in the south. With the advent of spring, the stimulus for reproduction drove them northward again.

Modifications of this theory postulate causes other than reproduction and homing instinct as the stimuli for the original movements. Postbreeding wandering and search for food, for example, have been suggested as the causes for the northward movement, and adverse, seasonal, climatic conditions and search for food as the causes for the southward movement.

In general, theories of this type recognize the two important phases in the annual cycle of birds—the reproductive, or breeding, phase and the postbreeding, or winter feeding, phase—each with its own requirements. Such theories postulate further that originally one area sufficed for both phases, as it does today for many nonmigratory birds, but eventually two areas were occupied annually.

The migratory routes under these circumstances are supposed to have developed with the spread of the species into the new area. The birds of today, therefore, are believed to be following the path of great racial movements that took place in the distant past.

This second type of theory of the origin of migration is supported by much of our knowledge of the behavior of birds and their response to environmental factors. It is, nevertheless, inadequate. It fails, for example, to account for the remarkable routes of migration over large bodies of water, for the great distances that separate the breeding and wintering areas of many species, and for the cessation of breeding in the southern, ancestral area; and it fails to explain how the movements involved in the "expansion" and "retreat" of the species—an acquired characteristic—became hereditary.

The ends served by migration. That migration serves useful ends in many cases has not been doubted, for without usefulness, it has been argued, it would not have survived. But what tends to confuse the issue is the reasoning that the ends served constitute the causes of migration. This type of reasoning, for example, is responsible for the widely held but unsubstantiated view that the reproductive "urge" is the stimulus for migration.

On the whole, investigations of the usefulness of migration have been concerned with discovering and defining the effects of seasonal environmental factors on the life of birds because of the obvious correlation of migration with such factors. The results of such investigations have led to the conclusion that the purpose of migration is to secure a favorable environment throughout the year.

The annual stimuli for migration. The problem of the annual stimuli for migration has received the most attention in recent years, and much has been contributed to our understanding of this aspect of migration. The success of the investigations can be attributed in large part to the use of the experimental method and physiological studies of resident and migrant individuals.

Rowan (*3*), who was the first to use the experimental approach, concluded that spring migration is a part of the breeding cycle and is induced by gonadal secretions. The fall migration, however, he found to be independent of the influence of the gonads (*4*). The external factor which induced the development of the gonads was proven to be increasing day lengths. This external stimulus would, therefore, apply only to those birds that wintered north of the equator.

Almost 10 years elapsed before a further experimental analysis of the problem was undertaken by Wolfson (*9*). The results of these experimental and physiological studies did not corroborate Rowan's conclusion on the role of the gonads in migration. Instead, the new facts, which stressed the total physiological condition of the bird, pointed to a maximum body weight, due to a heavy deposition of fat, as the diagnostic feature of a readiness to migrate. Its significance was further attested by the fact that nonmigratory races of the same species do not show such deposition of fat or marked seasonal variations in weight.

There is no doubt that the annual stimulus for migration arises from some physiological change which is induced by increasing day lengths of winter and spring. The fact that residents and migrants differ in their weight responses would seem to favor the view that a maximum body weight, and not the gonad, is involved in initiating migratory behavior.

Studies of the annual stimulus have contributed little toward the elucidation of such problems as the origin of migration and the path and goal of flight, but one is in a better position to speculate on the evolution of migration, for whatever theory is formulated, it must include some plausible explanation of the evolution of the annual stimuli which are operative today.

The path and goal of flight. This final problem has been under careful investigation since the introduction of banding and other marking techniques. Through the use of such techniques, as well as extensive field observations, the breeding and winter ranges and the path of flight between them are well known for many birds, especially those which breed in the central and northern parts of North America and Europe.

This knowledge has served to impress ornithologists still further with the extraordinary nature of migration, but, again, other fundamental problems have not been elucidated. Instead, new and perplexing ones have been added to an already enigmatic phenomenon.

How was one to explain, for example, the evolution of the amazing flight of the arctic terns (*Sterna paradisaea*) that breed in northern North America, then fly *eastward* across the Atlantic to Europe, and finally *southward* along the African coast to their winter home in the Antarctic region; or the flight of the Pacific golden plover (*Pluvialis dominica fulva*) which breeds in Alaska and adjacent portions of Siberia and either makes a nonstop flight across the Pacific to Hawaii or travels along the eastern coast of Asia as far south as Australia, New Zealand, and Tasmania? The routes of other birds and the distances flown are equally remarkable.

An explanation of these routes, it is generally agreed, can be found only in the history of the species.

THE CONCEPT OF CONTINENTAL DRIFT

The theory of continental drift, also known as the displacement hypothesis, includes all hypotheses postulating a large amount of horizontal movement of land masses and not merely the better-known conceptions of Taylor and Wegener.

Taylor, who was the first to present a definite and convincing hypothesis in 1908, was followed by Baker in 1911 and Wegener in 1912 (see *1* for review).

Wegener, because his ideas challenged more directly the recognized principles of geology and because of the various incongruities and inaccuracies in his works, was primarily responsible for provoking a strong reaction.

The outline of the concept presented here is taken from Du Toit and portrays in broad outlines the present status of our knowledge. The fundamental features of this concept follow.

(1) Two great land masses, a *northern* one, *Laurasia,* and a *southern* one, *Gondwana,* were present throughout the Paleozoic and most of the Mesozoic. These two major units were separated by a vast sea known as the Tethys. Its trend was generally east-west; its depth varied in space and time, and several times its shallowing at some points put Gondwana into connection with Laurasia for short periods. By the Tertiary it was reduced considerably.

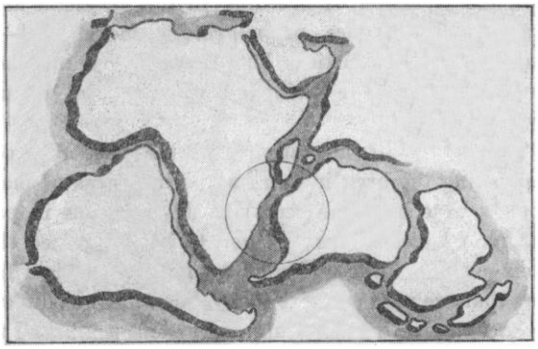

FIG. 1. Gondwana during the Paleozoic and early Mesozoic. The space between the various portions was then mostly land. (Redrawn from Du Toit, 1937. Based on Lambert's Equal Area Polar Projection.)

(2) During the Cretaceous these parent masses fragmented, and the resultant parts drifted.

(3) With reference to the land masses as we know them today, from Gondwana the following evolved: South America, Africa, Arabia, Madagascar, peninsular India, Australia, and Antarctica. From Laurasia evolved North America, Greenland, Europe, and Asia.

(4) To indicate how the fragmentation occurred and the movements of the fragments, attempts have been made to reassemble the parts.

Reassembly of the parts of Gondwana is illustrated in Fig. 1. It should be noted that the entire mass was located in the southern hemisphere. The drift of the parts, with the exception of Antarctica, was dominantly northward. At the same time, there was an eastward and westward drift, South America drifting *westward,* and Africa and the other fragments drifting *eastward.* The result of the fragmentation and drift of the parts was the creation of the *South Atlantic* and *Indian Oceans,* the original parts being eventually arranged about them in their present positions.

(5) Reassembly of the fragments of Laurasia is shown in Fig. 2. The fragments, it is noted, were not as widely dispersed as those of Gondwana, but the same relative pattern of drift took place—namely, a northward, and an eastward and westward movement. North America moved ultimately *northwestward,* while Eurasia moved *northeastward.* The result of fragmentation and drift was the creation of the *North Atlantic* and *Arctic Oceans.* The southern part of the present North Atlantic was originally a small ocean (Poseidon), and it is generally accepted as the locus at which rifting started.

FIG. 2. Laurasia during the early Mesozoic. The space between the various portions was partly land, partly sea. (Redrawn from Du Toit, 1937. Based on Lambert's Equal Area Polar Projection.)

Greenland may be considered as a point of reference from which North America drifted farther westward and Eurasia, eastward. The broad region extending from Portugal through Ireland to Scandinavia, which was land throughout the Triassic, represents the subsequently torn-off margin of North America.

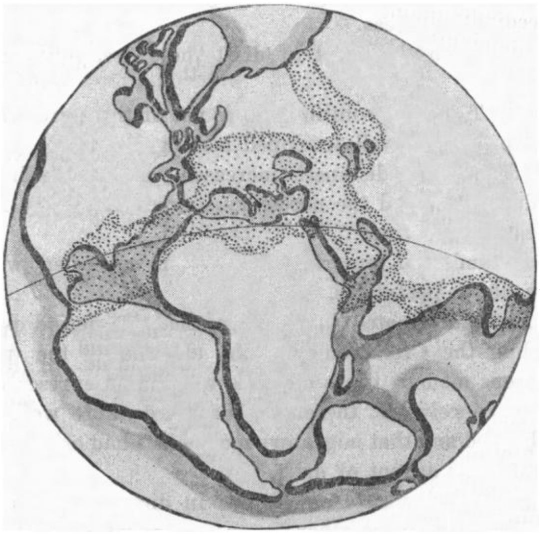

FIG. 3. Reassembly of Gondwana and Laurasia to indicate the position of the equator during the Cretaceous. Stippled areas represent shallow seas of the Eocene. (Reconstructed from Wegener and Du Toit.)

During the Mesozoic, and before then, Laurasia lay *farther to the south,* with much of its southern margin reaching or *extending across the equator.* At Cretaceous time the equator is regarded as running through Central America, North Africa, Southern Europe, Persia, and Himalaya. Laurasia, then, since Cretaceous time has been displaced northward approximately 35° of latitude (Fig. 3).

(6) Laurasia and Gondwana are viewed as *separate* and, in certain respects, independent masses belonging to the Northern and Southern Hemispheres. Although the fragments of both show the same drift pattern, their displacements have not been equal or simultaneous.

(7) The rate of movement in drifting is considered as being extremely slow at all times.

Migration in Relation to Drift

In past theoretical discussions it has been assumed that migration arose in stationary populations because of the "separation" of originally coincidental or adjoining nesting and feeding areas. The result of the separation was the origin of *short,* periodic flights such as are known in many tropical species today.

This assumption has been generally accepted to explain the *origin* of migration, but it has never been adequate to explain the *evolution* of migration.

The evolution of migration according to the present hypothesis is envisaged as follows:

(a) Before the advent of continental drift many birds were performing short flights between breeding and feeding areas.

(b) With the onset of drift these areas diverged slowly.

(c) The birds continued their use of these areas because of their well-developed homing instincts.

(d) As the distances increased, only those individuals that had the necessary sources of energy for the flight survived.

A number of important facts are in agreement with the above postulates.

Birds originated in the Jurassic, the period preceding the Cretaceous, and by the end of the Cretaceous modern types of birds were well represented. It is conceivable, therefore, that birds were well established and that migratory movements had originated *before* the advent of drift.

Homing instincts are known in diverse groups of animals, but in no other group is it as well developed and of such general occurrence as it is in birds. This behavior of returning to a known territory or "home" has been shown to apply not only to the nesting area but also to the feeding area in the winter range. Unquestionably, it forms the foundation for all types of migratory movements.

As the nesting and feeding areas diverged, one can conceive of the birds making the trip successfully only if they had the necessary sources of energy for the flight. Only those individuals that had suitable hereditary variations in this direction would have survived as the distance became greater. Inevitably, natural selection would have resulted in the survival of a population that developed sufficient energy reserves at the proper season. Recent studies have demonstrated the correlation between the onset of migration and a heavy deposition of fat, and there can be no doubt that such fat provides the energy for the migratory flight.

In the earlier discussion it was pointed out that current theories were inadequate because they failed to account for the remarkable routes of migration over large bodies of water, the great distances separating the breeding and wintering areas of many species, the cessation of breeding in the ancestral area, and the inheritance of migratory movements—an acquired characteristic. Let us now examine these problems from the point of view of the present hypothesis.

The routes of migration and the vast distances separating the breeding and wintering areas of many species have been the great stumbling blocks in past theoretical discussions. It had to be recognized that their evolution was undoubtedly due to historical factors that are not operative today, but what was difficult to accept was that the migratory movement and the route that eventually evolved had survival value. This difficulty arises from the fact that many birds fly much greater distances and subject themselves to more rigorous conditions than seems necessary to find suitable breeding or wintering grounds.

When we examine some of the remarkable routes of migration and the vast distances between breeding and wintering areas, and *think of them as evolving in response to drifting continents,* what heretofore has been enigmatic becomes explicable.

The migratory species that perform the longest flights and, hence, demonstrate the development of migratory behavior in its highest form are those belonging to the group known as the shore birds. Consequently, it is from this group that a number of the following examples have been chosen.

(1) Three species that have as great a migratory range as any others known are the turnstone (*Arenaria interpres*), the sanderling (*Crocethia alba*), and the knot (*Calidris canutus*).

The turnstone is almost cosmopolitan in range, nesting in the far north to 70° latitude and probably farther. It migrates throughout the world, mainly along salt waters, and its wintering range extends as far as South Africa, Australia, New Zealand, and

Chile. The sanderling covers a similar vast area, nesting in the Arctic regions and wintering as far south as Patagonia, South Africa, and Australia. The knot, which is circumpolar in its summer range in the Northern Hemisphere, winters in the Southern Hemisphere as far south as the Cape of Good Hope, India, Australia, New Zealand, and Patagonia. The proximity of these winter ranges in the reassembly of Gondwana is striking!

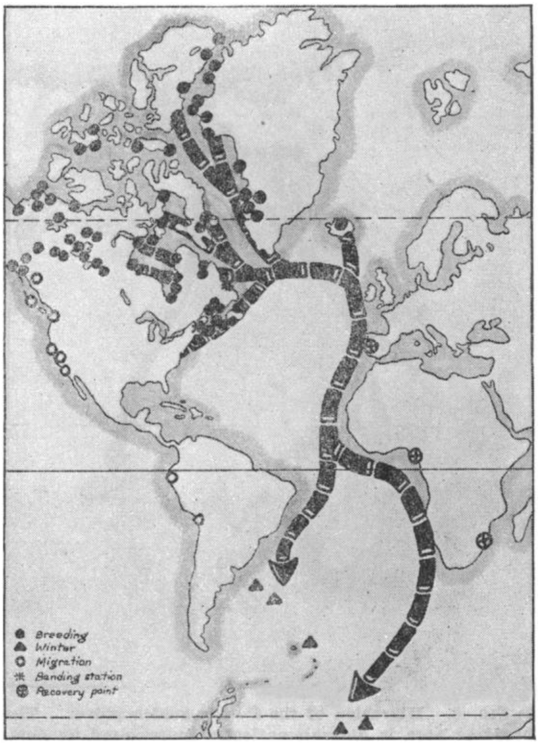

FIG. 4. Migration and distribution of the arctic tern of eastern North America. Recovery records are based on banded individuals. (From Lincoln, 1935, with modifications.)

In terms of the permanence of the continental masses and ocean basins it is difficult to explain these widespread distributions and migrations. However, in terms of an original Gondwana and Laurasia, their subsequent fragmentation and northward drifting, these distributions are readily explained.

Gondwana may be thought of as the original site of an extensive population that eventually spread into Laurasia, breeding as far as its northern margin, but returning to its ancestral site to feed. As Gondwana fragmented, *each part was still retained as a division of the wintering range* and, hence, the present widely scattered wintering area. The extreme northern breeding ground can be accounted for by the northward displacement of Laurasia and its eventual fragmentation to form much of the Arctic Ocean around which these species breed.

(2) The species that performs the longest flight among all birds is the arctic tern. It breeds in the circumpolar region of the Northern Hemisphere as far north as 82° latitude and in winter ranges from the tropical Atlantic to Antarctic Oceans as far south as 66° latitude. A distance of about 10,000 miles separates the extremes of its breeding and wintering areas.

As with the species mentioned above, the *extent* of migration is readily explicable in terms of continental drift, but what is more remarkable is the correlation between drift and the *path of flight*.

In North America this species breeds as far south as Great Slave Lake, in the interior of Canada, and on the Atlantic coast as far as Massachusetts. It also breeds commonly on the west coast of Greenland and in Iceland. When the fall migration begins, these birds do not fly southward, as one might expect, but fly *eastward* across the North Atlantic to the shores of Europe, and *then southward* along the African coast to their wintering area in the South Atlantic and Antarctic regions. Some individuals may cross to the eastern coast of South America south of the Azores and then continue southward (Fig. 4).

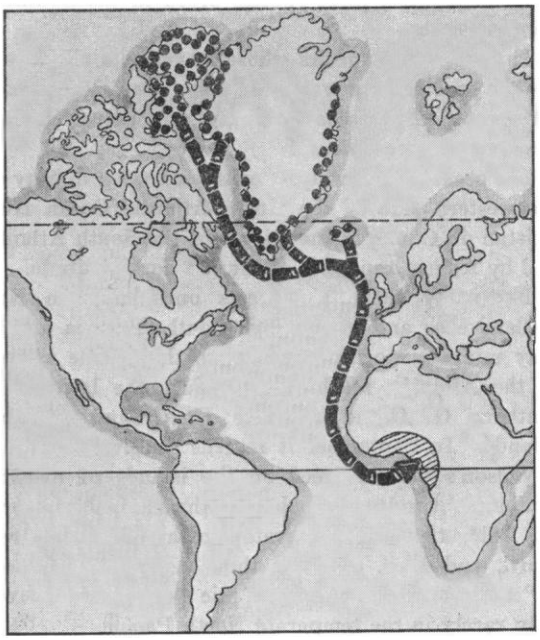

Fig. 5. Migration of the Greenland wheatear. Breeding and wintering areas are diagrammatically represented by dots and diagonal lines, respectively.

Is it merely coincidence that the direction of flight is in accord with the pattern of drift? If so, how, then, can one explain the east-west flight across the North Atlantic and the vast distance between the breeding and wintering grounds?

According to drift, the present wintering area would represent that part of the South Atlantic produced by the drifting of the Gondwana fragments. The flight across the North Atlantic would represent the east-west drift of the parts of Laurasia. Thus, the route seems to be the natural consequence of drift, the birds following their breeding grounds as they drifted westward.

Other species also perform this east-west flight across the North Atlantic, and among these the flight of the Greenland wheatear (*Oenanthe oenanthe leucorhoa*) is worth noting. This species breeds regularly in Ellesmere Island, Greenland, and Iceland. After the breeding season it flies eastward, migrates through the British Isles and France, ultimately reaching West Africa, where it spends the winter (Fig. 5). Again, there can be no question of the coincidence of the pattern of drift and the route of migration.

(3) There are other species which also seem to have followed the development of the Atlantic Ocean according to drift, but instead of breeding in the Northern Hemisphere, these species breed in the Southern Hemisphere.

Three of these species whose movements are known are the greater shearwater (***Puffinus gravis***), the sooty shearwater (*P. **griseus***), and Wilson's petrel (*Oceanites oceanicus oceanicus*).

The greater shearwater moves northward in May on the western side of the North Atlantic Ocean from Tristan da Cunha in the middle of the South Atlantic and by August ranges to about 60° north latitude.

The sooty shearwater nests on islands in New Zealand seas and in southern South America and in May migrates northward through the Pacific as well as the Atlantic, reaching eventually the latitude of southern Greenland and the Kuril, and Aleutian Islands. In September it returns southward.

Wilson's petrels breed on the islands of extreme southern latitudes, probably southward to the shores of Antarctica, and migrate northward in March, April, and May, checking their movement at about 50° north latitude in the Atlantic Ocean. They occur only rarely in the temperate North Pacific.

The fact that these species migrate so far northward *after* the breeding season is readily explicable in terms of drift and the hypothesis presented.

(4) Another remarkable route of migration which has defied explanation is that from Arctic regions to the islands of the South Seas, extending in some cases to the eastern atolls of Polynesia. A number of species perform this flight regularly, some of them, such as the Pacific godwit (*Limosa lapponica baueri*), reaching as far south as New Zealand.

The Pacific golden plover, one of the better-known species which uses this route, nests along the Bering Sea Coast of Alaska and in northeastern Siberia. After the breeding season the species travels south along the eastern coast of Asia as far as Australia, Tasmania, and New Zealand, and through the Pacific Islands from Hawaii southward. The individuals which reach Hawaii are believed to fly nonstop from Bering Strait, thereby covering a distance of about 2,800 miles over the open sea and without landmarks (Fig. 6).

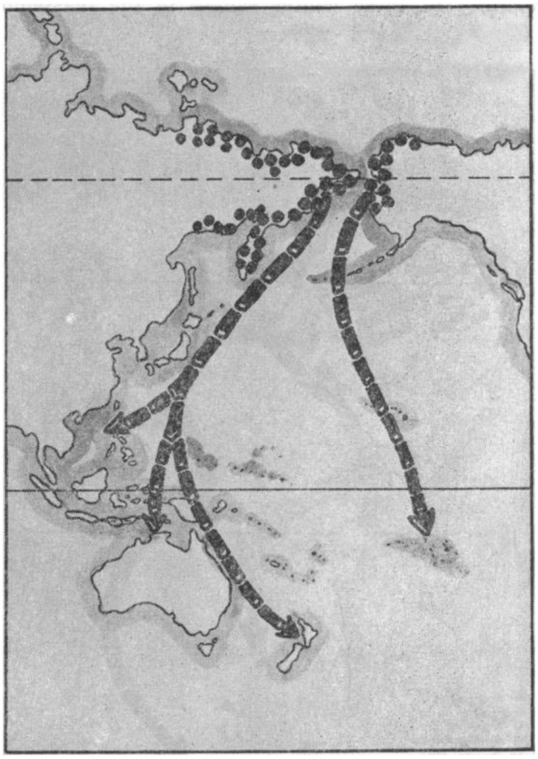

FIG. 6. Migration of the Pacific golden plover. The breeding area is diagrammatically represented by dots, with the more western portions omitted.

How can one explain the evolution of such routes from the viewpoint of permanent ocean basins and continents? According to drift, the path of migration becomes explicable, even though some of the details may be obscure.

Before drift occurred, Laurasia lay far to the south of its present position, an estimated 35°–45° of latitude. This displacement southward would alone decrease considerably the distance between the Pacific Islands and northeastern Siberia and Alaska. Taking into account some meridianal drift, the amount and direction of which is difficult to estimate, the present wintering and breeding grounds were conceivably much closer together at one time. The evolution of the route of migration could then have occurred *gradually* as Asia and North America drifted northward.

In addition to these specific routes, two other general features pertaining to the direction and extent of migration are readily explicable in terms of drift and, conversely, support the hypothesis presented. These features are: (a) the general trend of migratory routes in North America and Eurasia, and (b) the extensive development of migration as a *northward* movement.

When one compares the general trend of migration in North America and Eurasia, some rather fundamental differences come to light. In North America the general trend of many migratory routes in the spring is from the *southeast* to the *northwest,* and in a few instances there are marked westward flights along some routes. In Eurasia the general trend in the spring is from the *southwest* to the *northeast,* and many species fly directly eastward for a part of their route.

Is this agreement between the general trend of many migratory routes and the resultant directions in which North America and Eurasia were drifting merely coincidental?

One of the most puzzling facts about migratory behavior which previous theories have not accounted for is that migration is essentially a *northward* movement, irrespective of how far south a species may winter. Whereas many species that winter in the temperate latitudes of South America and Africa migrate to the Northern Hemisphere to breed, *few species* that "winter" in northern temperate latitudes migrate into the Southern Hemisphere to breed.

If migration developed because of range expansion from tropical and subtropical breeding grounds, why did it not develop equally toward both poles? Again, is it merely coincidental that extensive migrations are northward and all of the continental masses (with the exception of Antarctica) drifted *northward* since the Cretaceous?

It must be pointed out that migration does occur among species that breed in the Tropics and Southern Hemisphere, but in most instances these are comparatively short flights, and in only a few cases do these birds cross the equator. These flights from southern temperate latitudes, it should be noted also, are northward and coincide in some cases with the northward flight of those migrants that will fly to the Northern Hemisphere to breed.

In considering the next problem, the cessation of breeding in the ancestral area, the question arises, first, as to whether the present breeding grounds represent the *ancestral* range or the *acquired* range. Implicit in the present hypothesis is an *origin in the Southern Hemisphere* for those migrants that winter there today. That these migrants breed now in the Northern Hemisphere is explained by the effect of day length on the breeding cycle of birds.

As the birds crossed the equator it is held that their breeding cycle was altered so that eventually they bred only in the Northern Hemisphere. Since birds normally have only one breeding cycle a year, the cessation of breeding in the ancestral area would have resulted.

Supporting this contention is experimental evidence of the effect of changes in day length on the breeding cycle; the fact that populations of the same species breed at opposite times of the year when their breeding grounds extend to both sides of the equator; and the fact that some species, when transported from the Southern Hemisphere, where they normally occur, to the Northern Hemisphere, show a reversal of their breeding cycle to conform with the seasons of the Northern Hemisphere.

If it is true that migratory individuals developed within stationary populations that originated in the Southern Hemisphere, as this hypothesis maintains, then it follows that surviving nonmigratory populations of the original stationary stock should be located in the southern part of the range. An examination of a large number of cases substantiates this conclusion, and it is evident in such cases that migratory behavior has been an important isolating factor in speciation.

This conclusion would also apply in those instances where a species originated in northern land masses that were formerly connected, and we would expect to find insular areas, particularly with a highly mixed avifauna in regard to migration. This is especially true of Great Britain, where a number of species are represented by both resident and migration populations. Some of the migrants winter there, while others breed there. It is interesting to note that the migrant populations that breed in England come from Ireland in the west and France, Spain, and Portugal in the south.

Since the migration of the arctic tern has been given in detail, it may be noted further that the antarctic tern (*Sterna vittata*), a closely related species that breeds primarily on the islands in the Antarctic Ocean, is comparatively nonmigratory and has evolved into several subspecies because of its strong "attachment" for particular islands as nesting grounds.

The final problem of the inheritance of an acquired characteristic does not exist under the present hypothesis. Migration *originated* in those groups that had an *inherent pattern of behavior* of regular, short flights to and from the breeding area. It *developed* to a great extent in those groups (a) that responded to drifting of continental masses, (b) that had the hereditary pattern to provide for the energy sources needed in migration, and (c) that had the physiological mechanism to correlate the occurrence of these resources with suitable seasons for migration and breeding.

SUMMARY AND DISCUSSION

The present hypothesis for the evolution of migration is founded on three premises: (1) that the inherent behavior of moving to and from nesting and feeding grounds had appeared soon after the origin of birds; (2) that many birds returned to the same feeding and nesting areas even though they became divergent; and (3) that only those individuals survived as migrants that developed the necessary sources of energy to enable them to complete the flight between the diverging areas.

It is postulated that the cause of the divergence was the drifting of continental masses and the concomitant development of oceans.

That such drifting played an important role in the evolution of migration seems attested by the extent, direction, and general pattern of migration and the correlation of these features with the evolution of the continental masses, temporally and spatially.

That the establishment of energy resources played an important role in the evolution of migration is attested by the occurrence of periodic fat deposition in migrants, its absence in closely related resident forms, and the correlation of fat deposition and migratory behavior under natural as well as experimental conditions.

Various causes for the *original movements* may be postulated, but whatever the cause of these movements —and there is no reason to believe that it was identical in all migratory species—the salient feature, the gradual divergence and northward drifting of land masses, would still provide the stimulus for the evolution of extensive migratory flights.

Migratory behavior, according to the hypothesis presented, did not evolve into its highly developed forms because it served useful ends, but was the natural consequence of an inherent behavior pattern responding to the drifting of continental masses. The "adaptive features" of migration, such as leaving an area with the approach of winter, are, therefore, the *result* of natural selection and *not the cause* of migration as implied in previous discussions of the ends served by migration.

Although Pleistocene glaciation has been emphasized in the past to explain the origin and evolution of migration, it seems rather that it was only a *modifying* factor. It is beyond the scope of the present paper to discuss its role, but one point is relevant.

Although the glaciers would obviously have claimed the breeding and feeding areas of many species, many of the shore birds and other aquatic species would not have been affected. They still could have bred at the edge of the glaciers as they do in Greenland and Antarctica today. This observation, plus the evolution of migration according to drift, would account for the fact that migration in its most highly developed form occurs commonly among the shore birds and other aquatic species that feed in marine waters.

Other investigators, who have been primarily concerned with the origin, dispersal, and evolution of particular faunas, such as birds (*2*), mammals (*7*), amphibians and reptiles (*6*), and fishes (*5*), have found that it is not necessary to invoke drift to interpret their data. While that may be true, by *not* considering drift they are left with a number of significant problems which have necessitated, in some cases, the postulation of some rather extraordinary concepts.

Having examined these problems and concepts, I believe that a re-examination and re-evaluation of the pertinent zoological facts in relation to drift will show that drift is not only logically equivalent to current explanations based on permanence, but, *at the same time,* it provides solutions for the enigmatic problems that result from the point of view of permanence.

It is recognized that the reception afforded the hypothesis presented will be considered by some to rest in no small measure on the fate of the concept of continental drift. There are many biologists who believe that the establishment of the validity of drift must come first from the geologist before they can consider it in relation to their problems of evolution and distribution. On the other hand, if biologists have an adequate knowledge of the properties, requirements, and behavior of organisms and have confidence in that knowledge, they can make a substantial contribution to our knowledge of the earth's history. Thus, that birds migrate along the routes indicated and show certain distributional patterns seems to me to constitute prima-facie evidence for the drifting of continental masses.

References

1. DU TOIT, A. L. *Our wandering continents.* Edinburgh-London: Oliver & Boyd, 1937.
2. MAYR, E. *Wilson Bull.*, 1946, **58**, 3–41.
3. ROWAN, W. *Proc. Boston Soc. nat. Hist.*, 1929, **39**, 151–208.
4. ROWAN, W. *Proc. nat. Acad. Sci., Wash.*, 1932, **18**, 639–654.
5. SCHAEFFER, B. *Bull. Amer. Mus. nat. Hist.*, 1947, **89**, 1–40.
6. SCHMIDT, K. P. *Copeia*, 1946, No. 3, 144–152.
7. SIMPSON, G. G. *Bull. geol. Soc. Amer.*, 1947, **58**, 613–688.
8. THOMSON, A. L. *Problems of bird migration.* London: Witherby, 1926.
9. WOLFSON, A. *Condor*, 1940, **42**, 93–99; 1942, **44**, 237–263; 1945, **47**, 95–127.