

## 2.—THE INDIVIDUAL vs. THE SPECIES IN MIGRATION STUDIES

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INITIATION of migration studies of individual birds is a definite corollary of the development of the banding method. Previously most contributions to this subject were the result of fortuitous circumstances, and frequently by their very nature, they could be only doubtfully accepted as applicable to the species as a whole or even to that element of the species contemporary with the cited example. Consequently, it is not surprising to note that nearly all the studies made during recent years have been based upon this means of investigation. Although the migratory movements of individual birds have only occasionally been treated as a distinct subject, nevertheless, numerous contributions have been made by both American and European students.

In some respects it is by this contemplation of the known movements of individuals that the migration of birds reveals its great magnitude. The spring and fall movements, considered *en masse*, are spectacular, but they become even more impressive when reflection is given to the travels of each individual that goes to make up the flocks. With some birds that perform long migrations, including most of the shorebirds, it would seem that a considerable part of their lives must be spent in travel at the expenditure of vast amounts of energy. Furthermore, since this almost constant motion unquestionably adds to the hazards of existence of such individuals, so it must also increase the dangers to the species as a whole.

The study of the migration of individual birds shows a change with age, whereas that of the species itself may be resolved into fixed routes, orders, terminals, and dates of arrival and departure. The classic American example, determined through extensive collecting, is the Golden Plover, the adults of which migrate in fall earlier than do the immatures, a large number of which also travel southward by a different route. It is now known that this also is true of several other species of shorebirds and probably of some members of other families. Here, of course, we are considering the species as a whole, but when we study individual birds we find that although a year-old bird may arrive later in spring than those fully adult, the second spring it is itself fully adult and so may arrive at an earlier date at the exact site where it established its first nest. Similarly, its dates of departure for winter quarters undergo corresponding changes.

These facts would seem to indicate that the exact time control is internal and dependent upon gonadal development. In this connection it is worthy of note that Meinertzhagen, writing in 1930 on the birds of Egypt, stated as a general conclusion his belief that although it may be common for the

adults and immatures of many species to start their migration together, it appeared that frequently the stronger adults, particularly the males, would outdistance the others, and possibly made fewer stops en route. He recognizes, however, that in some cases the immature birds migrate before their parents. Weigold, analyzing the data accumulated at the bird observatory on Heligoland, found that during the autumn migration the first arrivals for four species of perching birds and one raptore were immature individuals and that the last of these species to arrive were old males. For twelve other species the immature birds came first, followed by mixed flocks of those that were adult and immature. Among several species of shorebirds he found the order to be: adults only, mixed adult and immature, and a sort of rear guard of adults only.

This variation in migration according to the age of the individual is well illustrated also by the Herring Gull, which has been banded in large numbers throughout its entire American breeding range. Practically all those banded were marked as chicks in their natal colonies, and it has been a conspicuous feature of all Herring Gull bandings that the recovery records showing the greatest distance traveled, are of birds recaptured during their first winter. The returns from two-year-old birds have invariably disclosed greatly reduced distances, and those from fully adult gulls have usually been received from the general area in which the banding was done. In other words, the data indicate that although immature Herring Gulls may be extensively migratory and that yearlings are partially so, the adults are either sedentary or only slightly migratory.

Reference may also be made to the post-nuptial movements of several species of herons. Both observation and banding data have demonstrated that most of the birds that late in summer travel long distances north of the breeding range are young of the year. Practically none of the many young Black-crowned Night Herons banded in Massachusetts and subsequently recovered in Maine, Ontario, Quebec, and the Maritime Provinces were two-year-old or adult birds. The Little Blue Herons that every summer are locally common from Maryland and Virginia north to New England are chiefly immature, as shown by their white plumage. Strangely enough the young Night Herons raised at colonies in the extreme northern part of the breeding range, as in Saskatchewan, are not known to move northward in the manner of their more southern nesting relatives.

From a consideration of these data, especially those applicable to the Herring Gull, it would seem that for these species, migration may be inherited by the individual as a recessive character, which it largely outgrows as it reaches maturity.

The effect of the sex of an individual upon its migration has perhaps been better recognized, particularly in those species that exhibit conspicuous

sexual differences of plumage or song. The early spring arrival of male Red-winged Blackbirds, Orioles, House Wrens, and others is now associated with the selection of nesting territory. Weigold in his studies of the data from Heligoland found that the order of spring arrival for twelve species was: first, males only; second, mixed flocks; and third, females only; for fourteen species: first, males only; and second, mixed flocks. Although he does not definitely say so, it seems probable that the males of those species migrating in company with the females were yearling birds returning for the first time to their breeding grounds. As has been previously pointed out by the writer (*Bird Banding*, 4: 149-155, October 1934) the weight of evidence from banding data indicates that the 'homing instinct,' or the return of a bird to the site or vicinity of its nest of the previous year, does not seem to operate until after the bird has first nested, and that the location of the first nest is largely a matter of chance in obtaining possession of unoccupied territory anywhere within the natural range of the species or subspecies, as the case may be. Accordingly, young males, not having the added incentive to return and claim their proprietorship of territory previously occupied, would tend to perform a more leisurely migration and so be inclined to travel with the later-arriving females.

It is, of course, not at all improbable that, having spent the period intervening between nesting seasons in more or less close association with other individuals from the same area in which it was reared, a yearling bird might come back to or near the area in which it was hatched, and finding unoccupied territory, proceed to establish its own territorial claims. The extensive work done by Mrs. Margaret M. Nice with the Song Sparrow demonstrates that this is not an infrequent happening (*Trans. Linn. Soc. New York*, 4: April 1937).

Although with most species of migratory birds the sexes probably winter together, there may be occasional segregation that will be discovered through banding data. Schuster in a study of the Hen Harrier found that the birds that failed to go south for the winter were chiefly females, the percentage running from 75 to 80. Comparable data for the American prototype, the Marsh Hawk, do not thus far support this statement, but admittedly the available material is incomplete because most Marsh Hawks and other birds of prey have been banded as nestlings when the sex could not be determined.

In considering the effect of sex upon individual migration, cognizance must be taken of those birds whose period of courtship is during the winter months. For most species it is hardly credible that the mated pair traveled southward together, and as the winter range is usually but a fraction of the breeding range, it is possible that the male and the female may represent distributional extremes. Under such circumstances, in the ensuing spring migration one bird influences the other to the extent of altering both its

migration route and its breeding area. Such a situation may go so far as the irregularity Dr. A. Landsborough Thomson has called "abmigration," wherein a resident bird mates with a winter visitor to that area and in the ensuing spring migrates northward to a region it has never before seen. It is probable that this occurs occasionally among many kinds of birds, but it is most frequent among migratory waterfowl. The evidence now available indicates that among ducks the influence of the female is the determining factor in the route of the migratory flight.

The investigation of individual migration must also be considered from the viewpoint of heredity. There seems reason to believe that although the migratory impulse is basally inherited by each individual and that the act of migration is brought about through the operation of a complex series of stimuli, there is, nevertheless, much individual variation in the effectiveness of the physiological and seasonal rhythms that actually initiate the movement. Certain individuals for one reason or another fail to respond to the changing seasons. This does not appear to be correlated with either age or sex, and in its most common manifestation is responsible for the summer or winter residences of birds far outside the normal range of the species at that season. Different species of shorebirds offer notable examples.

It has been generally postulated that not only is the instinct to migrate hereditary, but that there is also an hereditary instinct or knowledge of the route to follow and the means for keeping on it. Possibly in the light of our present knowledge that is the best we can do, but studies of the recovery records of banded birds from a single brood that have been retaken at widely separated points suggest the operation of other factors. An outstanding example of this nature is that of a brood of European Widgeons banded in Iceland, the individuals of which were subsequently recaptured in both Europe and the United States. This problem offers a fascinating field for investigation, as it may be approached only by comparison of the routes of travel of banded birds that are members of the same broods.

Among the extensive files of banding data there are now sufficient records to indicate that an individual bird *usually* behaves the same way in successive seasons. The word "usually" must be emphasized, as there are cases sufficient to prove that no hard and fast law can be established to account for the migratory movements of any one individual bird. Outstanding among such material are the life-history studies made on the Song Sparrow by Mrs. Nice. In her investigations of this species she found that "the difference between migrating and non-migrating" birds in that locality (Columbus, Ohio), had "nothing to do with age and also is not a matter of inheritance." In summing up her data she found that seven resident fathers had seven resident sons, and that four migratory fathers had four migratory sons. On the other hand, two resident fathers had two migratory

sons, and five migratory fathers had seven resident sons. Among 61 males, 24 remained consistently resident, 31 always migrated, and the other six changed their status from resident to migrant or vice versa. Of the females, only five were consistent residents, 37 always migrated, and one changed her status from resident to migrant.

Although it may seem trite to discuss further the comprehensive analysis already made of these data, the following possible hypothesis occurs to the writer. Generally speaking, the Song Sparrow is not a species with a well-developed migration, and the instinct might accordingly be considered recessive, for there is a vestigial remnant of what earlier may have been a more uniform migratory movement. With this assumed delicate balance between resident and migrant, it might well be that a slight change in the climate, in the nature of the food supply, or even in the physiological condition of the individual bird at the time migration would normally take place would be the deciding factor in any particular season. In the absence of definite proof one way or the other, such suggestions have their chief value in pointing to the need for further study. We now have a method for the study of individuals in migration and it remains to be seen how well we shall use it.

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