BIRD MIGRATION FROM THE STANDPOINT OF ITS PERIODIC ACCURACY.

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ONE must confess to a feeling of trepidation on entering into such a dangerous field of discussion as bird migration, especially in its theoretical aspect, for perhaps no scientific subject has been so flooded with wild speculation, dogmatic assertions and poetical fancy. This is natural, because the facts cannot fail to come to the notice of every lover of nature, and their æsthetic quality makes them attractive material for thought and discussion.

Bird migration touches many interesting provinces of science, such as zoögeography, geology, meteorology, evolution and comparative psychology. What has recently excited the writer's curiosity is the meaning of the time sense of certain species of birds, especially where such an accurate sense does not seem to be warranted; in a word, where it seems more highly developed than is compatible with adaptive necessity.

In the past decade many of the facts of migration have become common knowledge, but when these facts are completely grasped, and even when the movements of the individual bird have been thoroughly studied, *the* great problem of migration is likely to remain as much unsolved as ever, for the sense on which distant orientation depends, and the instinct which starts the travellers are beyond the reach of our present methods of investigation. Instinct itself is of course the fundamental problem, a problem as deep and obscure as any in the realm of philosophy. Bergson says: "*The intellect is characterized by a natural inability to comprehend life.* Instinct on the contrary is moulded on the very form of life. While intelligence treats everything mechanically, instinct proceeds so to speak organically. If the consciousness that slumbers in it should awake, if it were wound up into knowledge, instead of being wound off into action, if we could ask and it could reply, it would give up to us the most intimate secrets of life." [1]

[1] Bergson, Creative Evolution, p. 165.

But though the nature of instinct is so far beyond us, the direction of its efforts can be studied, and as far as the writer can see they are held by students of animal behavior to be of a purposeful and adaptive nature; if not for their present needs, then possibly through persistence they may show a glimpse of what was their past necessity or specialization. Comparing instinct with intuition Bergson says again: "Without intelligence, it (intuition) would have remained in the form of *instinct*, riveted to the special form of its *practical interest* and turned outward by it into movements of locomotion." [1] (Italics mine.)

Holmes says: "Salmon begin their up-stream migration, the male frog develops his tendency to clasp the female, birds herald the advent of the breeding season with courtship and song, and the males of many mammals show at this season an unusual degree of belligerency. The change in instinctive behavior during the breeding season may be due to the production of internal secretions which influence the irritability of certain parts of the nervous system, but however caused, it is, like the varying responses to food, water, etc., *pretty closely subservient to the needs of the species.*"[2] (Italics mine.)

In the same vein we might quote from Lloyd Morgan who in contrasting reflex with instinctive actions, says of the latter: "Instinctive activities are those organized trains or sequences of co-ordinated activities which are performed by the individual in common with all members of the same more or less restricted group, in *adaptation to certain circumstances,* oft-recurring or *essential to the continuance of the species.*" [3] (Italics mine.)

Whether we regard migration as the operation of a pure instinct, or complicate it with reflex action brought about by various tropisms, and even influenced by a certain element of choice (intelligence), we must admit, I think, that its foundation is adaptive and useful. It is true that it is often difficult to see why bird migration has been so persistently carried on, especially in cases where part of the individuals of a species are local in their habits and part are migratory, for no reason that seems a necessity, but this is very

[1] *do.* p. 178.
[2] Holmes, The Evolution of Animal Intelligence.
[3] L. Morgan, Animal Life and Intelligence, p. 422.

likely analogous in a certain way to evolution of form, which as embryology shows us so well, is forced into the repetition of ancient and disused types.

Professor Wheeler in his book on ants gives a very concise discussion of instinct, with some excellent definitions. He points out various grades of degenerating instincts in these animals, some of which can be brought back into activity under proper conditions. According to him, instinct, "the combination of complexity with automatic fixity," has been studied from four different points of view, ethological, physiological, psychological and metaphysical. We are naturally concerned now mostly with the physiological side.

We must bear in mind that the regularity of instinctive behavior has probably been somewhat exaggerated, and as Jordan says, an instinctive action is subject to variation like all other characteristics of animals.

Individual birds show peculiarities of behavior in nest building, song and other actions. Hodge has shown that a great difference in power of orientation exists for homing pigeons. Also, in animals as high in the scale of life as birds, there cannot fail to be some "power of choice" in almost every stereotyped activity.

This brings us back to our enquiry into the mechanism by which birds are enabled to arrive each year at a given locality at almost exactly the same time. From a physico-chemical standpoint the accuracy of time sense in certain species is little short of marvelous and is well shown in the familiar Baltimore Oriole and the Bobolink, which are both late arrivals in the north. Mr. Brewster very kindly allowed me to see his notes on the arrival of these species at Concord, Massachusetts, for long periods of time. From 1900 to 1911 his earliest record for the Bobolink is May 3, and his latest May 11. For three years the arrival was May 8, and for two years May 7; the average being May 7. Just as remarkable is the Oriole at Concord. From 1900 to 1911, the earliest is May 3 and latest May 14. The average is May 8, and the species appeared twice on this day, twice on the 9th, once on the 7th, and once on the 6th. An earlier period including the years '86, '89, '90, '91 and '93, gives the average date of the Oriole near Boston as May 6, with the greatest variation at six days.

Examples of this great potential accuracy could be multiplied indefinitely, but we will confine ourselves to some of the most striking. Cooke's report of Bird Migration in the years 1884 and 1885 bear out the wonderful uniformity of progression of the Oriole. Cooke says[1]: "Were the surface of the earth level and the climate absolutely uniform, birds would arrive at a given place on approximately the same day each year.... In the records of the Biological survey the best example of uniformity in arrival is that of the Chimney Swift at New Market, Va., as noted by George M. Neese. The dates of each year from 1884 to 1906 are respectively, April 16, 16, 15, 16, 16, 11, 9, 15, 21, 14, 15, 14, 12, 7, 16, 14, 16, 12, 11, 9, 12, 12, 10."

Dixon[2] quotes the case of the Puffins which arrive at St. Kilda very regularly on the first day of May, while the Bartailed Godwits reach the south coast of England so near a certain date that the twelfth of May is known as 'Godwit-day.'

Think for a moment what this means; a start from a more or less changeless climate, where environmental stimuli can hardly account for any of the accuracy we have pointed out, with a journey of two thousand miles or more, fraught with innumerable variations in wind, precipitation, food supply, etc., and in the case of these first instances, an arrival at Boston, estimating the total journey to occupy about two months, with an average error of only 9%. This is comparable to a train being thirteen and one-half minutes late in a journey of one hundred miles at forty miles per hour. Yet if we take into consideration that the bird has no watch to start on, we ought really to figure its possible error of spring arrival as the per cent of its total sojourn in winter quarters, plus the time of its northern journey, which total period must be reckoned to be nearly eight months. This gives us an error of only 2.4%. With the case of the Chimney Swift the actual average error as Cooke remarks is only 2.2 days in the whole period of twenty-three years.

It is natural that a very exceptional season, such as the cold May of 1907, may have a very marked effect on bird arrivals.

[1] The Migratory Movements of Birds in Relation to the Weather. Year-book of Dept. of Agric., 1910, p. 386.

[2] Dixon, The Migration of Birds, 1897. p. 134.

Eifrig's observations at Ottawa, Canada,[1] show that this exceptional season delayed some birds, like the Hummingbird, for two weeks, while other species were very little affected. This, however, only means that the racial accuracy of the species was forcibly interfered with from outside, in some cases far more seriously than in others.

We must, however, now consider another side of the question. So far we have been dealing with 'first arrivals.' What we should like, of course, would be individual arrivals, but until we have some definite information on this point, which can only be supplied by the return of banded birds to nesting sites, we must content ourselves with the consideration of the possible errors in recording first arrivals, and also with the highly interesting 'bulk arrivals,' or dates of greatest frequency of transient migrants.

The question of the error of first arrivals has been discussed by Messrs. Stone and Cooke. Stone found [2] that many eyes were better than one, and Cooke [3] states that where one observer was operating, his dates of first arrival were apt to be over a day late on an average. Cooke's method of averaging migration arrivals [4] consists in throwing out dates which are more than six days out of the way, his experience teaching him that "birds seldom vary on account of the season more than six days either way from the average date of their arrival." This method may seem to some, as to the writer, rather arbitrary.

Mr. Stone gives a good discussion of the problem of recording early arrivals in the 'Proceedings of the Academy of Natural Sciences of Philadelphia' for 1908. In it he shows that to get at the actual date we must combine the records of many observers at different points a few miles apart, and combine them in certain definite ways, so as to throw out stations in which individual error or incompatibility of surroundings delayed the detection of the species in question. By 'bulk arrival' Mr. Stone means the date on which the species has arrived at half the stations in a given restricted area. He regards the bulk arrival, or greatest frequency as recorded only

[1] Auk, 1908, p. 1.
[2] Stone, W., Condor, 1906, p. 88.
[3] Cooke, W. W., Auk, 1907, p. 346.
[4] Cooke, W. W., Auk, 1908, p. 485.

by a single observer, as much too variable a quantity to be of practical use. By his methods of estimating the dates from year to year he obtains an extraordinarily slight arrival variation.

Thus it is probable that ordinary dates of arrival as given by single observers increase rather than diminish our knowledge of the actual potential accuracy of the species.

In 'Cassinia' for 1911 arrivals in the Philadelphia region are tabulated for the years 1906–1911. Below are given in a table four species which are remarkable from our point of view. The figures are the actual departure in days from a ten year average for the species. They are based on Mr. Stone's 'bulk arrival.'

	1906	1907	1908	1909	1910	1911
Yellow Warbler	0	0	+4	−2	0	0
Ovenbird	0	0	+4	−1	0	−2
Baltimore Oriole	+2	−5	+4	−1	−3	−2
Canadian Warbler	0	0	−1	+1	−3	+1

In glancing down the 'Cassinia' table one sees immediately that groups of species arriving at nearly the same time are often very similarly affected by the season, and will be either late or early according to the year. Within the same year, however, the early or March migrants may be affected in an opposite direction from the late migrants; thus early species may be late and late species early, for the same season. This is merely more evidence to show that at least some of the observed arrival error is meteorological rather than instinctive; and external instead of internal.

In the same paper Mr. Stone notes that in computing the ten year averages it is interesting to see how the average of 'bulk arrivals' based on the method given above, coincides with the average of first arrivals at stations where there have been a number of accurate observers. On page 47 is a table which shows the 10 observation stations near Philadelphia, with dates of arrival for 9 common birds. The 'bulk arrivals' here are either the same or only *one* day later than the average first arrivals.

Taking a single species, the Brown Thrasher, a bird easily seen and almost impossible to identify wrongly, the ten year arrival records are given in detail. For this period there are 10 stations and 22 observers at work. Each of the stations has its own average and the greatest error is +2 days at George School, and —3 days

at Concordville. The Grand Total is April 22 for first arrival, while the grand computed 'bulk arrival' is April 23 for the entire period. This shows that first arrivals are not mere stragglers, for if they were, the records of the different Philadelphia stations would not give such uniform results.

In Stone's 'The birds of Eastern Pennsylvania and New Jersey, 1894' are given lists of arrival at Germantown, Pa., for 50 species from 1885 to 1892. Those showing great constancy are the Chimney Swift, Baltimore Oriole, Barn Swallow, Yellow Warbler, Blackpoll Warbler, Oven-bird, Redstart and Catbird. These records of course are not the work of so many observers as the 'Cassinia' records.

For the period 1893–1900 there is another set of arrival records [1] which shows as very accurate birds, the Chimney Swift, Baltimore Oriole, Barn Swallow, Wood Thrush and others. We note that the same species come up with accuracy performances at different times and in different localities.

Mr. Brewster [2] has called attention to the probable dependence of species upon each other for purposes of guidance. He shows how flocks are made up of many species and how rare stragglers are always found in the company of other species. He also mentions the case of lost birds, that is, rare stragglers, almost always turning out to be the young of the season. It is of course apparent that many species migrate together. On the great May rush several species arrive each day on an average. From the 'Cassinia' table of 1911 we get 4 species on May 4, 2 May 5, 2 May 6, 1 May 7, 5 May 8, 2 May 9, 1 May 10, 2 May 11 and 2 May 12. This refers to common species only, exact dates for rare birds being much harder to compute. But however dependent species are upon each other during their journeys, we cannot escape from the fact that each has its characteristic time period, for if it did not, we would get a very different picture of migration. The birds would then come in great scattering waves, transient migrants would be longer in passing a given point, and the whole phenomenon would lose much of its present orderliness. Of the 14 common Hunga-

[1] Cassinia, 1901, p. 37.
[2] Memoirs of the Nuttall Club, No. 1, 1886.

rian migrants to be referred to later, no two fall upon the same day. They begin with *Alauda arvensis* on February 28 and end with *Coturnix coturnix* on April 29.

There is much to be learned as to the nesting localities of late and early arrivals inside a given species. It is certain that some birds wintering in Central America arrive in temperate summer haunts and begin nest building almost before others of the same species start from winter quarters bound for sub-arctic regions, the north bound birds starting later and traveling faster.

As Cooke remarks in speaking of the Robin [1] "The first robins that reach a given locality in the spring are likely to remain there to nest, and the advance of the migration time must await the arrival of other birds from still farther south. Therefore each robin undoubtedly migrates at a faster rate than the apparent movement of his species as a whole. This is true of most, if not all, of the other seemingly slow migrants."

We may now refer to the most elaborate study of migration yet attempted, that outlined by Otto Herman in Hungary [2] and given in 'Aquila' from year to year. Enormous numbers of stations are in use and stress is laid on the common species. It must be confessed however that the actual significance of these records from our point of view is hard to determine because most of the observers appear to have been masters of elementary schools and others not skilled in field work. It is more than likely that many stations would show a delay in arrival not actually present. In Vol. XII, 1905, p. 226, there is, however, a table showing the combined dates of arrival of 16 species from 1894 to 1903. The average yearly error, as compared with a ten year mean date of arrival, has been computed, and shows as very constant birds the following species: *Turtur turtur* and *Oriolus oriolus* with an error of 1.5 days and *Coturnix coturnix* with an error of only 1.4 days.

I have computed the average error of these same species for a later period, 1904 to 1910, using the 'Aquila' tables and find it to be 2.2 days for *Turtur*, and 2 days each for *Oriolus* and *Coturnix*.

Vol. XVIII, 1911, of 'Aquila' gives on p. 138 a large table show-

[1] Yearbook of Dept. of Agriculture, 1903, p. 383.
[2] Proc. 4, International Ornith. Congress, p. 163.

ing 15 years of work summed up, with actual numbers of individuals included in five day intervals. A rough idea of dates of greatest abundance is thus obtained. These 15 year bulk arrivals are compared directly with the results of the previous year 1910. On the whole this table shows a pretty orderly invasion and departure for each species, although of course the country covered is a large one with much mountainous territory, naturally tending to lengthen out the passage of migrants a great deal above what it would be if a small area had been used for tabular work.

Another way of getting some light on the orderliness of the species in migration is by comparing in a long series of years actual first arrivals with average first arrivals. In Cooke's various papers in 'Bird Lore' on the migration of N. A. Sparrows there is a large number of such records. We will take only a few of the most striking cases where observations extend over a long period, so as to get the greatest possible chance for departures from the normal.

Rose-breasted Grosbeak at Wasington, D. C., 18 years; earliest, May 1; average May 5. For the same species observed at Englewood, N. J., 12 years; earliest, May 1; average May 6. Ballston Spa, N. Y., 14 years; earliest, May 4; average May 10. St. Johnsbury, Vt., 12 years; earliest, May 6; average May 10. Chicago, Ill., 21 years; earliest, April 25; average May 3. Warterloo, Ind., 11 years; earliest, April 28, average May 2. Aweme, Manitoba, 16 years; earliest, May 12, average, May 16.

For the White-crowned Sparrow at Ottawa, Ontario, 24 years; earliest, April 30; average, May 7. For the White-throated Sparrow at Ottawa, Ontario, 27 years; earliest, April 15; average, April 26.

For the Blue Grossbeak at Raleigh, N. C., 21 years; earliest, April 25; average May 2. St. Onaga, Kan., 15 years; earliest, May 1; average May 5.

Indigo Bunting at Raleigh, N. C., 23 years; earliest, April 23; average, May 1. Renovo, Pa., 16 years; earliest, May 2, average May 9.

In thus considering a biologic problem such as migration, it is as well to remark here that we are laying ourselves open to the just criticism which biometricians incur when they rely solely on figures. This we realize fully. Perhaps data from individual birds, which

will one day be forthcoming, will show us that we have greatly exaggerated the individual potential accuracy, but on the other hand may it not be possible that in some cases we have underestimated the case, for as suggested above the first arrivals of a species flight may prove to be always the same birds, bound for a definite latitude and locality.

From Cooke [1] we get the impression that birds cannot in any way predict weather conditions, as has so often been claimed for them, and that such birds as the ducks and geese are much more liable to take advantage of weather conditions, open water, etc., than are the passerine birds. And were this accuracy of the passerines correlated in any way with an increased intelligence, we would certainly expect to see it manifested in birds like the Canada Goose and the ducks, whose superior mental endowment none can doubt. But here we seem to see it least, for in the migration of these independent fowl there is often an error of weeks as contrasted with days among their more trustful and less intelligent brethren. Has not this very intelligence tended in some subtle way to deliver the geese from the bondage, so to speak, of a hide-bound time sense, and allowed them a greater scope to grapple with seasonal conditions? This has nothing to do with the evolution of the species considered: it simply means specialization in a given direction. So also it seems to the writer that the 'potential accuracy' of birds like our Bluebird is probably much greater than we think, but the species is subjected to such a grave variation in season on account of its early arrival in the north, that it, so to speak, does merely the best it can.

Another question occurs at this point, which is really not within our enquiry, but may be mentioned, and that is the reason for the widely different migration times of different species.

Loomis [2] saw in this phenomenon an indication of an orderly depopulation of the North in order to prevent over-population, and he attributed all that we see now to an equalization of distribution through diversity in the time of southern migration, evolved by the progress of ages and perpetuated by the require-

[1] W. W. Cooke, Yearbook of the Dept. of Agriculture, 1910.
[2] **Auk**, 1894, p. 94, Loomis, L. M.

ments of winter. In other words, a huge and far-extending altruism, with nothing left to chance or to orthogenetic tendencies. This view is, I think, farfetched, for one cannot see how the earliest spring movements are the necessary outcome of a rush to occupy all available territory. We should suppose that many more birds could migrate at the same time without disturbing the geographical economy of seasonal dispersal.

Loomis saw in the case of the Canada Goose a continuous migration, not subject to a sudden arousing of the migratory impulse. The impelling force came in this case, he thought, more from without. But here it seems he is only partly right, for this species is certainly subject to great and sudden migratory impulses, only, as we have mentioned above, there is added an element of choice, or an ability to profit by external conditions which is not often easy to see in other birds.

Loomis's various papers in 'The Auk,' in so far as they refer to the erratic movements of birds, and peculiar periodic dispersals, are very interesting, but cannot be considered here. See also an instructive paper by Whitaker on the great invasion of southern Europe by Crossbills in 1909.[1] Even such cases of sporadic invasion of new territory may show an orderly progress and just as orderly retirement.

Many theories of course have been put forward to account for the start of vernal migrants from winter quarters. An ingenious one is that of Taverner[2], who saw in the breeding of tropical species an actual stimulus to wintering migrants. This stimulus was, he thought, brought about by pressure of numbers and lack of food owing to increase in resident numbers by their early breeding, the pressure extending outwards (northwards) to the limits of populated ground. Other writers have seen in the failure of the food supply in the South after the advent of the dry season, a sufficient inciting cause, but it is hardly probable that any of these reasons could account entirely for the orderly procession of different species, and their appearance at allotted times.

It remains to search for other examples of a physico-chemical

[1] Whitaker, J. I. S., Auk, 1910, p. 332.
[2] Auk, 1904, p. 322.

periodicity to compare our time sense with. There occurs to one immediately the phenomenon of ovulation and menstruation in man, and the appearance of rut in other mammals. But such appearances are notoriously liable to time error, and easily affected by changed conditions, disease, season, etc. Variation in periods of gestation and incubation are, it is true, extremely close to the mean for the species, but these periods are coupled and timed by very marked changes in circulation and metabolism, and are scarcely comparable with the migrating period of the bird, which has nothing but the very doubtful stimulus of the developing sex glands to check and control the migration once it has started, and even this is sometimes not present at all. I use the word 'nothing' as meaning nothing that we know of at present. It would indeed be interesting if we could subject castrated birds to experimental conditions in order to test the strength of their migratory impulses, but this could hardly be accomplished. All we know is that young birds belonging to migratory species, though they do not themselves breed during their first year, come north with the others, perhaps by imitation.

We acknowledge the dominating power of sexual 'hormones' in instituting spring migration in birds, for the instinct of reproduction is the dominant instinct in animals, and all others may be classed as secondary to it. What we cannot account for is the controlling and regulating power which must be constantly at work once the journey is begun, in order that a certain latitude may be reached at a certain time.

For instance among warblers Cooke tells us[1] that the Black and White Warbler, an early migrant, occupies a whole month in going from North Carolina to Massachusetts, averaging only 13 miles per day, while the Blackpoll Warblers that nest in Alaska make the last part of their journey, 2500 miles, in not over two weeks, or about 200 miles a day. Some Yellow Warblers accomplish the last part of their journey to Great Slave Lake more than twice as fast as the average advance of spring over the same region. From New Orleans to Great Slave Lake they are continually meeting colder weather. Even the same species shows very different rates of advance in different parts of the country.

[1] Chapman's 'The Warblers of North America.' 1907.

We have, it must be said, various other periodic reflexes, dependent on feeding habits, the diurnal movements of lower organisms following the light, and the tidal movements of various littoral creatures, with very likely a host of others. But none of these so far as I am aware exactly fits our case in birds. In fish, it is true, especially in the salmon family, we see an accurate periodic movement, often begun months before the spawning time, and therefore hardly carried out alone by a direct stimulus from developing eggs or milt. Ocean fish, like the herring of Europe, show characteristic spawning times and spawning places for each closely related race. Bats and fur-seals among mammals are other examples but as to the accuracy of arrival of these animals I am not informed.

I think it is plain, then, that the migratory impulse in birds is not to be explained on the basis of a purely physico-chemical response to an internal secretion, at least not that phase of it which pertains to potential accuracy. This may be a part but not the whole story. Nor does one wish to drag in by the heels any question of intelligent effort, for this would not help us in the least, and would tend to diminish rather than increase the time sense. I say *diminish* because instinct appears so much more mechanical, regular and blind than intelligence ever does.

If one accepts Darwinism in so far as it applies to the selective value of useful variations, it seems hard to see how this chronometer-like accuracy can have been evolved; or even assuming it to have arisen through an adaptive necessity, it is still harder to see why it should remain in its present perfection, for the most enthusiastic Darwinian could scarcely picture it as a matter of great moment to the species if it arrived one week early or one week late, with the whole season before it. We must grant of course one great source of error in our conception of potential accuracy, for as stated above, we are forced to deal with groups instead of individuals; still with a long series of years it seems as if one might gain a pretty correct impression of the accuracy of the individual bird itself.

The writer is familiar only in a general way with the subject at hand, and has merely attempted to call attention to an aspect of migration which does not seem to have been much discussed. Whether it is even worth discussing in the light of our scant knowl-

edge of instinctive actions and their causes is doubtful. With the masses of facts being brought constantly to light relative to bird travels, we are perhaps a little apt to lose sight of some of the old time mystery of the subject. The modern tendency seems to be to sniff at the word 'mystery' as applied to any phenomenon of bird migration. This is merely a question of where the word is applied; if to the actual facts, then it is hardly warranted, but if to the causes, then it is certainly as applicable now as ever. Supposing the facts all at hand, what would the student know about the actual inherent impetus, the heritability of instinct, or the powers of orientation and their mechanism? Would he be one whit better off than the present day systematist who with all his finely cut races does not really know how or why a new species arises?

Mystery there certainly is, and mystery there will always be as long as *the* great biologic problems remain unsolved. The formation and maintenance of this time sense is only one of those activities of nature which tend to make the sternest advocate of mechanism doubtful of its all-sufficiency. It is so much easier to find behind that clock-like movement a vital impetus, 'a guiding unity.'

"It (the evolution of life) is a creation that goes on for ever in virtue of an initial movement. This movement constitutes the unity of the organized world — a prolific unity, of an infinite richness, superior to any that the intellect could dream of, for the intellect is only one of its aspects or products." (Bergson.)