

SOME ANGLES IN THE PROBLEM OF BIRD
MIGRATION.

BY JOSEPH GRINNELL

It has been suggested that when the emotion of wonder or marvel comes over a person, said person tends to lose all rationality—he is, for the time being, of unsound reason. If this be true, then the state of mind in which one marvels or wonders over natural phenomena is not a state of mind in which one can permit himself to indulge and at the same time expect to develop soundly scientific interpretations from the sets of facts he gathers.

There is on our library shelf a large amount of literature concerning the subject of bird migration; and from year to year this mass of print is growing. The majority of the authors represented in this field of literature handle the subject of bird migration in the popularly appealing, romantic way. A common literary device employed in this method is the one inducing in the reader the emotion of wonder—startling queries left unanswered, ideas akin to supernaturalism invoked if not out and out expressed. Examination of books and articles on bird migration, with this point in view, shows that, with very few exceptions, they open and conclude with exclamations of wonderment! “The marvel of nature” is their main selling point. And natural history in general, as a really worthy field of scientific enquiry, I may as well admit has been suffering from the same sort of thing.

A substitute for the emotion here called in question, and one, I think, quite different and altogether consistent with rationality, is what has been well termed scientific curiosity—that calm and unexcited attitude of mind in which a person wants to know, with confident expectation ultimately of finding out. Regarding this subject of bird migration, freely admitting it to be one of manifold complexities, let us begin and carry on our enquiries with rather bold assurance that, sooner or later, we are going to find satisfactory answers to every question, down to such as relates to the very smallest detail. At least, this attitude cannot fail of being the really safe as well as profitable one.

We now have, right at hand in published form, large accumulations of well attested facts concerning the habits and individual behavior of birds. Good observers are increasingly numerous; and methods are improving, for example in the employment of banding, or ringing as the Englishmen say. What we need in improved measure is the exercise of those faculties which will enable us slowly, critically, and explicitly to derive interpretations from these facts. We also need to draw upon the correlated knowledge afforded in general biology, in addition to what we can learn alone from the bird itself.

We learn from general natural history that often when an animal group gains increased ability for locomotion on the part of its individuals, other factors remaining equal, it gains ascendancy in the struggle for persistence over related groups which lag in this respect. The class of birds outstandingly, among all the vertebrate groups, has acquired the ability individually to move from place to place, and the individuals of this class do so chiefly through the air. Indeed, we may say of birds that all of their class attributes have to do with this perfected function of rapid aerial locomotion.

Aerial locomotion requires high-power engines. The prime and unique structural feature of birds which allows them to develop power with economy of weight is their covering of feathers; for this envelope of feathers enables them to maintain a higher bodily temperature than is found in any other animal group. Citing some facts from Bergtold and from Wetmore, in the ordinary run of passeriform birds the body temperature ranges, in different species, where definitely ascertained, from 105 to 112 degrees F., with a mean of 108, a temperature quickly fatal to the human mammal. And a major feature of structure in the thermo-regulatory system of birds which prevents lowering of the temperature below the optimum for them is their equipment of feathers; a feature of structure which helps to prevent the temperature mounting excessively during extreme exertion is the air-sac system. Heat conservation, insulation, means economy of fuel consumption plus maximum production of power. Relatively to the remaining warm-blooded group of animals, the mammals, birds possess much greater rates of action and reaction in all respects.

Let us recall here that certain law of the acceleration of chemical

reactions with increased temperature. In the activities of living muscular and nervous and secretory cells and tissues, just such behavior of reaction is involved. I have been told by a friend in chemistry that an increase in temperature from 98 degrees F. to 108 degrees F. means in the inorganic world roughly doubling the rate of chemical reaction. In organisms, where various chemical activators also operate, there is surely no less increase of rate with rising temperature. In other words, a bird like the Junco, which Wetmore found to have a temperature of 108 degrees F., probably lives at least twice as fast as does a human being. In matters of awareness, quickness of perception, decision (in the instinctive sense), ability to get under way and to change direction, in potential speed of movement, the bird is the superior by a huge margin.

It is one characteristic of birds, then, that ordinary physical barriers such as deter or outrightly stop non-volant, terrestrial animals are easily crossed over. The immediate problem of gaining a livelihood on the part of the individual bird thereby becomes greatly simplified; for the bird can easily extend its search for food—can shift its daily forage beat altogether, seek food where most readily obtainable, even far from the safe roosting place to which it must return each night, in certain cases go across miles of country to get the food with which to supply its young which have been hatched on an island or in an aerie selected for essential safety from enemies. Birds, by reason of their successful solution of the problem of transportation, are able to *commute* in degrees far exceeding our own celebrated accomplishments in this line.

Migration as regards any given species in which this habit is highly developed is a pouring or streaming of a population with more or less *seasonal* regularity from one territory where subsistence of the requisite kind is failing into another territory where subsistence of the same kind is obtaining. Sometimes the pouring or streaming of emigrating populations follows single narrow, well-defined channels, as when paralleling coast lines, river-valleys or mountain chains; often the routes of travel are broad, covering extensive and topographically variable terrain thinly; sometimes they break up into numerous trickles or streamlets, separating and uniting in approximate conformity with the configuration of the land or with resources of subsistence along the way; sometimes

there is merely an irregular drift of individuals across or over the land or the sea from winter to summer habitat or vice versa. And in many species there is no regular, migratory movement, but a tendency to wander, irrespective of season or place—avian vagrancy.

It is significant here for me to point out that the classical cases of migration forming the usual basis of discussion are those of birds which show the habit in extremest degree, as regards length of route traversed, or as to seasonal regularity of accomplishment, or both. Also, the latitudinal position of the usual station of observation, namely, in the north temperate geographic zone, is so located as to give maximum opportunity for perceiving of the phenomenon, because there involving the greatest percentage of far-migratory species, and most individuals of these species; and also, *there*, are located the greatest number of thinking, or "marveling," human observers.

We must constantly keep in mind, as full of meaning for our thesis as I try to develop it, that when we consider all the birds of any one locality and more especially all the birds of the entire territory in so far as we know it from the equator to the north pole we find every conceivable intermediate degree from the extreme of far-distance and great regularity of migration down to the condition of absolute sedentariness of entire population with only a meager evidence even of vagrancy. Indeed, on checking over groups among all the species of the northern hemisphere I feel safe in saying that the majority (and this applies to aggregate of the individuals as well as to species) are either wholly sedentary or are only partly or slightly migratory. Thus, I would say that migration in its more extreme manifestation is *exceptional* rather than the rule among birds.

By my interpretation, then, we are to look upon birds, all of them, as uniquely, inherently and primitively capable of easy locomotion. The only exceptions or near exceptions are where other factors have induced, *secondarily*, a condition of near or absolute flightlessness, as exemplified in certain insular genera and in certain birds of huge size and highly developed foot power. Here in California, even in our most resident species, like the Brown Towhee, we observe exercise of a high degree of locomobility, as attested of late by the observations of bird banders.

The individual Brown Towhee has in reality a wide latitude of movement, it is able quickly to adjust itself to locally varying food supply and shelter, and it thereby improves its chances of surviving the dangers of locally and recurrently shrinking subsistence.

The factors delimiting the geographic ranges of all our birds, the most sedentary as well as, and in like measure, the farthest migratory ones, are as follows: (1) food of the right kind in sufficient amount, (2) appropriate shelter, meaning safety refuges for individuals, and (3) breeding places or nurseries of appropriate kinds. Territory providing all these factors is occupied to its limit. The distributional occurrence of a species at any moment of the day or on any day of the year is controlled by the co-existence, within coverable distance, of all three of these factors, which together may be termed subsistence. If any one factor of them fails in any direction, the individual bird must withdraw from the territory affected or else die. If, on the other hand, from day to day, and from year to year, changing conditions result in the opening up of new habitable territory, that is, if favorable conditions precedently lacking become provided in it, then individuals from each species affected will promptly fill in the new increment to the general range. Because individuals are able to circulate readily, in groups and individually, and by reason of their geometric ratio of reproduction, their populations may spread within a very few generations to almost any limits. Far more quickly than in the case of other vertebrates, I think, birds are able to take advantage of new territory offering. They are superior opportunists.

Bird populations, then, are blessed with an extraordinary fluidity as regards both time and space—by reason not only of wing power but of superior reaction rate. A factor in the group of features which makes for elasticity of distributional behavior in birds, even in the most sedentary of our species, is comprised in the proneness to wander on the part, especially, of birds-of-the-year. By this process, individuals of each species are continually exploring the frontiers of the general range of the species—seeking to find new ground where, even temporarily, according to season, competition against other animals and against other individuals of their own kind, for subsistence, is not so keen. Huge numbers of individuals are continually, from generation to generation, being

fed into this particular trial-and-error mode of progress, which obtains of course in more or less degree with all other animals. Vagrancy, or pioneering, if that term sounds better, is certainly more conspicuous, and probably more effective, in birds because of the possession by the individual bird of superior ability quickly to go out of ordinary bounds.

To repeat: the most sedentary of our local birds are able to cover much ground daily, to commute, as it were, between resting and breeding places, between resting places and forage grounds, between forage grounds and breeding places. Large areas, producing special kinds of food supply, become accessible, even though far from breeding places, and this ability to reach them means the existence of larger and larger numbers of individual birds, than would otherwise be the case, as the system becomes perfected. Here we see a reason for so much of the flying that is going on—birds going to and fro, not at all for the joy of living or because of excess of vigor—but because it is in the long run absolutely necessary in their scheme of living to do so. They are conspicuously “on their way,” but with a justifying purpose; not joy-riding, but as a matter of life, versus ever-impending death, of their species. Daily, the birds go to and fro, over many routes, these determined upon in part by conscious choice, for the birds are keen quickly to fall in with any change that brings improved conditions of subsistence locally—better feeding ground, safer resting and roosting place, safer nesting place.

With all birds, then, much movement is involved in the *daily* program. Let me here try to picture the locomotional behavior of a bird which is selected from among those members of our *Campus avifauna* which show no truly migratory tendencies whatsoever. This is the diminutive Bush-tit (*Psaltriparus minimus*); and I doubt if any individual of this species during its whole life-time gets beyond a mile from where it was hatched. Yet each individual covers a surprising amount of ground in the course of its daily foraging.

During three-fourths of the year, June to February, the Bush-tits associate with one another in flocks of from 15 to 40 individuals. Each of these flocks ranges in a day over a more or less definite area of live oak, chaparral, or, in the upper edge of the town, culti-

vated shrubbery. In February the flocks break up into pairs, for the breeding function, but as soon as the young are out, new companies assemble. Although we call these companies flocks, the birds are never seen to bunch closely together and to mount on the wing high in the air to take any prolonged flight. Rather, do the birds form loose, scattering droves, loitering along widely spread through several oaks or brush-clumps. There will be noted a general onward movement of the group as a whole, but the striking thing is the incessant and independent movement of each component individual. The food of the species consists entirely of animal things, plant-lice, scale-insects, and the like, of to us minute size, gleaned from the surfaces of leaves and stems. To find these objects in sufficient amount to sustain super-active life, especially during the winter season, day-long activity seems necessary: the individual Bush-tit is continually intent upon its near-sighted scrutiny of leaf-surfaces, especially the under sides which some other foliage-foragers largely miss; thus a Bush-tit's movements bring it very often into the inverted position of body characterizing also its relatives, the Tit-mouses, widely known in North America and Europe.

Incidentally, this close and incessant scrutiny, necessary for successful food getting of the kind described, may expose the Bush-tits to a serious measure of danger from their hereditary enemies, the Sharp-shinned Hawks (*Accipiter velox*). This danger is minimized by the habit of flocking whereby the individuals keep within hearing of one another so that the entire group profits by the warning given by the first one to apprehend danger. There is an elaborate "language," consisting of constantly uttered location notes, to keep the flock within bounds—to prevent loss from it of individuals out of sight of one another because of intervening foliage—of loud alarm notes, and of a most effective, effacing chant or confusion-chorus, combined with the "freezing" of the birds.

But to return to their locomotion: The flock as a whole moves but slowly, and it moves in an irregularly circuitous course, determined by such factors as food-productiveness of leafage, and fear of open spaces on the part of the birds. As worked out by my one-time student, Robert C. Miller, in his inquiry as to the so-called "mind of the flock," the total distance covered by one com-

pany of Bush-tits in a day may be less than one mile and by reason of doublings and zigzaggings cover all told less than 50 acres. Yet the individuals, each on its own independent course, have traveled a far greater distance.

The other day, with watch in hand, I observed some Bush-tits with this point in view. A given Bush-tit was seen to shift its position in extent more than a hop, so that the use of the wings was involved, eighteen times in one minute—this therefore in addition to the many more movements involving shift of foothold; and I estimated each of such major shifts to average ten inches. Carrying out a computation on the basis of these figures, for an eleven-hour winter day, brings us to a total daily extent of travel for each individual, of very close to two miles, or upwards of a thousand miles per year, if we figure in the greater length of summer days. The so-called sedentary Bush-tit is thus really pretty much of a traveler even though within small radius.

E. M. Nicholson, perhaps the foremost present-day student of bird behavior in England, in his recent book, "How Birds Live," cites an observation of a pair of Long-tailed Tits which required an aggregate of journeyings, in order to collect the materials for their nest, amounting, when the nest was completed, to over six hundred miles of travel. In another case a pair of Blue Titmouses made thirty-five journeys an hour to their nest, and covered sixty miles daily for every one hundred yards that the food supply was distant from the nestling brood. The point, again, in these cases of the Bush-tits and Tit-mouses is that, while these species are sedentary, non-migratory, yet in normal course of daily routine they individually cover in flight great distances.

The energy involved in the so-called "marvelous" examples of migration is, therefore, even in a conspicuous case, say that of the barn swallow, no single terrific test of endurance; to quote Nicholson, "It is the energy of everyday life concentrated in one direct aim," and involving only a period of days, rather than a single day. "It would hardly be exaggerating to say that a great part of migration is performed simply by the travelers keeping to one appointed direction instead of traveling round and round one little area."

I want now to cite some facts and inferences from studies of sub-

species, and of local populations, pertinent to the better understanding of the nature of migration. We observe that in a number of geographically variable groups certain of the subspecies are conspicuously sedentary while others in the same genus and same species are habitually and regularly far migratory. For example, among the subspecies of Song Sparrow (*Melospiza melodia*) here in California, the race *fisherella*, of the Modoc region, is altogether migratory, while the race *pusillula* of the southern San Francisco Bay marshes is altogether resident. Among the Horned Larks (*Otocoris alpestris*) of western North America, *arcticola* of Alaska is far migratory, while *rubea*, of the Sacramento Valley, is perfectly sedentary. It would appear from a consideration of numerous cases of this sort either that the migratory habit is quite as easily lost as other features shown by slightly differentiated subspecies, or, with the same significance, that it is as easily gained as those features which distinguish slightly different subspecies.

We can go farther, and examine the local population within a single subspecies. Take the Brewer Blackbirds (*Euphagus cyanocephalus*) of the Pacific coast race *minusculus*: those individuals which summer and breed in northeastern California and along the high Sierra Nevada move west and south for the winter season, then occupying common ground with those individuals identifiable as of precisely the same race which stay summer and winter in the lowlands of western and southern California. Then, the Western Meadowlarks (*Sturnella neglecta*) of the various parts of the range of that species in western North America show varyingly, in response clearly to varying need, the predilection for migrating; some individuals, those in southern parts of the general range, are quite resident, while those summering at the north and at high altitudes on the Sierra are regularly migratory.

It would appear from this category of facts that the habit of migration is in most kinds of birds a perquisite easily and quickly taken on or put off. The physical equipment for migration is in nearly or quite adequate measure already possessed as a common attribute of birds, one of primordial standing. In the continual play of factors of existence consequent upon the continual changing of general and local environments, birds, by reason again of their endowment of motility, of sensitiveness, of extreme alert-

ness, are able quickly to make adjustments. We may, indeed, say that the easiest thing they can do toward maintaining successful existence is to transfer their behavior from that of a population shifting annually to the condition of continual residence of their populations, subject only to daily and local circulation. And quite as easy is the reverse adaptation.

A conclusion, then, that seems to me warrantable is that there is not the least need of resorting to any theory of ancient establishment of specific habits of migration. It is unnecessary to appeal to conditions in past geologic time to account for the varying extent of migration in the different species at the present time, as has been done by very many writers on this subject. In the one genus *Sterna*, the Terns, which affords the classic example of the Arctic Tern (*S. paradisaea*), some individuals of which are thought to make an annual circuit of 22,000 miles, we also have the Forster Tern (*S. forsteri*), some individuals of which probably make no migration drift at all; but the latter individuals are probably almost if not quite as much on the wing day by day as the individuals of the former species.

In summary: The problem of bird migration is to be dealt with as a subject without any quasi-mystical attributes, one to go at with full confidence that it can be understood eventually in all its details upon the basis of facts discriminately gathered and rationally interpreted. This is a complex problem, one of many, many angles. The nature of a few of the phenomena which are dealt with in the present paper, and something as to their interpretation, is indicated in the following statements.

(1) Birds are primordially equipped easily and quickly to cover territory by flight through air; and this all kinds do, save for the very few, mostly insular forms, where very special conditions of existence have led secondarily to flightlessness.

(2) Birds, by reason of their high body temperature, react in all sorts of ways with exceeding speed and accuracy; they are far and away more alertly responsive to environmental stimuli than we clumsy humans, perhaps two to one; they are observant and heedful beyond the degree shown in any other animal.

(3) No so-called sixth sense, or sense of direction, *has* to be invoked to account for birds finding their way during long seasonal migratory flights any more than in their courses of daily movement.

(4) The factors that induce, maintain, and modify habits of migration are at the very least as effective now as they ever have been in past time; and they are in all likelihood precisely the same as those which control general geographic distribution in all the higher vertebrates.

(5) Adjustments of populations to changing conditions of food, shelter, and safe breeding places are, by birds, readily met; seasonal movements of populations, easily acquired or discarded as habits, give birds a great advantage over any other group of animals yet evolved. It may be suggested that, in consequence, an Age of Birds is in the ascendancy.

But, be it said again, the above are offered only as *some* angles in this big problem of bird migration.

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RUFFED GROUSE (*Bonasa umbellus umbellus*) PHOTOGRAPHED ON ITS DRUMMING LOG, MONROE CO., PA., BY HENRY R. CAREY, MAY 12, 1930, AT 4.39 P.M. PHOTOGRAPH TAKEN WITH CAMERA TRAP SPRUNG BY THE BIRD AFTER BEING SET FOR SEVEN AND A HALF HOURS.