

## ANIMAL MIGRATION—PERIODIC-RESPONSE THEORY

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THE object of this paper is to review available data pertaining to migration, to reorganize and restate the background material, to present a new theory of migration to be called the periodic-response theory, and to point out ways and means by which the theory can be subjected to scientific experimentation. The writer is indebted to the following for suggestions and criticisms: A. S. Pearse, F. C. Lincoln, Clarence Cottam, May T. Cooke, Walter Cottam, W. W. Newby, William H. Behle, Don M. Rees and others.

It is becoming increasingly clear, as Dixon (1897), Nicholson (1929), Grinnell (1931: 32) and others have indicated, that the migration of animals must be explained upon the basis of natural processes still at work. Migratory movements occur in so many different groups of animals, that the conclusion seems inescapable that the process of migration has arisen independently many times and probably in many ways. There is such wide divergence in the degree of development and methods employed in migration among different groups of animals that it becomes extremely difficult to delimit the concept and define the term. Cahn (1926) considers migration as "a periodic passing from one place to another." Coward (1912: 1) says that "migration is the act of changing an abode or resting place, the wandering or movement from one place to another, but technically the word is applied to the passage or movement of birds, fishes, insects and a few mammals between the localities inhabited at different periods of the year."

The idea of two-way movement is not included in Williams's (1930: 9) concept of migration, which he says "is a periodic, more or less unidirectional continued movement, assisted by the efforts of the animal, and in a direction over which it exerts a control, which results in the animal passing away from its previous daily field of operations." This was obviously designed to include certain insect movements which could not be proved to have a return. It also excluded daily movements, which Cahn included.

The author believes that migration may be considered as periodic passing of animals "from one place to another" in which movements are timed to fit with some periodic rhythm or cycle of the environment, or timed to fit with some stages or steps in the life history of individuals making the migration. This correlation with periodic rhythm implies two-way movement and this in turn implies some

sort of directional control of movements—not merely drifting with the forces of the environment. In some insects, the return movement may be performed by a different generation. Periodic dispersal without return may be considered as 'emigration' in accordance with the definition of Heape (1931).

#### BIOLOGICAL RHYTHMS

In accordance with this definition, it becomes desirable to take stock of biological activities that are rhythmic or periodic. All activities may for the purposes contemplated here be grouped in a graded series under three headings: non-rhythmic activities, environmentally controlled rhythms, and inherent (hereditary) rhythms. In the first group are those activities that are not correlated with periodic events of the environment, as for example the activities of human growth. In the two other groups are included regularly recurring biological rhythms (cycles) that may be correlated or timed to coincide with such regularly recurring events as day and night, wet and dry periods, tides, the lunar month, annual seasons and longer secular periods. Among these biological rhythms are some that are active as long as the periodic event continues but cease if the event discontinues its periodicity. There are certain snails (Pearse, 1939: 104) having both 'lungs' and gills between which they alternate breathing when living in the intertidal zone at the seashore, but in certain protected estuaries where there is no tide they use gills only. These are examples of the second group. There are many biological rhythms correlated with the periodic events that persist even when removed from the influence of such events. Some persist for short periods, others for longer time and some permanently.

*Daily rhythms.*—Welsh (1938) in reviewing the field of daily rhythms has shown clearly that many kinds of biological rhythms correlated with day and night persist in the absence of alternating conditions. These changes include such things as biological light production, changes of color, changes in the rods, cones and pigments of the eye, the resting-activity cycle, and other metabolic relations. The mechanisms causing the different cycles may not be the same in all animals but the net response—persistent 24-hour cycles—seems to be similar. The human daily rhythm of activity varies considerably in different latitudes, being strong in the tropics and nearly absent in the polar regions.

In some cases, the phases of a cycle may be experimentally altered, but the tendency to return to normal when opportunity offers seems to be present. Johnson (1940) demonstrated that deer mice (*Pero-*

*myscus*) kept in continual darkness will continue to exhibit their daily rhythm in which the active period occurs at night, but since they are not necessarily accurate time-keepers, they may gradually get out of phase with actual day and night in absence of the photic stimulation of day. When exposed to continuous light, the active period was postponed slightly on each successive day by increasing the length of the quiescent period. The greater the intensity of the light, the more the active period was retarded. It also tended to break up long active periods into shorter ones. This may be interpreted to mean that light appears to have an inhibiting effect upon the mouse activity, delaying the activity period in continuous light; or in alternate dark and light periods restricting its appearance to the dark. The conclusion seems inescapable that the external stimulus of light in the case reported tended to regulate the rhythmic appearance of the biological cycle.

Despite the fact that daily-movement rhythms are not usually considered as migrations, there is much in common in the general nature of the phenomena and the differences are largely matters of detailed adjustments to different kinds of environmental periodicities. In many cases, the daily movements of animals represent in miniature movements similar to migration, and require similar mechanisms of operation. In lakes and ocean, there are certain daily movements of plankton rising to the surface or sinking into deeper water, that are often called daily migrations.

The daily movements of blackbird flocks (*Agelaius phoeniceus*) may serve as a better example, and may be considered a prototype of the seasonal migratory movements of the same birds. The nocturnal roosting place in cat-tail marshes serves as the home base from which the birds start out in a 'daily migration'. They fly to some distant place with which they may or may not already be acquainted. There may be some mechanism of guidance in either case. After foraging, resting or wandering, a return journey to the swamp must be undertaken. This may be described in almost identical terms with their seasonal migration—a two-way journey from the home base to some distant place and return.

This, of course, is not a definition of migration and it is discussed only for the purpose of showing the inherent similarities of the two patterns, and in a simple way laying a foundation to which more complex patterns may be compared.

*Lunar rhythms.*—In the intertidal zone on the seashore are many animals with rhythms correlated with the tides which are chiefly influenced by the moon. Certain crabs (Pearse, 1939: 104) can breathe

by means of either gills or 'lungs' and serve as good examples of animals with biological rhythms that depend exclusively upon the external controls for their alternations. If kept constantly in either air or water the biological rhythm initiated by the tides disappears. The periwinkle, *Litorina littorea* (Pearse, 1939: 92) moves up and down the rocky shore as the tide flows and ebbs. Some podurans move up the sandy beach and burrow several inches in the sand when the tide comes in and then emerge after it has ebbed. These are sometimes called tidal migrations.

While the foregoing examples illustrate adjustment to the tidal rhythms as such, some of the animals in the intertidal zone show rhythms which are not only correlated with the tides but also with the daily rhythm. The naked pulmonate snail, *Onchidium floridanum* (Arey and Crozier, 1921: 483) living in protected colonial homes in crevices, emerges for short foraging expeditions during the daytime when the tide is out but is not known to emerge at night. The rhythm disappeared in the laboratory.

Perhaps the most striking lunar responses are found in the marine palolo worms and the grunion fish (Pearse, 1939: 175), in which the responses occur not only correlated with the moon's phases but also with seasons. The Pacific palolo in the southern hemisphere rises to the surface to spawn in great numbers when the moon is full during October and November but the Atlantic palolo in the northern hemisphere picks the time near the moon's last quarter in July. These may be considered as vertical migrations, correlated with moon phase and season.

The grunion rhythm is much more complicated (Thompson, 1919). The small fishes of the species *Leuresthes tenuis* come to the California coast to spawn from March to June each spring. The fish ride the high waves up the beach until they are left stranded. The spawning takes place in the sand near high-tide mark during the nights immediately following the high tides of the full or dark moon. The male is partly wrapped around the female during the act of spawning, during which the eggs are buried in the sand, and are buried deeper by successive lower waves. Two weeks later the eggs are ready for hatching, which cannot take place in the sand. The high tides of the next dark or full moon actually wash out the eggs and release them for hatching. Thus the spawning cycle appears to be correlated not only with season and lunar phase but also with high tides of the full or dark moon that will bury the eggs deeper in the sand and which will be followed by high tides two weeks later that will wash the eggs out of the sand and permit hatching.

*Seasonal rhythms.*—Woodbury and Hardy (1940) have shown that there is a seasonal cycle of movements in the desert tortoise (*Gopherus agassizii*), in which the tortoises congregate in dens (long horizontal tunnels) in the winter, move out in the spring on to open terrain where they spend the summer, digging short individual burrows when summer gets too hot, and seek the winter dens in the fall. This represents a very primitive type (prototype) of seasonal migration of very limited scope. The seasonal migrations occurring in March and October between the winter dens and summer range, are of very limited distance, usually not over one-quarter mile, but in proportion to mobility and time consumed, the movements of the tortoises may be on a par with the short migrations of some birds. In any event, the behavior patterns are essentially similar in response to season but also have certain problems in common, namely: initiation of movement, determining direction and distance, cessation of movement, initiation of return movements, and so on. Despite these essential resemblances, such movements of tortoises are not generally regarded as migration, but may serve as a type of what may be termed local migration.

Unpublished investigations of the writer have disclosed that some snakes in the temperate mountainous regions of the western United States make similar seasonal local migrations covering somewhat greater distances. Wintering dens have been found containing Great Basin rattlesnakes (*Crotalus v. lutosus*), Western striped racers (*Masticophis t. taeniatus*), and the Great Basin gopher snake (*Pituophis c. deserticola*), which must have concentrated from many square miles surrounding the dens. More than 320 such snakes taken from a single den under conditions which make an estimate of 500 to 1000 snakes a probability, give a basis for estimating that they must migrate up to several miles to spread out over the summer territory and return again in the fall.

Allen (1939: 253) indicates that some bats have similar habits of concentrating in caves for hibernation in the winter and spreading out over the surrounding territory for the summer. The distances traversed in such migrations are much greater than in the snakes, but essentially the same pattern of behavior is presented. The difference in distance traveled is proportionally as much greater than the snakes' as the snake distance is greater than the tortoises'. All three are probably correlated with locomotive ability. Other bats are known to make latitudinal migrations similar to those of birds.

Among the more outstanding biological rhythms correlated with season, in the temperate zone may be mentioned the deciduous habit

among trees, the hibernation and in some cases estivation of cold-blooded animals (also some mammals), the changes of fur and feathers in warm-blooded animals and the ordinary migrations of birds, certain mammals and certain insects. It is, of course, the last type that is of primary interest here but the others are mentioned because they represent phenomena essentially similar in pattern of response to season but employ different methods in effecting the response. The movements of a bird that nests in the temperate or frigid zone and moves toward the equator or to warmer climates to spend the winter and then returns to the breeding area the next season may be considered as typical migration. Consideration of seasonal migration will be deferred for special attention in a later section of this paper.

Some border-line cases may be considered at this point. The activities of certain young spiders and gypsy-moth larvae in spinning long silken threads which they use in 'ballooning' to carry themselves down wind can scarcely be considered as migration. Even though such activities occur regularly correlated with the seasons as typical migrations are, yet there are differences that are significant. In typical migrations, the animals, at least in part, determine their direction and furnish the motive power, whereas in these cases, the spiders and larvae do neither—they are carried and directed by the wind. In true migration, wind at best can only be a favoring circumstance and at worst, can only retard or stop the movement.

*Secular rhythms.*—Some biological rhythms express themselves periodically in cycles of longer duration than one year. These are not all of the same length and great difficulty has been experienced in finding correlations with or the causes of such cycles. Many attempts have been made to correlate some of them with various phases, fractions or multiples of the sunspot cycle, a full unit of which is believed to take about 45 years, but with at least ten sub-cycles ranging in length from  $8\frac{1}{4}$  months up to 23 years (Abbot, 1940 lecture), of which the 11-year cycle appears to be more or less primary (De Lury, 1938).

It has been abundantly demonstrated (Clements and Shelford, 1939) that there are secular cyclical fluctuations in population numbers in many animals. Green and Evans (1940) have concluded from their study of fluctuations in the snowshoe-hare populations that with a relatively constant death rate and biotic potential in the adult population, it then depends upon the rate of survival of the young what the trend of the population will be. Since survival of the young depends so much upon competition for food, success of

predators, and other biotic factors, it may be interpreted to mean that the population rhythm of numbers may be so closely correlated with biotic events and so remote from secular periodic events of the physical environment that correlation with the latter in many cases may not be recognizable. Under such conditions, the correlation with biotic events may be more profitably studied.

It is well established that many animals when at peak numbers in the population cycle respond to the population pressure by some kind of movement. Such movement is usually concomitant with hunger and may result in either individual or group activity. In many cases, the movement actually takes the animals away from the home area of their development into new places. Such movements not involving a return journey are sometimes called one-way migrations but a better designation would be secular emigrations. Such emigrations may be either irregularly sporadic or rhythmic, i. e., repeating at more or less regular intervals. An example of the former is the mouse plague of Tulare, California (Hall, 1927) and an example of the latter is the story of the lemmings which has received so much attention in the literature (Heape, 1931: 75). It has been shown, however, that not all animals resort to movement when crowded. The Kaibab deer (Clements and Shelford, 1939: 201) when overconcentrated and starving on their winter range failed to emigrate in search of better places.

Among the insects, secular emigrations appear from time to time in the grasshoppers, dragonflies, moths and butterflies. Some are sporadic and some appear to be rhythmic, but many of them are difficult to classify. Williams (1930) has shown that many moths and butterflies have secular movements which he terms migrations but it seems probable that some examples are only emigrations. At least, a return movement has not been clearly demonstrated, as in the case of *Pieris brassicae* in Europe. In other cases, it seems probable that a two-way migration may exist even though it may not be fully demonstrated. The migrations of the painted-lady butterflies, *Pyrameis cardui* (*Vanessa cardui*) furnish examples. Secular outbreaks occurred in 1879, 1903, and 1926 in which migration flights were reported as common in many parts of the world except South America. Some flights at other times have been reported but they were much less numerous, and tend to emphasize the cyclical nature of the great migrations. It seems probable that peak populations in those years originated in Africa in the spring and spread northward across Europe during the summer. Although there are only slight indications, it also seems probable that there may have been

return migrations in the fall, but the peculiar thing about it is the fact that if so, a different generation performed the return journey. Similar secular migrations have been shown for grasshoppers (Packard, 1880) in which the return migration made by the next generation derived from eggs laid by the migrating individuals occurred in the following year. It should be noted that when these secular migrations develop they are correlated with the proper season of the year in which they occur.

Secular migrations among birds are illustrated in the Snowy Owls which leave their northland habitat in certain winters whenever their lemming food supply becomes too much depleted and return in the spring when other conditions are more favorable.

#### SEASONAL MIGRATION

Seasonal movement is so common and so important that it will be given special attention. The seasonal rhythm in Nature is so widespread in temperate and frigid regions, that it has produced a large number of responsive biological rhythms. Those that have resulted in migrations have produced some remarkable movements.

In considering responses to seasons, care must be taken to recognize the components of seasonal change: the change in length of the alternating day and night periods, the march of the seasons, the diurnal as well as the seasonal changes in temperature and light, and the wet-dry periods of the tropics. It should be remembered that length of day and night varies from a constant twelve hours of each at the equator through all gradations of intermediates to day and night six months in length at the poles. In addition, it should not be overlooked that the relatively more constant climate of the tropics would not be expected to produce as much rhythmic response as the much less constant climates outside of the tropics. Chapin (1932) quotes Sclater (1905) as estimating that of the 814 African birds, only about 150 showed any migratorial tendencies, and of these, at least half were Eurasian migrants, leaving 71 African species that were wanderers, partial migrants or migrants. This decided contrast with temperate Eurasia or America may be explained as the result of more response to wet and dry periods and not so much to temperature rhythms. Zimmer (1938) has pointed out the fact that south-temperate breeders of South America resemble north-temperate breeders in migration characteristics.

*Moisture rhythm migrations.*—Spruce (1908) reports that the American Wood Ibis as well as many other waterbirds regularly move between the Orinoco and the Amazon Rivers in South America at such



times as to utilize the stream banks during low water. This is obviously a two-way series of movements correlated with the wet-dry rhythm of the tropics.

Chapin (1932) states that many shorebirds regularly follow the exposed stream-banks in the equatorial regions of Africa shifting back and forth with the fluctuations due to the shifting of the wet-dry cycle. He indicated that there were more sedentary types on lakes with slight variation than on streams with shifting water level but even on the lakes there were more shorebirds when the water was low. The phase was reversed, however, on the Nile River in northern Africa where the birds were more numerous in the flood stage. At that time, the water spread out over the wide flood-plains and made possible the development of a huge food supply that could not appear in the desert without water. Chapin (op. cit.) concludes that "true forest birds are nonmigratory. It is only pronounced seasonal change in weather that causes the birds of the tropical zone to migrate."

In discussing tropical regions, Wetmore (1926: 31) says: "Climatic conditions there are quite uniform, divergence from a level mean being found mainly in the amount of precipitation that marks wet and dry seasons. In careful observation over a limited area certain birds may appear extremely rare for the greater part of a year. Suddenly some forest tree will come into flower or fruit, and immediately these same birds flock, at times in abundance, to feed. They remain common for a period and then disappear."

*Seasonal wandering.*—There are many examples (U. S. Fish and Wildlife Service files) of birds that show from banding returns a remarkable degree of seasonal wandering without much evidence that the movements follow a consistent directional migration pattern. The returns from Redhead Ducks banded at Bear River Refuge in northern Utah indicate a widespread dispersal in almost every direction where suitable habitat occurs. While such movements are seasonal in nature, there appears to be no correlation with either a directed species movement or a consistently better habitat at different seasons of the year. There is, of course, a return migration to the breeding ground, which constitutes a two-way movement for individual birds and collectively may constitute a two-way migration for the species despite the fact that they seem not to have acquired a consistent directional control.

*Food migrations.*—The peculiar wanderings of the Red Crossbills have been interpreted by Griscom (1937) as coordinated with food supplies. Being highly specialized for conifer-seed extraction, they seem to be largely dependent upon the conifer seed-crops for suste-

nance. The inconstancy of seed production makes sedentary living in a given spot almost impossible. Apparently then, they have developed a wandering or migratory habit not correlated with seasons but rather, with the occurrence of seed-crops in various localities, which enables them to adjust their movements to the vagaries of seed production. Thus, their movements do not show regular migration rhythms, but do seem to indicate a definite pattern of movements that take them to the areas where and at the time when seeds are available. They are probably in the nature of food migrations correlated with very irregular cycles of food production, which of course, are mainly seasonal or secular.

*Altitudinal migration.*—Altitudinal migration occurs in many mountainous regions. It is a well-known phenomenon in the mountains of the western United States (Rockies, Wasatch, Sierras) and occurs in the Himalayas in Asia, the Andes of southern South America and possibly elsewhere. The significant thing about altitudinal migration in temperate regions is that it gets temperature effects similar to latitudinal migration in much shorter distance without noticeable change in day length. Chickadees, kinglets, rosy finches and juncos are believed to illustrate this type of migration in the Wasatch Mountains of Utah and the Black and White Redstart in the Himalayas of Asia.

In mountainous regions of the tropics where day length as well as temperature are relatively more uniform, there would theoretically be less expectation of altitudinal migration than in temperate-zone mountains. It is, however, likely that high altitudes within the tropics but at some distance on either side of the equator will show seasonal changes in temperature which may be instrumental in developing altitudinal migration even within the tropics. So far as known, altitudinal migrations are seasonal in character.

*Longitudinal migration.*—It has recently been established from some of the writer's color-banding operations in Great Salt Lake that young California Gulls reared in rookeries on islands in the lake migrate westward to the Pacific coast in late summer and fall. Records of young gulls banded in June and taken at Seaside near Portland, Oregon, August 3, observed at San Francisco, California, October 25 and 28, and at Monterey, November 15, are quite conclusive evidence that there is, as had been suspected, some longitudinal migration exhibited in this species. The implications of this movement have not yet been studied but it seems clearly evident that young birds leaving the Great Salt Lake in August would find

no significant change in either temperature or day length westward on the Pacific coast.

East-west migrations are, of course, known to occur in other species and at other places. Such migrations across the English Channel (Clarke, 1912) are noteworthy. The Bobolink pursues part of its way (Lincoln, 1939: 161) westward through Wyoming, Utah, and Nevada after coming northward from the Gulf through the Plains States. Files of the U. S. Fish and Wildlife Service show many examples of individual birds making longitudinal migrations, but also show the custom to be fairly common in such species as the American Coot, Purple Finch, and Evening Grosbeak.

*Vertical migrations.*—Seasonal effects seem much less pronounced upon aquatic animals, but nevertheless, seasonal rhythms do exist. Certain vertical migrations seem to be correlated with changes in surface temperatures of water, due largely to preponderant heat-absorption at the surface in summer and heat-loss in winter or to shifting of surface water by currents. In temperate regions, some animals such as fishes, lobsters, crabs, prawns and squids (Pearse, 1939: 184) living along the shores when surface waters are warmer than underlying waters, descend into deeper waters when surface waters become cooler than those underneath. Similar vertical migrations of pulmonate snails, *Phryganea* larvae and possibly others occur in freshwater lakes where surface water is warmer in summer and cooler in winter than that below.

*Anadromous migrations.*—Perhaps the most outstanding ocean migrations for purposes of this work are the long-distance migrations of fishes that take them from ocean to freshwater and vice versa across great osmotic barriers. Many freshwater fishes migrate inshore or up small streams to spawn. In the case of anadromous fishes such as salmon, the young fishes hatched in the small freshwater creeks or tributaries at the heads of large rivers make their way slowly downstream more or less independently of the current despite the fact that they are going with it. Eventually, they reach the mouth of the river and enter the ocean without any apparent difficulty with the problem of osmosis. After development in the ocean over a period varying from one to several years, the sexually mature adult individuals make their way back to the mouths of the rivers (may be the same rivers), recross the osmotic gradient and make their way up the stream against the force of the current to the headwaters of the stream where spawning takes place.

While this is a very generalized account, and there are many variations and details not described, nevertheless it illustrates the prob-

lems involved. The spawning, hatching of the eggs, migration down stream and the return migration up stream are all more or less correlated with season. In many species, spawning migrations occur every year despite the fact that it may take several years for one individual to become mature. In such cases, there must be a crop maturing each year; otherwise it would be a secular phenomenon coming in occasional years. There are examples of anadromous fishes such as landlocked salmon and brook lampreys, in which the young never reach the ocean and yet are able to propagate and maintain the species.

*Catadromous migrations.*—In the case of catadromous fishes, such as the Atlantic eels, the process is reversed. The newly hatched conger eels in the deep waters of the Atlantic Ocean between Bermuda and the West Indies make their way slowly over a period of three years toward the North American and European coasts where they also cross the osmotic gradient into freshwater streams. Ascending the rivers, the eels spend from five to twenty years in development before they undertake a return migration. In this case, the eels have to face the current while young and descend with the current as adults in contrast with the salmon. After reaching the ocean, the adults must make a long journey before reaching the spawning deeps between Bermuda and the West Indies.

*Latitudinal migrations.*—Most important of all are the seasonal migrations that are primarily latitudinal in movement. The seasonal response has had a much larger outlet on land via latitudinal movement than by altitudinal, longitudinal or drouth responses. It is here that the greatest variety of conditions illuminating migration may be found.

The northern hemisphere with its immense area of land in the temperate and frigid zones exposed to great periodicities of the environment should be a fertile field for the development of latitudinal seasonal migration. Because of the immense difference in size of areas in temperate zones of the two hemispheres, it would be an interesting study, if information were available, to compare the number of southern-hemisphere nesting birds that move northward for their winter with the numbers of northern-hemisphere nesters that move southward.

Among the northern-hemisphere migrants, nesting occurs all the way from the tropic line across the temperate zone and beyond the arctic circle as far as land is available. Some of the nesters migrate short distances southward, remaining in the same zone for winter. Others move southward into the tropics, some north of the equator

and some south of it. Still others move into the south-temperate zone and a few others into the antarctic.

Williams (1930) reports a case of the monarch butterfly in latitudinal migration with a behavior pattern somewhat resembling that of birds. According to his evidence, it seems that the newly matured adult butterflies of northern United States and Canada tend to aggregate in flocks in late summer and fall. With approaching cold weather, the flocks migrate southward to suitable wintering grounds of the southern United States stretching from Florida to California, usually south of latitude  $31^{\circ}$  N., but extending northward up the California coast as far as Monterey and up the Atlantic coast as far as North Carolina. After a more or less inactive period (semi-hibernation) from November to March, the butterflies become active again and begin a return movement (often individually), gradually spreading northward as their milkweed host-plant (*Asclepias*) becomes suitable for egg laying. The young larvae hatching from the eggs develop *in situ* on the milkweed, pupate and complete the cycle by transforming to adult butterflies. This complete migration in one generation resembles that of birds and differs from the other insect migrations already discussed in having both journeys of the migration performed by the same individuals. This is a case in which an obligate vegetarian limited to one scattering host-plant has been able better to utilize the milkweed crop by means of migration. This migration differs from that of birds, however, in that they perform only one migration in a lifetime. There is no learning from experienced individuals. Each generation in turn must find its own way.

*Arctic breeding ground.*—An area occupied by birds in summer for nesting in the polar regions north of the arctic circle would have almost continuous daylight during the early part of the summer, after which the day length would gradually decrease to twelve hours by late September and finally to continuous darkness by late December. This would be accompanied by a generally equable climate in summer, in which the fluctuations between day and night temperatures would be much less than that expected in temperate climates. The long daylight periods of summer would give the green food-making plants opportunity for long hours of work, resulting in rapid growth of food, part of which would be quickly transformed into insect, rodent or other animal life. Thus the arctic nesting ground furnishes to the bird nesters an equable climate for rearing the young, long hours of daylight in which to tend the young and a rapidly multiplying food supply at the time when the young are growing

vigorously and increasing tremendously the demand on the food supply.

After September, conditions rapidly change—the days grow shorter, the nights get colder, the food supply diminishes, cold-blooded animals hibernate or perish, and much of the area becomes covered with snow. The ideal conditions of summer are almost completely reversed thereafter.

*Temperate breeding area and wintering ground.*—Nesters of the temperate areas have day lengths in early summer in which to rear the young varying between twelve hours at the edge of the tropics to twenty-four hours at the arctic circle, the length depending upon the latitude. The night temperatures are much cooler than those of the day, differences of 40° F. being not uncommon in some continental areas. The spring-and-summer increase in food supply lasts over a longer period, is more steady and not so meteoric as in the arctic. The nesters spread their breeding periods out from early spring to late summer, some raising more than one brood.

With the approach of winter, snow usually covers the ground in northern areas but its effect usually varies with latitude and altitude, southern portions often being without snow and often without frozen soil. Winter temperatures vary tremendously, being much more moderate in the South. The winter food supply also varies considerably, especially from north to south. Most of the plants are deciduous and become dormant for the winter as do the cold-blooded animals. Warm-blooded birds and mammals are usually the only ones active. Buds, seeds and dried fruits from the plants, eggs, dormant pupae and hibernating adults among the insects and the active rodents are the principal foods available for wintering birds.

*Tropical wintering grounds.*—Birds of the tropics live under nearly constant temperatures throughout the year. The day and night lengths are nearly equal, not varying much from twelve hours of each, except, of course, as the tropical limits are approached either north or south of the equator, when slight differences become more emphasized. The reproductive cycle in nesting birds functions in regular biological rhythms but seems not to be correlated with any seasonal temperatures, consequently nesting activities are likely to occur at any time of the year whenever the internal rhythm of the bird dictates. They may, however, be correlated with food supply or wet-dry cycles and thus restricted to specific times of the year.

Migratory birds which 'winter' in the tropics are subjected to summer conditions. Since their reproductive cycles do not call for nest-

ing during that period, they are more free to move about than the resident nesting birds with which they may be in competition.

*Comparative conditions in moving.*—Birds that nested in the arctic or sub-arctic and migrated southward in the fall would leave a region at a time of rapidly shortening days, increasingly colder nights, decreasing daily temperatures, and rapidly depleting food supplies. If they stopped in the north-temperate zone for winter, they would find temperatures somewhat higher but also gradually decreasing both in day and night, day length approximately the same but shortening more slowly, and summer food supplies on the wane but with winter foods still intact.

Other birds that passed them by and went on to the tropics to winter would find little change in day length (late September or early October) but would find relatively constant temperatures considerably higher than those left behind. The tropical food supplies would be relatively constant and available, but migrants would have to compete with resident birds.

Other birds that went from the arctic to the south-temperate zone would find conditions reversed from the north-temperate. It would be like jumping from fall into spring. The day lengths would be increasing; the daily temperatures would be rising both day and night; and the food supplies would be on the upswing after the winter dormancy.

Those birds that went on to the antarctic would find a repetition of conditions of the arctic except that there would not be as much room; the land habitats are much more limited in extent, and there would be no young to rear, consequently no increasing population to expand at the expense of a limited food supply.

*Conditions of return.*—Birds returning from all these various wintering places where mostly they have avoided winter, must reach the summer arctic and sub-arctic nesting grounds at approximately the same time in order to complete the rearing of the young in the short time available during the summer season. Allowing for considerable variation in the rate of return travel and some variation in time of arrival, there yet remains a considerable degree of parallelism in the times at which the various birds must begin the return journeys.

Those from the antarctic would have to leave at a time when conditions were similar to those prevailing in the arctic when the southward migration was undertaken; namely, rapidly shortening days, declining temperatures both day and night, and depleting food supplies. They would have to cross both the temperate and the tropical regions—a tremendously long journey. Those returning from the

south-temperate and those from the north-temperate zones would be faced with reversed conditions at starting time. The southern birds after spending the summer would be leaving in the southern fall when days were shortening, temperatures lowering and food supplies shifting to the winter condition, whereas the northern birds after spending the winter would be leaving as spring opened, when days were lengthening, temperatures rising, and food supplies flourishing.

Those returning from the tropics would have to initiate their return under conditions relatively similar to those obtaining when they arrived. About the only variable conditions that might need consideration are the periodic fluctuations in the wet and dry cycle, but these vary in time of fluctuation with the latitude and may consequently be considered negligible.

To summarize, all birds leaving the arctic or sub-arctic must initiate migration with inactive gonads under conditions of shortening day length, lowering temperatures and depleting food supplies. After migrating to new areas in temperate, tropical or antarctic regions vastly different from the prospective northern winter conditions which they avoid and spending the winter period under much nearer optimum conditions in other parts of the world, they then must all initiate return migrations at nearly the same time of year under a great variety of environmental conditions in temperate, tropical or antarctic regions. The gonads of many birds may be swelling as a preliminary to later reproductive activity but this may be only a coincidence rather than a causal activity. The great variety of environmental conditions relative to day length, temperature, and food supplies found in antarctic, south-temperate, tropical and north-temperate zones does not stop the return migration and probably has little bearing on its initiation.

#### PROBLEMS AND THEORIES

*Ends served by migration.*—Obviously, the chief ends of migration are served by making better use of places or areas that are not equally valuable the year round or that are not equally valuable at all times in their life history. Migration enables mobile populations to shift from one portion of the world to another to take advantage of the opportunities offered. Undoubtedly a greater population density can be maintained by such shifting.

Concomitant with more efficient use of the earth is an obvious advantage from obtaining more favorable, comfortable or optimum conditions of life. Migration leads many birds away from cold



winters and keeps them in almost continuous summer, grasshoppers away from congestion and depleted foods into new areas, and takes salmon or eels from fresh water into sea water or vice versa. This does not imply that they always attain the objective ends, nor that there is any consciousness of the objectives.

*Problems of migration.*—The principal problem involved in migration is that of providing movement for a population so that areas may be utilized to better advantage of the species than if continuously resident thereon. There may be some exceptions to this general statement, which may be illustrated by landlocked salmon that appear to survive successfully despite the loss of access to the sea. The movement twice a year from place to place and even from one hemisphere to the other is a tremendous task.

The energy involved in migration is enormous. Such an expenditure of energy must be worthwhile to the species. Can it be that migration pays for itself in advantages brought to the migrators? Might the expenditure of energy, for example, in certain juncos, be much more efficiently utilized in migration than in hunting for extra food to maintain the much higher rate of heat radiation from the body in the Far North?

The great orderliness of the migrations seems to indicate that the movements are made with considerable precision and that the great majority of migrants either know the way or are able to find it. The precision indicates that the migrants are somehow oriented in time and finding the way indicates that they are oriented in space.

In moving from place to place, migrants are faced with the problem of geography, especially in relation to feasible routes and avoidance of barriers. The longer the migration the more complex does the problem become. The problem of finding mouths of rivers by eels and salmon, scattered host-plants by monarch butterflies, and Patagonia in southern South America by Golden Plovers seems to present excessively complex enigmas which the migrants must be equipped to solve. Such long journeys, or even shorter travels are bound to take aerial migrants through great varieties of weather and climate. Changing barometric pressures, sunshine, fogs, clouds, high or low humidity, rain, winds, or even hail and snow may be encountered. Changes in temperature are bound to occur and frost or freezing may be part of the lot of migrants, especially if they are delayed in fall or arrive too early in spring.

Both Alexander (1938) and McMillan (1938) suggest that birds make use of wind by utilizing the moving currents of air to help them drift along their way and thus save energy and avoid certain dangers.

Nevertheless, no matter how much they utilize wind in their movements, it seems certain that there must be inherent dangers connected with the air barriers between differing winds and the weather produced by them. The flight speed of birds in calm air would in all probability be maintained by the bird in winds, but the actual distance traversed would be a resultant of the flight speed as modified by the drift of the bird due to the wind. The flight speed is probably greater than the implications of McMillan indicate.

The daily and seasonal periodicities are certain to affect migration travels on land. The problem of whether to travel by day and rest at night or vice versa is one that is solved in different ways by different species. Sometimes it may be necessary to fly long distances without rest as when land birds cross barriers such as the Gulf of Mexico. Arctic birds going to the southern hemisphere have to cross the tropics with season and climate vastly different from that at either end of the journey.

The food supply along migration routes may or may not be greatly different from the usual fare. In some cases, food may actually be unsuitable or unavailable in certain places. Most migrants forestall such possibilities by storage of fat supplies in the body before starting on their journeys.

Many migrants are subject to predation by natural enemies that either follow them or are stationed along the way. Such enemies usually take toll from the passing hosts. It is entirely possible that the weak, the sick and the tired are most likely to be taken by the predators but it is within the realm of possibility that a well-equipped and wary predator such as a Duck Hawk may take almost any individual duck or other bird that it selects from a flock.

There are also physical dangers along the way that may take toll from the moving population. Unfavorable weather conditions, long flights across the ocean, winds from the wrong direction, lighthouses, fogs, storms, and many other conditions hold potential dangers to migrating birds.

From the standpoint of human problems in studying bird migration, Thomson (1926) suggests in addition to his first question of what are the useful ends served by migration, three other problems, namely: what originated and developed the migration custom, what evokes its periodic manifestation in the individual, and how do migrants find their way or what determines the way to be found?

*Historical theories.*—There have of course been many attempts during human history to explain the riddle of migration. One man after another has contributed thoughts on the subject. These in turn

have been worked and re-worked time after time trying to find an answer. If one may be pardoned for prognosticating, this process will continue indefinitely into the future. Each contribution but serves to make a little larger base for the successive workers in the field.

A review of the principal theories dealing with migration was published by Walter (1908). No attempt will be made here to repeat his work, but certain aspects of older theories must be summarized as background for new interpretations. Little need be said about the ancient Greek and Roman theories of hibernation, transmutation and transportation except to indicate that while they may not have been actually disproved, yet positive proof in support has not been found and they have been gradually relegated to a status of useless or outworn.

Many writers (e. g., Seebohm, 1888; Gätke, 1895; Dixon, 1897; Coward, 1912; and others) have regarded migration as instinctive, but others (e. g., Thomson, 1926: 261) have been more cautious and called it migration impulse, racial custom or some other noncommittal designation. There seems to be, however, an almost unanimity of opinion that there is something hereditary about it. Many writers fail to indicate how it may be transmitted in heredity, others leave it vaguely as an inherited instinct (a cloak of ignorance on the subject), but Cahn (1925: 548) suggests that it may be a "behavior expression of physiological change accompanying gonad activity" which may be inherited. "Everything points to the conclusion that migration is a custom which forms part of the inheritance of the species and which is evoked to repeated activity by periodically recurring stimuli" (Thomson, 1926: 273). There is a whole series of theories based on the idea that external periodically recurring stimuli such as changing length of day, seasonal temperatures, barometric changes, depleting food supply including suitability for nestlings, glacial fluctuations and secular crowding may have been originating causes. None of these is universally applicable to all migrants and consequently they fall of their own weight as causative stimuli although, as will be pointed out later, they may act as regulators. While many writers have considered migration behavior as hereditary, and some have even considered it as induced by physiological conditions, Cahn (*loc. cit.*) seems to have been the first to point out the possible internal mechanism which might be responsible for its induction.

A few theories are more or less based upon vague generalities or else imply human attributes of intelligence. The premonition theory that animals can forecast coming events to be avoided, the homesick theory that they long to return to the land of their birth, the theory

that animals desire to disperse from their homeland, the theory that birds migrate to find safer nesting sites, and the theory that they move to fill up a vacuum are all in this class. No matter whether the ideas behind these theories have factual basis or not, they are not universally applicable to all migrants. It is difficult to see how any of them could be considered as causative agents. The overpopulation theory is based upon the idea of crowding after reproduction, the surplus being forced away from the crowded area. This assigns a reversed motive from that of the desire-to-disperse theory. It fails, however, to make a satisfactory explanation for the return migration to the area of overcrowding.

Another group of theories is based upon supposed historical considerations that may no longer be operative. Graser's theory (1904) held that birds developed migration in Tertiary times by flying from island to island. The logical implication that birds are becoming less and less migratory today will hardly find approval among present-day zoologists.

The Deichler-Jager northern-home theory and the Dixon-Braun southern-home theory are diametrically opposed to each other in the fundamental assumptions, the one assuming that birds arose from reptiles in the North and spread southward as migration developed, whereas the other holds that birds developed in the South and pushed northward into new breeding grounds as migration grew. The Kobelt-Duncker theory held that there was evidence of both. Glaciation in the ice ages played a large part in the previous ancestral-home theories as well as in independent theories. Wherever used, the ice-age theory is based upon the assumption that birds moved north and south with the fluctuations in the front of the glaciers. A fundamental weakness in this theory is the failure of correlation between migration and glacial movements. They do not operate simultaneously. Migration movements are semi-annual in general, but semi-annual glacial movements are insignificant. Significant movements of glaciers occur in secular cycles (Tarr, 1912).

Mayr (1937) refers specifically to the visual-orientation theory, the retracing theory and the knowledge of geographical position theory of guidance in migration. More recently (1938) both Alexander and McMillan have suggested that wind currents and barriers between them have played an important part in guiding and developing migration routes.

#### PERIODIC-RESPONSE THEORY

The author now presents his periodic-response theory of migration. In adding another theory to the imposing list from the past, the

writer is fully aware that it is not a complete answer to the riddle of migration, but hopes that it will lead the way to clearer thinking on the subject and may stimulate others to clarify its deficiencies.

In brief, the periodic-response theory is based upon the following steps: (1) the periodicities of the environment drive animals into rhythmical behavior patterns of movement that tend to be correlated with the periodicity; (2) the development within such animals by independent agencies (mutations) of hereditary behavior patterns which drive the animal to make such movements automatically; (3) natural selection would tend to perpetuate those that were lucky enough to acquire such hereditary behavior patterns; (4) the periodic events would act as regulators and moulders of the hereditary pattern to keep the two in tune; (5) once established, migration routes might be modified in length and direction by other means.

While it seems plausible that those migrations geared to periodicities probably originated in accordance with these steps, it seems necessary to start with step number 2 in order to explain such migrations as those of the eels in which the migrations are in gear with certain stages of the life history instead of with environmental periodicities. In such cases, perhaps the hereditary mechanism would drive the animals out of a more or less uniform environment to a point where periodicities would be encountered.

*Nature of migration.*—Many writers have contributed ideas useful in the delineation of this theory. Regarding the nature of migration, Coward (1912) quotes Seebohm (1888) that “the desire to migrate is a hereditary impulse, to which the descendants of migratory birds are subject—a force almost, if not quite, as irresistible as the hereditary impulse to breed in the spring.” This theme is further elucidated by Dixon (1897: 76), who says “. . . the impulse to migrate is unquestionably instinctive, in the sense of being an hereditary desire transmitted from parent to offspring, which has become so deeply rooted in the uninterrupted course of countless ages to and fro, that in many species nothing but death can eradicate it. Migratory birds if kept in confinement begin to grow restless and unsettled as the usual period of their departure draws nigh; the same irresistible desire is reflected in the gathering of the swallows in autumn; and the unwonted activity of other little feathered voyagers among the trees and hedges may be remarked by anyone who takes the trouble to observe it. This desire to migrate gradually becomes an overwhelming desire, before which all other inclinations bow, and at last, the great flight is commenced.”

After citing examples of closely related forms of Song Sparrows,

Horned Larks and Meadowlarks that are partly sedentary and partly migratory, Grinnell (1931) says “. . . the habit of migration is in most kinds of birds a perquisite easily and quickly taken on or put off . . . 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 . . . upon the basis of facts . . . rationally interpreted.” He bases his argument upon four principal ideas, namely, that (1) factors of migration are probably as effective now as ever; (2) the high metabolism of birds making them exceedingly heedful and observant, and (3) the great mobility of birds because of flight allows them to (4) make such population adjustments as may be necessary by means of their own inherent powers.

A working hypothesis is advanced by Wetmore (1926: 29) in which he holds “that migration has arisen from movement induced by seasonal and climatic change developed in certain species until it has become hereditary instinct.”

*Theoretical basis.*—Any adequate theory of migration should be able to offer a plausible explanation for the origin of the custom, its growth and development, its mode of operation and a plausible justification for its existence by means of the ends served. The very making of such a theory implies that it should be open to experimental testing and that the only corroboration can come from evidence to be found in Nature either through observation or experiment. In other words, it must stand or fall upon the basis, not of opinion, but of scientific investigation.

This, then, assumes with Grinnell, that the answer to the riddle of migration must be sought in the realm of natural law and not in mysticism. It is not difficult to find in Nature large series of behavior patterns which grade insensibly from strictly non-migratory into complex migratory types. If it may be assumed that such patterns give the best clues to evolutionary changes, it then follows that the more complex patterns of migration have probably evolved through some such similar steps as are indicated by the simpler behaviors. Some patterns, such as the catadromous migrations of eels, are so complex that there is scarcely any inkling of their origins. Fossil evidence, indicates that birds arose from a group of reptiles which in all probability were non-migratory. Such an assumption, however, should not exclude the possibility that declines in migration may also have occurred.

*Establishment of biological rhythm.*—Many writers (Pearse, 1939: 169; Welsh, 1938; Johnson, 1939) have called attention to the fact that biological rhythms exist, and that some of them are correlated

with periodic events and some are not. Examples were given earlier in this work. The crux of the matter of origin of migration is to show the plausible establishment of a biological rhythm of movement correlated with a periodic event. Changes in migration after such establishment would be a logical part of the problem of growth and development of routes.

Explanation of the establishment of any biological behavior rhythm involves an interpretation in terms of the laws of heredity. The laws of heredity involve the very foundations of metabolism, especially the activities of the chromosomes in guiding the organization, growth, development and behavior of individual animals as well as the process of maturing and fertilizing germ cells for reproduction. It seems consonant with the laws of heredity to postulate that psychological behavior like physiological activity is concomitant with morphological form, i. e., behavior and activity result from certain types of structure in tissues of a body. Such structures nearly always have considerable leeway of activity. There is generally an optimum and a pessimum which may lie near either maximum or minimum. Morphological structures are recognized as potentially transmissible in heredity in accordance with certain laws.

*Hereditary transmission.*—Now if a species of animal, bearing any type of non-migratory activity such as may have been transmitted by the reptile forbears to ancient primitive birds (probably similar to certain birds of today), transmits its genetic constitution from generation to generation, the non-migratory activity is bound to be transmitted with it. But such non-migratory behavior undoubtedly would have considerable latitude of adjustment between optimal and pessimal activity. This is well supported by observations and experiments on many species of animals. There are, moreover, great varieties of present-day behavior patterns indicating great departures from the primitive type of pattern and this needs explanation. It brings up the fundamental question of evolution and any explanation of the establishment of the migration custom depends upon the state of knowledge of the fundamentals of biology, especially physiology, genetics, evolution and ecology.

Under the present state of knowledge, three methods of changing heredity between one generation and the next are known. These are: (1) new combinations of hereditary traits normally transmitted by two unlike parents, (2) accidental changes or aberrations in the normal set of chromosomes to make abnormal arrangements which thereafter may be transmitted as normal, and (3) chemical changes or mutations in the genes of the chromosomes which result in some

change in the hereditary traits. The first method is a normal process taking place in every sexual reproduction between two unlike parents. It provides for the continual mixing and rearrangement of the diverse hereditary traits in a breeding population. As a result, the leeway of activity of one individual may be quite different from the leeway of another. A breeding population would therefore present a series of individuals differing slightly from one another and having slightly different optima and pessima. If such a breeding population be exposed over a large area, the environmental conditions encountered by some are bound to be different from those encountered by others. Assume for the sake of example that non-migratory birds once covered the lands of both tropical and temperate zones. Then those of the tropics would encounter relatively uniform conditions and those of the temperate lands would be exposed to varying degrees of periodic changes of the environment.

*Adjustments.*—In order to explain simply, it becomes necessary to assume that animals had already acquired many characteristics by similar methods to that being elucidated. Cahn (1925: 544) points out that an animal has various regulatory mechanisms that tend to make it respond by appropriate activity to external changes in the environment. He says, "... every animal has the capacity to regulate its conditions, but this regulation is limited to the usual fluctuations of its natural and normal environment. When fluctuations pass beyond that point the animal can not adjust to them. Thus an animal regulates through behavior by the following steps: (1) certain processes are going on within the animal; (2) external changes affect the rate of these processes and upset them; (3) the result is movement of the animal in an attempt to adjust to the changes; (4) these movements bring the animal into various conditions, one of which may relieve the disturbance, in which case the disturbing factor being removed, movement would cease, as the equilibrium between processes and environment is established. By these steps we see that the environment of an animal may be regulated by behavior, e. g. movement."

*Natural selection.*—The temperate-zone animals would be driven to movement to seek adjustment more than those of the tropics. If the extremes of the temperate zone went beyond the pessima of all individuals, they would undoubtedly wipe out the race and the area would be occupied by a race that could meet the conditions. If the extremes went beyond the pessima of only part of the individuals, then there would be chance for natural selection to operate, and in accordance with the Darwinian principle, it could be confidently



expected that there would be a gradual elimination of those whose hereditary limitations could not withstand the extremes and a concentration of those that could. Thus there would tend to be moulded because of the environment a population that could meet the extremes.

But countless ages of such natural selection could probably never bring any additional improvement without the help of methods 2 and 3 of changing heredity between generations. It is the combined effect of aberrations and mutations that allows of the introduction of new or increased abilities for meeting the exigencies of the environment. They make it possible for improvement to occur but they do not assure it. They also make it possible for degeneration to occur but natural selection is likely to prevent survival of such in Nature just as it is likely to insure survival of any improvements.

This implies, then, that continued advancement in adaptation to fit or control environment is probably at the mercy of fortuitous aberrations or mutations. Such is probably the case if judgment can be rendered on the basis of observed phenomena of Nature. The whole graded series of characteristics displayed by organisms seems to suggest that at almost every stage of development some forms have been able to improve and some have not. It seems impossible that beneficial adaptations could come with need. Rather, lucky are those who obtain them and survive because of them, and unfortunate are those who need but do not get and perish for the want. This is a far cry from the philosophy of those who must see a purposive plan in the process of Nature.

*Process of adaptation.*—The process of establishing biological rhythms in harmony with periodic events in the environment (akin to the origin of migration) seems to involve (1) the exposure of a behavior pattern already developed to the stimuli of periodic events to which it is not yet adapted. This induces the animal to (2) execute movements designed to make itself more optimal or comfortable, thus making an adjustment of the behavior pattern within its hereditary leeway limits. To transform such a voluntary cycle of movement into an hereditary rhythm to be transmitted from generation to generation requires (3) change in the genetic constitution sufficient to make the behavior pattern of succeeding generations automatically respond in a similar way. (4) The appearance of such changes in chromosomes or genes is not necessarily dependent upon the needs of the organism but comes from the exigencies of the hereditary apparatus. (5) Natural selection helps to fix changes in hereditary mechanisms, but cannot of itself initiate such changes.

This outlines a method believed to occur in Nature which not only serves as a method of initiating new behavior patterns but also at the same time serves the additional function of providing a method of successive modifications and improvements. It is only necessary to explain the establishment of a two-way movement rhythm of the migration pattern to account for the origin of migration. Such rhythms may have been initiated many times and in many places. Once established, the course of development can be charted with plausible accuracy.

*Independent migration rhythms.*—The establishment of a migration rhythm by the method indicated might have been induced by any one or more of the several periodic events of the environment, such as temperature, changing day length, food supply and moisture cycles or possibly by internal rhythms that spur the individual animal into behavior adjustments as Cahn suggested. When such a rhythmical behavior adjustment was transformed into a fixed hereditary cycle, then such a cycle would persist through its own hereditary mechanism independently of the periodic events which might have originally acted as the stimulator to adjustment. Consequently, in searching for the cause of migration, it should not be expected to be found operating upon species with well-developed complex migration, but rather on those species that have incipient migration, those such as Grinnell indicated that are partly migratory and partly non-migratory, that can easily put on or take off the migration perquisite, and those that Lincoln (1939: 84–87) describes with short migrations or partially sedentary habits.

*Incipient migration.*—In studying incipient migration among birds, care should be exercised in distinguishing between those species that are in process of becoming migratory and those becoming sedentary. Historical perspective based on fossil evidence suggests that the latter type has probably been in a decided minority, because in transforming from the primitive non-migratory reptile-like types to the complex migratory populations of today, there must have been a decided expansion in migratory species.

It may be confidently asserted that precisely the same environmental periodicities that are operative today upon sedentary or incipient migratory species were probably the same periodicities that were operative in the period of migratory origins extending down to the present time. Faced with the periodicity extremes of the temperate zones, various animals have taken different methods of meeting them. Some were doubtless exterminated, many cold-blooded animals hibernated or estivated, some warm-blooded animals developed ways and

means of changing fur or feathers to match extremes, but others developed movement into migration as a method of meeting the changing effects of the periodicities, no matter what kind.

The type of response was undoubtedly geared to the inherent potentialities determined by the hereditary traits as already outlined. The distances covered in migration could not outrun the potentialities of mobility. The development of flight whether of birds, bats or insects made long-distance migration a potentiality but did not assure it. That had to await the combination of the driving forces of the environment with the fortuitous changes of heredity as previously indicated, probably a matter of long-time development.

Gadow (1913: 63) must have had some inkling of this process when he wrote: "What we usually understand by periodic migration cannot have sprung into existence suddenly; it is more like the cumulative effect of the doings of countless generations. The faculty of shifting the abode was of course always there, the necessity of moving further on was also present, and those members of a species which went in the wrong direction came to grief, whilst the others flourished and could return with their progeny. At first, they did not cover great distances, but just enough to find unoccupied ground. The annual repetition became an established habit, at last an ineradicable instinct."

Nichols (1918: 168) suggested that the Red-breasted Nuthatch may point the way to the development of migration. During years of scarcity, there is little or no migration, but at other times, it does show definite migration.

*Hereditary control.*—As the once-adjustable behavior habits became gradually transformed into hereditary biological rhythms, the animal must have come more and more to depend upon the internal hereditary stimuli to initiate the behavior and less and less upon the periodic stimuli of the environment. This implies that there has been a gradual increase in hereditary control at the expense of environmental control. Such an interpretation seems to be warranted as a corollary of a general interpretation of evolution that each successive step in the increasing complexity of animal organization has been paralleled by an ever-increasing control of and independence from the environment.

When an hereditary migratory rhythm was once established, thereafter the periodic events of the environment would be expected to operate only as regulators or modifiers of the rhythm and no longer as initiators, despite the necessity of considering the whole sequence as a continuing process through the past ages down to the present

and into the future. Such migratory behavior would then depend upon some internal mechanism to initiate the movement in opposite directions at two different times of the cycle.

*Environmental regulation.*—The question may well be asked, if migration behavior depends upon an internal rhythm, then how does that rhythm keep in tune with the environmental periodicities? The theoretical answer is that the periodic events, as hinted earlier, act as regulators. If the internal rhythm keeps behavior regulated properly, it may never come into conflict with the periodicities, but as Johnson's (1939) study showed with daily periodicities, his mice were not accurate time-keepers and after several months in darkness got out of tune.

May not the same principle apply to other than daily rhythms also? There is good evidence to indicate that this is so. The records of the U. S. Fish and Wildlife Service are replete with examples indicating that the date of earliest return of birds to their breeding territories varies greatly from year to year in some species. The general average seems to vary about one week on each side of the mean, thus giving a period of about two weeks through which dates of earliest arrival usually vary. However, the bulk arrival which is more important to the species probably varies in a similar way.

It seems conceivable, as an explanation, that the earlier arrivals stand in much greater danger of perishing from inclement weather, lack of food or other inherent dangers of the environment than those that come with the mass migration. Nonconformists with the environmental periodicities would under such conditions tend to be culled, thus continually eliminating those in which the hereditary rhythm did not conform.

There is, of course, the alternative explanation that differences in date of return arrival may be due to the regulative action of weather or other factors on the rate of migration. While that may account for the differences in some early-arriving species or in those with poorly developed hereditary rhythms, it will hardly account for species that come late enough so that weather makes little difference or for those with well-developed hereditary rhythms, such as is indicated by the Blue Goose which remains on the Gulf Coast long after the local birds have started breeding activities and then migrates when its own breeding area in the Far North is ready.

There is considerable evidence to show that even in mass migrations, the great bulk of the migrating population may face dangers that produce wholesale slaughter. Roberts (1907) reports a case in which an unusually wet snowstorm in Minnesota struck the main

migration wave of Lapland Longspurs and killed an estimated million birds. A case in which thousands of Eared Grebes were lost in a late southward migration in Utah and Nevada (December 13, 1928) by a similarly tragic snowstorm is reported by Cottam (1929).

An unusually late spring in 1917 with cold rains and snow that prevented normal development of vegetation and insect life in the New England region (Forbush, 1917) resulted in the death of enormous numbers of birds of at least 61 species. Among these, the Purple Martins were almost decimated and seem not to have recovered in that area since (Lincoln, Cottam, Cook, personal communications). Such disasters in spring would leave mainly the later migrants for propagation, which would perhaps tend to retard future migrations in generations descended from them, but this tendency would be reversed by disasters in the fall or winter for southward migrants.

On the other hand, it is conceivable that in other years when the season was earlier than usual, the late-migrating birds might find their insect-food supply so far advanced in its life cycle that food would become scarce before the family rearing was finished and thus act in a similar manner to push the arrival time in the opposite direction—earlier.

Both Alexander (*loc. cit.*) and McMillan (*loc. cit.*) have indicated that wind currents may have played an important part in regulating the times of arrival and departure, i. e., birds take advantage of favorable air currents (usually accompanied by favorable weather) in timing their migrations. Their implication is summed up by McMillan (1938: 403): "The bird's arrival and departure dates fluctuate just as the schedule of the winds fluctuates. Spring and the birds came early in 1938. Was one the cause and the other the effect? Why not say both are effects of the same cause—that the influx of tropical air came early this year? The birds migrate and the winds migrate."

His explanation, however, overlooks the larger aspects of the problem. Wind may serve as one of the regulative or culling factors but can hardly be considered as the only one. In all probability, expression of the migration movement is a composite resultant of all the pressures being exerted by all the factors.

*Restatement.*—The periodic-response theory is based upon the idea that the periodic events of the environment have acted as initiators, moulders and regulators of the migration phenomena by first inducing migratory-habit patterns within the limits of the hereditary mechanism possessed by the animal, then by natural selection perpetuating any hereditary mechanism developed by independent

agencies that tended to transform the habit into an hereditary behavior pattern. The migration behavior thereafter was moulded and guided in its extension, growth and development by the periodic events, which also acted as regulators to keep the hereditary rhythm in tune with them. This means then that the environmental periodicities through their incessant hammering at the biological rhythms have been able to select and guide the development of those animals who were able by independent means to present hereditary mechanisms accompanied by biological behavior rhythms that would coincide with the rhythms of the environment. This may be considered as environmental induction but it is not Lamarckian. It works through independent hereditary mechanisms, the critical thing overlooked by Lamarck. There is, however, another alternative that migratory movements may originate directly from hereditary means.

*Origin of migrations.*—This periodic-response theory was first announced as the seasonal-response theory by one of the writer's students (Brown, 1938: 141), but further study has convinced the writer that it is of wider application than merely seasonal and that migrations have originated in many places, wherever environmental periodicities have warranted and organisms have been equipped, whether it be on land or in water, in tropical, temperate or frigid zones. In connection with bird migration, it seems reasonable to assume that with the acquisition of flight, birds spread to all habitable portions of the land both north and south of the equator, no matter where they originated, and have since kept the world continuously stocked.

Bird migration, then, may have arisen in almost any place, but the amount of migration expected in any given place would be roughly proportional to the periodic events occurring at that place, conditioned, of course, by the numbers of animals equipped to meet the periodicities and the number that had pushed there in migration from elsewhere. On this expectation, there should be more migrations arising in the temperate and frigid zones than in the tropics and more in the northern hemisphere (on land) than in the southern. Those originating in the temperate or frigid zones of either hemisphere would be based primarily on daylight, temperature, and food rhythms and these might drive the migrants to any distance. With this interpretation, both the southern-home and northern-home theories lose their significance.

*Secular applications.*—The periodic-response theory has been stated in general terms as a general theory intended to apply to a wide variety of rhythms—daily, lunar, seasonal, secular—but it may need special application in certain cases. Such rhythms may differ considerably

in their expression in the ocean from those on land but they seem to have been effective in both, for migrations appear to be very common phenomena. The daily, lunar and seasonal migrations in the ocean can perhaps be covered satisfactorily by the theory as stated.

The anadromous and catadromous migrations of fishes, however, may call for further elaboration. Most of the marine or lake migrations from shallow to deep water and return or vice versa are seasonal in nature. The freshwater-seawater migrations already discussed are really secular as far as an individual fish is concerned even though the phenomena may be manifested seasonally each year by the species. The secular nature appears to be produced by the sequences of the life-history stages. The periodicity between freshwater and seawater is produced not by the environment itself but by hereditary mechanisms through migrations which take the fish periodically from one into the other. The origin of such migrations is difficult to understand, but it may be that they originated through hereditary mechanisms instead of through adaptable behavior.

The application to secular migrations and emigrations on land is not so clear. There appear to be two possible interpretations of such phenomena. Under one interpretation, population pressure resulting from crowding during a secular peak forces the animals to resort to an ancestral custom now abandoned except in crisis. Under the other interpretation, the animals have an established rhythm of local movement, into which the excess population cannot be accommodated. This forces a break with custom and the resulting movements are erratic and unpredictable. Perhaps there are examples of both.

#### GROWTH AND DEVELOPMENT OF MIGRATION

Once given established seasonal migrations, no matter how short, then as Brown (1937: 32) says, "it is only necessary to show possibilities of extension and change of direction to account for the migratory routes of today." The environmental conditions found at each end of the route would be important moulding and guiding influences in determining the location of the summer or winter home areas. Each end would be more or less independent of the other and could move about in various ways as needed to fit the exigencies of the situation as it changed from time to time. The route between the two areas would in part be determined by the positions of the ends but conditions along the route might be instrumental in determining its exact location. It seems conceivable that land topography or

water may have a good deal to do with it, but Alexander (loc. cit.) and McMillan (loc. cit.) indicate that both air and water currents may be very important.

*Geological effects on migration.*—There is good evidence for believing that the geological history is replete with cases that have forced adjustments and changes in routes, and that they have probably been the greatest cause of such modifications. The raising or lowering of land into the ocean, the building of mountains or their erosion, and the ice age are examples of geological phenomena which might change the contour of the land or modify the habitats upon it that migratory animals could use. The ice age, for example, undoubtedly pushed the breeding range of adjacent migratory birds slowly southward as the glaciers advanced and allowed them slowly to expand as the glaciers retreated, thus first gradually shortening the migration route at its northern end and then lengthening it again some thousands of years later. With this interpretation of the effect of glaciers the theory of the ice age as an originating cause may be considered as outworn.

If the West Indies are considered as the remains of partly sunken land, then the migration routes across them from North to South America now involving ocean passage may be considered as the continued persistence of a modified land route. Cooke (1915: 35) regards as a possible explanation of the route across the Gulf of Mexico, that it may be a short cut to Central America gradually transformed from a longer route by land around the west side of the gulf. McMillan considers it a direct use of wind.

*Lengthening routes.*—These are examples of modification of established routes by means of geological phenomena, but they do not account for the establishment of such routes. Assume for the sake of example that a bird had a short migration route established in the north-temperate zone. How could it be extended to make a long journey beyond the equator and back?

Always contingent upon the bird getting the proper hereditary mechanisms by independent means, then theoretical explanations may be made. If there are advantages by moving south in the temperate zone for winter, would there not be additional advantages by moving farther south? If so, natural selection (other things being equal) would tend to favor those with the longer migration in that direction. Such lengthening of the route would of course be contingent upon favorable conditions of many other factors such as competition, food supply, favorable air currents and so on.

But that would account only for reaching the tropics. How could



routes be lengthened to cross the equatorial regions? Obviously there could be no special advantage from temperature by moving farther south. There may be critical things among other factors which would favor lengthening of the route. Among these, competition for the food supply suggests itself as a possible explanation. If two species using at least in part the same food occupy either the same or adjacent areas in the tropics during their non-breeding residence there, and one is more successful than the other in taking the competitive food, then natural selection would tend to favor those who went beyond the competitive species. By this method, the southern terminus of the migration route might be pushed about almost anywhere within the tropics or even into the south-temperate zone. By the same line of reasoning, migration routes might be shortened or changed in direction by the same process.

An interesting example of lengthening of a route northward is furnished by F. C. Lincoln of the U. S. Fish and Wildlife Service, who reports (personal) that the early records of the Service indicate that the Canvas-backs were not important components of the waterfowl fauna of the Athabasca Delta in northern Alberta in the early years of this century but that the birds have become of major importance within the last few years. The explanation for such a lengthening northward appears to lie in the drying or draining of the marshes of southern Canada and northern United States on which they formerly depended for breeding habitat. It is all the more interesting by comparison with the Redhead which, faced with similar loss of habitat, has failed to extend its migration route in a similar manner.

#### PERIODIC-RESPONSE MECHANISM

The enunciation of a theory of migration would scarcely be complete without at least suggesting a possible mechanism through which it might work. This is the critical aspect which would provide the basis for experimental or observational testing of the theory. The actual mechanism is so complex and information available so meager that suggestions or hints of the mechanism are about all that can be given. The work of both Rowan and Bissonette has been important in stimulating such studies.

*Metabolism.*—"It appears manifest that metabolic condition is the crux of the matter," say Clements and Shelford (1939: 216). Metabolic condition is difficult to evaluate. The periodic-response theory involves an hereditary mechanism which automatically motivates metabolism at the critical periods. How this operates is at least

partly a matter of speculation although the speculation may be well based on genetic and metabolic principles.

It is generally agreed that primary control of behavior is vested in the relatively stable nervous system but in the vertebrates at least, primary behavior may be modified by endocrine secretions and may be conditioned by environmental influences.

*Nerves and hormones.*—The nervous system of an animal is, of course, a product of its hereditary mechanisms, as are also the endocrine glands which provide hormones that modify or condition the nervous control of activity or possibly even initiate certain types of activity.

The control of the hereditary migration rhythm is probably vested somewhere in this nervous-endocrine complex, and it may act in very different ways in different animals such as insects, fishes, birds and mammals. The question of hormone secretion is not very well understood in insects and it seems possible that insect migration may have its control in the central nervous system although such a condition seems doubtful.

In the vertebrates, it seems likely that the control is bound up with cycles between the two—the nervous system and the glandular secretions. It seems almost certain that behavior controlled by the nervous system alone is much more stable than behavior influenced by endocrine secretion which is known in many cases to be fluctuating or cyclical in nature. It may be that endocrine secretion is a means of introducing variable behavior into a more stable type controlled by the nervous system.

*Hormones and migration.*—Such a point of view may serve as a base for suggesting that migration can be initiated and controlled in the individual by cyclical endocrine secretions which cause the migratory behavior. If so, it is probably independent of the action of the gonads which have been studied so much in this connection. Many young birds migrate before the gonads are completely developed. Migration may be synchronized with fat production. What the secretions are and how, when or where they are liberated is a matter for further investigation and experimentation.

Grinnell (1931) has pointed out that there is probably little difference in the actual amount of wing work and flight between the shorter-migratory Forster's Tern and the longer-migratory Arctic Tern. The difference probably lies in the control that is directed over activity. This is such a complex metabolic matter that it may take long experimental work to elucidate.

Might it be that the secretion governing migration is such that

it initiates action that can only be satisfied by travel, and the quantity of the secretion or the time during which it is secreted determines the duration of flight or the length of the journey? If so, experimental work would first have to determine or isolate the secretion and then test quantitative injections in large numbers of birds to see if length of migration were proportionate to quantity of hormone.

*Finding the way.*—But even if this theory provides a plausible explanation of the regulation of migratory movement, it still does not explain how migrants find their way or as Thomson (1926: 264) re-phrased it, "What determines the way to be found?"

Some writers have maintained that birds must find their own way by the use of their ordinary senses. Grinnell (1931) indicates in the case of birds that they are exceedingly heedful and observant implying that they can find their way with their ordinary senses without calling upon the aid of a special 'sixth sense.' A similar point of view is revealed by Dixon (1897: 131). "Birds, then, perform their migrations by the aid of extremely acute powers of observation, their inborn aptitude for recognizing landmarks, in other words an intensely receptive memory, the result of experience, a keen knowledge of locality, which civilized man can never hope to realize. But all these wonderful powers would be absolutely at fault on a strange road, so that each individual bird keeps close to a certain route that has been slowly formed during the range expansion of the species." But Dixon (loc. cit.: 76) also indicates that what he calls the migratory instinct is not infallible. "Birds blunder, lose their way and perish in uncounted hosts."

This same theme is amplified by Walter (1908: 266) who says: "Finally, it must be remembered that all who start upon this winged crusade do not reach the holy land. The annual loss of bird life during migration is unquestionably enormous. Birds are not driven by an unailing instinct that carries them all automatically to their destination. The blunderers and the stupid ones are relentlessly eliminated in countless numbers. The more resourceful ones, the quicker witted, the more vigilant, accomplish the grand tour amid perils innumerable with many a hair-breadth escape and the survivors are those choice spirits who, having thus won their spurs by noble effort, or because they possess the birthright of a superior endowment over their fellows, become the ancestors of other birds. So it is that winning qualities are engrafted upon the race by hereditary transmission. Is it to be greatly wondered at that, after ages of such rigid selection, we should at last have birds today whose performance is so

remarkable that we are tempted to attribute it to powers uncanny and unknown?"

*Theories of guidance.*—But despite these samples from the many who believe in the natural and non-mysterious explanation of migration, there have been many who invoked occult senses or left it to the operation of unknown instinct. There have also been suggestions of tangible mechanisms for guidance. These include according to Walter (loc. cit.: 262) an unknown magnetic sense, semicircular-canal guidance, a sixth sense of direction, following familiar landmarks, and following leaders who have been over the way before. Mayr (1937) added to these the visual-orientation theory, the retracing theory and knowledge-of-geographical-position theory. Alexander (1938) and McMillan (1938) suggest that birds are guided by air currents and barriers between air currents.

The magnetic theory, although extensively investigated, has found no experimental support. The semicircular canals will help birds keep their gravitational balance but will not help in directional orientation, and even if they did furnish a good explanation for birds, they would not help with insects.

It is to be expected that there will be various grades of development in the ability of animals to guide themselves and determine their whereabouts. Might it not be possible among birds that those with short migrations could get so well acquainted with their range, that the young could become perfectly familiar with the terrain through companionship with those who were already acquainted? And might it not be possible that even longer journeys might be accomplished in the same manner? If so, would such an answer apply equally well to those that had a narrow well-defined route and also to those that advanced in parallel series over a broad front? This implies that many birds use a combination of companionship, familiar landmarks and follow the leader, but might also use air currents and air barriers.

*Direction finding.*—But will such an explanation hold for birds with longer migrations and more complex routes? Will it apply to insects, fishes, mammals and snakes returning to den? And will it apply to cases in which young birds migrate ahead of their parents (Thomson, 1926: 36) or as in the case of the European Cuckoo migrate much later than their parents? Furthermore, will it apply to birds flying in a dense fog as reported (Walter, 1908: 264) by the Harriman Expedition in which murrelets flying from their nesting area on Unalaska Island to their feeding grounds on another island sixty miles away, repeatedly caught up with the ship, passed it and went on ahead

out of sight, "flying as steadily and surely as if by compass although it was possible to see hardly more than a boat's length ahead?"

No attempt will be made here to account for the direction finding of salmon, eels or other fishes. Noble and Clausen (1936) have shown that certain kinds of snakes are able to trail one another by smell. This, then, is a mechanism which could theoretically lead young snakes to a den. It is well known that butterflies and moths have keen chemical receptors in the antennae equivalent to smell. Whether they use this sense in migration has probably not been experimentally determined.

*Orientation ability.*—Rabaud (1928) from the study of many invertebrate as well as vertebrate animals, concluded that animals studied found their ways by means of nervous complexes derived not by summation but by integration from all sensory material. Such ability may be interpreted to consist of more or less subconscious mental organization of all orientation bearings brought in by the senses. It seems reasonable to assume that some animals have an orientation ability much better developed than others. The mayflies, *Heptagenia interpunctata*, studied by Wodsedalek (1911: 270) showed a graded series of phototaxis reactions in experimentation. By adding certain chemicals to the water, they could be changed from negative darkness-hunters to positive light-hunters at different concentrations of the chemicals. There are certainly great differences in the orientation ability of different members of the human race. It is a common experience for many people to be 'turned around,' in which this supposed synthetic orientation ability fails to correspond to actual direction and it is easy then to 'get lost.'

May not birds have a similar synthetic orientation ability which varies not only in different species but also among individuals? If so, would it not account, if exceedingly well developed, for such cases as murrets flying in the fog? And if poorly developed, might it not help to account for the great number of accidentals, stragglers and stray birds that are being constantly reported out of their regular range? Some estrays are undoubtedly led over unusual routes by following associated breeding-ground species as in the case of Harris's Sparrow, stragglers of which occur in Utah and Arizona in flocks of Gambel's Sparrows (Woodbury, 1939).

*Strange routes.*—There still remains the question of young birds migrating over strange paths without the guidance of older birds acquainted with the route. It has been well substantiated (Gross, 1940: 136) that young Herring Gulls exhibit stronger migratory tendencies than do older birds and make longer trips. This probably

applies to other gulls also. In one sense, this is equivalent to the experimental work on the homing ability of birds. In both cases, birds fly over unknown areas, but there is this difference, the homing birds would have familiar landmarks when they neared home; the young migratory birds would be going to a strange country.

The experimental results of homing indicate that the route home is in some cases at least entirely independent of the sensory experiences obtained on the way out, but they also indicate that not all birds can go unerringly back home. Some of them have to hunt, probably at random. Could the success of those that do return directly be related to superdevelopment of the orientation ability?

Could birds going to a strange country without guides be controlled by the inherent migration activators? If a secretion that stimulates flight at a given rate lasts a given length of time, might it not take birds the proper distance and leave them without urge to go further? If this be the proper explanation, will it not also explain the behavior of Rowan's (1926, 1929) juncos which lost their urge to migrate when held until November after their usual time? If so, may not the effect of the stimulating secretion have been frustrated by imprisonment in the cages and the birds left without urge to go when the opportunity offered?

Even if it be the proper explanation, it does not explain the still-open question of why they take the proper direction. Could it be possible that some mental reaction takes place in connection with the orientation ability and in response to sensory perceptions from the environment that determines whether they should avoid or follow ocean shores or rivers, should cross or follow mountains, should fly out over expanses of ocean, or should follow air currents and avoid air barriers?

*Experimental investigations.*—The problems involved and the questions raised suggest certain types of experimental investigations. One line might well proceed to test the migratory urge in many different species to ascertain its relation to heredity. One method would be to rear young birds or hold old birds under uniform (non-periodic) conditions artificially provided to see if migratory behavior develops in the absence of environmental periodicities. This should theoretically yield a series of patterns grading from those with almost no migration behavior through intermediates to those with very complex migration behavior.

Another method would be to rear young migratory animals in a new location to see what happens to the migratory urge, preferably far removed from the ancestral homes and routes. While this method

has been initiated by the U. S. Fish and Wildlife Service on a small scale, it could well be much extended to include transplantation from one continent to another, always selecting an ecologically equivalent habitat in the new location. Such selections should keep in mind not only the summer home, but also the migration routes and winter home as well. Transplantations might be made from Europe to North America or vice versa and might also include transplantations between the northern and southern hemispheres. The selections would also need careful consideration from the standpoint of economic as well as faunistic impact in the proposed new location. Such studies might well become world-wide in scope and should be fostered by some national or international agency. They would, no doubt, lead to many other problems. The results might have bearing on hereditary mechanisms, effect of environment, finding the way on strange routes and many other aspects.

Another line of investigation might be further pursued in the laboratory. Biochemical differences between migratory and non-migratory closely related animals would present baffling problems, perhaps too great to undertake under the present state of knowledge. It might, however, lie within the practical range of experimental investigation to undertake further studies of the relations of glandular secretions to migration, extending the studies to other secretions beyond those already studied. Such experiments as those of Wolfson (1940) and others might be widely extended.

#### SUMMARY

There are many biological rhythms which are correlated with periodic events of the environment, daily, lunar, seasonal and secular. Some occur only in response to the environmental periodicities, whereas others are so ingrained in heredity that they persist despite them but may be regulated and kept in tune by the periodicities.

Migrations are forms of rhythms that are correlated with these environmental periodicities, or with stages of the life history of individuals. Seasonal migrations are much more extensive than the daily, lunar or secular, and have become expressed as wandering, moisture-rhythm, altitudinal, vertical, local, food, anadromous, catadromous and latitudinal movements.

The latitudinal migrations are best developed and show the most complex patterns, especially among birds with great powers of flight. Such migrations may be illustrated by two-way movement for example from the arctic to the north-temperate and back, to the tropics and back, to the south-temperate and back, and to the antarctic and back.

The conditions of starting the return are vastly different in each place. Return cannot be explained as the result of periodic fluctuations in day length, temperature or food supply as uniform initiators.

Obviously, the ends served by migration must justify its practice, or it would be discontinued. Migration tends to produce benefits of two kinds: (1) better environmental conditions tending toward comfort and (2) more efficient use of areas at different times. These must offset the dangers to the species, which arise during migration from hostile environment and natural enemies.

As a further step in the integration of theories to account for the origin of migration, the writer suggests in his new periodic-response theory that it has arisen in many animal groups and at various points in time as a response to environmental periodicities which at first were merely conditioned-behavior patterns but which, through mutation and natural selection, have become so fixed in heredity of some animals, that they recur independently of the environmental stimuli because of hereditary mechanisms.

Migratory movements are probably held in tune with the periodic events either by their direct conditioning effect upon behavior or by natural selection for survival of those whose hereditary rhythm automatically keeps them in tune.

When once established, migratory routes may be lengthened, shortened, or direction changed at either end independently of the other by geological agencies such as glaciation or changes in land elevation or by natural-selection agencies such as climate and competition.

A combination of stable nervous system modified by fluctuating glandular secretions probably provides the metabolic mechanism which regulates migration. This is open to experimental investigation by holding animals under artificially regulated environment and by studying the differences between non-migratory, semi-migratory and completely migratory animals.

Migratory animals probably find their way and keep themselves oriented by learning from those already acquainted or by an orientation ability derived by integration of nervous complexes from all available sensory perceptions.

Many questions are left unanswered and it is suggested that certain types of experimental investigations be further developed in seeking for answers. These include field work designed to test animal-migration responses in new locations and under controlled uniform environment, and also include laboratory work designed to discover hormones that may be responsible for initiating or directing migration behavior.



REFERENCES

- ALEXANDER, KENNETH C.  
1938. The unseen roads of bird migration. (Résumé of unpublished book.)  
News from Birdbanders, 13: 24-29.
- ALLEN, G. M.  
1939. Bats. Cambridge, Mass., 368 pp., illustr.
- AREY, LESLIE, AND W. J. CROZIER  
1921. Natural history of *Onchidium*. Journ. Exper. Zool., 32: 443-489.
- BISSONNETTE, T. H.  
1931. Studies on the sexual cycle in birds. Phys. Zool., 4: 542-574.
- BROWN, MARY D.  
1937. Factors involved in bird migration. Master's thesis, mss. University of Utah.  
1938. Factors involved in bird migration Biologist, 19 (3): 141.
- CAHN, ALVIN R.  
1925. The migration of animals. Amer. Naturalist, 59: 539-566.
- CHAPIN, JAMES P.  
1932. The birds of the Belgian Congo. Bull. Amer. Mus. Nat. Hist., 65: 322.
- CLARKE, WILLIAM EAGLE  
1912. Studies in bird migration. 8vo, 2 vols., London, 1: 1-323; 2: 1-346.
- CLEMENTS, F. E., AND V. E. SHELFORD  
1939. Bio-ecology. Chapter on migration, 200-228. Wiley, New York.
- COOKE, W. W.  
1915. Bird migration. Bull. U. S. Dept. Agric., no. 185.
- COTTAM, CLARENCE  
1929. A shower of grebes. Condor, 31: 80-81.
- COWARD, T. A.  
1912. The migration of birds. Cambridge, England, 16mo, ix + 137 pp.
- DARLING, J. F.  
1938. Bird flocks and the breeding cycle. Cambridge, England, 124 pp., illustr.
- DE LURY, RALPH S.  
1938. Sunspot influences. Journ. Royal Astron. Soc. Canada, Dom. Observ.  
Reprint, 32: 1-50.
- DIXON, CHARLES  
1897. The migration of birds. London, xvi + 399 pp.
- FORBUSH, E. H.  
1917. Destruction of birds by the elements in the spring of 1917. 10th Ann.  
Rept. Massachusetts State Ornithologist, 1917: 13-24.
- FREER, R. S.  
1931. Ecological factors in migration. Wilson Bull., 43: 173-176.
- GADOW, HANS  
1913. The wanderings of animals. London, 150 pp.
- GREEN, R. F., AND C. A. EVANS  
1940. Studies on a population cycle of snowshoe hares on the Lake Alexander  
area. Journ. Wildlife Management, 4: 220-238, 267-278, 347-358.
- GRINNELL, J.  
1931. Some angles in the problem of bird migration. Auk, 48: 22-32.

## GRISCOM, L.

1937. A monographic study of the Red Crossbill. Proc. Boston Soc. Nat. Hist., 41: 77-209.

## GROSS, ALFRED O.

1940. The migration of Kent Island Herring Gulls. Bird-banding, 11: 129-155.

## HALL, E. RAYMOND

1927. An outbreak of house mice in Kern County, California. Univ. California Publ. Zool., 30: 189-203.

## HARDY, ERIC

1940. Bird migration. The Quart. Review, 274: 219-232.

## HEAPE, WALTER

1931. Emigration, migration and nomadism. Cambridge, England, 369 pp.

## HEWATT, WILLIS G.

1940. Observations on the homing limpet, *Acmaea scabra* Gould. Amer. Mid-land Naturalist, 24: 205-208.

## HUNTSMAN, A. C.

1937. Migration and homing of salmon. Science, 85: 313-314.

## JOHNSON, MAYNARD S.

1939. Effect of continuous light on periodic spontaneous activity of white-footed mice (*Peromyscus*). Journ. Exper. Zool., 82: 315-328.

## KENDEIGH, S. C.

1934. The rôle of environment in the life of birds. Ecol. Monographs, 4: 299-417.

## LEWIS, H. F.

1939. Reverse migration. Auk, 56: 13-27.

## LINCOLN, F. C.

1939. The migration of North American birds. Doubleday Doran, New York, 189 pp.

## MAYR, ERNST

1937. The homing of birds. Bird-lore, 39: 5-13, figs.

## MCMILLAN, NEIL T.

1938. Birds and the wind. Bird-lore, 40: 397-406, figs.

## NICHOLS, J. T.

1918. An aspect of the relation between abundance, migration and range in birds. Science, 48: 168-170.

## NICHOLSON, E. M.

1929. How birds live. London.

## NOBLE, G. K., AND H. J. CLAUSEN

1936. The aggregation behavior of *Storeria dekayi* and other snakes with especial reference to the sense organs involved. Ecol. Monographs, 6: 269-316.

## PEARSE, A. S.

1939. Animal ecology. McGraw-Hill, 642 pp.

## PHILLIPS, JOHN C.

1928. Wild birds introduced or transplanted in North America. Tech. Bull. U. S. Dept. Agric., no. 61: 1-63.

## RABAUD, ETIENNE

1928. How animals find their way about. London, 142 pp.

- RIDDLE, O., G. C. SMITH, AND F. G. BENEDICT  
1932. The basal metabolism of the Mourning Dove and some of its hybrids. *Amer. Journ. Physiol.*, 101: 260-267.
- ROBERTS, T. S.  
1907. A Lapland Longspur tragedy. *Auk*, 24: 369-377, pls. 13, 14.
- ROWAN, WILLIAM  
1933. Fifty years of bird migration. *Fifty Years' Progress of American Ornithology, 1883-1933*.
- RUSSELL, E. S.  
1937. Fish migrations. *Biological Reviews*, 12: 320-337.
- SCLATER, W. L.  
1906. The migrations of birds in South Africa. *So. African Ornith. Union*, 2: 14.
- TARR, R. S.  
1912. The glaciers and glaciation of Alaska. *Science*, 35: 241-253.
- THOMSON, A. L.  
1926. *Problems of bird migration*. New York, xv + 350 pp.  
1936. Recent progress in the study of bird migration: a review of the literature 1926-35. *Ibis*, (14) 6: 472-530.  
1936a. *Bird migration*. London, 224 pp.
- WALTER, H. E.  
1908. Theories of bird migration. *School Science and Math.*, 8: 259-266, 359-366.
- WELSH, J. H.  
1938. Diurnal rhythms. *Quart. Rev. of Biol.*, 13: 123-139.
- WETMORE, A.  
1926. *The migration of birds*. Cambridge, Mass., 229 pp.  
1937. *Bird migration*. *Science*, supplement, 85: 10.
- WILLIAMS, C. B.  
1930. *The migration of butterflies*. Oliver and Boyd, London, 473 pp.
- WODSEDALEK, J. E.  
1911. Phototactic reactions and their reversal in the may-fly nymphs *Heptagenia interpunctata* (Say). *Biol. Bull.*, 21: 265-271.
- WOLFSON, ALBERT  
1940. A preliminary report on some experiments on bird migration. *Condor*, 42: 93-99.
- WOODBURY, A. M.  
1939. Bird records from Utah and Arizona. *Condor*, 41: 157-163.
- WOODBURY, A. M., AND ROSS HARDY  
1940. The dens and behavior of the desert tortoise. *Science*, 92: 529.
- ZIMMER, JOHN T.  
1938. Notes on migrations of South American birds. *Auk*, 55: 405-410.

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