MIGRATION
A BRIEF CONSIDERATION OF CURRENT KNOWLEDGE

BY ROBERT CUSHMAN MURPHY

Chairman, Department of Birds, American Museum of Natural History
New York City

SUMMARY:

Migration is a periodical mass movement of an animal population in a definite direction. Typically, it involves a journey away from the area of birth and a subsequent return. In many instances the round trip is repeated within the life span of a single organism, and is attuned to the annual seasonal cycle, but there are numerous exceptions. North Atlantic eels, for example, have but one shoreward and upstream migration in youth, followed several years later, at sexual maturity, by a final retracing of the course to the depths of the sea.

Animals of most groups, including all five classes of vertebrates and a large proportion of lower types, perform migrations, but the phenomenon pertains to particular species rather than to families or orders. Closely related birds exhibit very different levels of migratory activity, and most migratory animals of all groups have «sedentary» relatives.

Migration is distinguished from casual movements of populations, such as the irruptions of locusts, sandgrouse, springbucks, or lemmings, by its regular and two-way course and its purposeful (*i. e.* serviceable) bearing upon the welfare of the species. The term does not properly apply to dispersal as a result of overpopulation, nor to drifting in wind or water. But the short spring or summer returns of toads to the ponds in which they breed, or of land crabs to salt water, are as truly migratory as the twice-yearly flights of the Arctic tern from one polar ocean to the other.

Biblical and other ancient references indicate that migration was first noted among birds. During the scientific age the subject has been critically investigated in insects, other

invertebrates, fishes, amphibians, mammals (especially seals, whales, ungulates, and bats), and, most of all, in birds.

Schneirla (1945) presents evidence that certain seasonally recurring movements of army ants *(Eciton)*, on a reproductive basis, constitute «rudimentary migration», and that the altitudinal shifting of the home site in different phases of their life history is «a biological equivalent of directionalization of migration and its reversal.» Even though the colonies of these insects may not revert to an identical locus, they seek one of identical ecological status. In the monarch butterfly *(Danaus plexippus)* and in day-flying moths of the genus *Urania*, migration has developed extent and seasonal character approaching the performance of birds, but the return flights are believed to be made chiefly, if not exclusively, by insects of a second generation.

Many fishes carry out migratory voyages of extraordinary precision. They include strictly marine species no less than river-spawning forms like the salmon, the reproductive regime of which is the converse of that of the ocean-breeding eels.

It is natural that the ease of mobility in air and water should favor impressive aspects of migratory behavior. Since more has been learned about the migration of birds than of any other animals, it will be advisable to develop this discussion mainly from ornithological data. Furthermore, the source of the migratory impulse (phylogenetically and in the individual animal) should be considered, as well as the problems of route-finding over long distances by organisms which in some instances possess neither experience nor guides.

Origin

Men living in temperate zones long ago recognized a causal association between rising temperatures, increasing availability of food, and the explosive spring migration of birds. The phenomena are most pronounced in the northern or continental hemisphere, but south of the equator many land birds migrate in mirror-image of the more familiar movements in Eurasia and North America.

Consonance between migration and temperature is evident to anyone who observes the stimulating effect of a warm night following a cool spell during the spring migration of birds, or of a sudden cold snap in autumn. It is such weather conditions which bring the great bursts or «waves» of migrants. The behavior of whales in the southern oceans confirms an equally fundamental relation between migration and

food supply. As the Antarctic winter sets in, the fin-whales retreat toward the tropics, where they fast much more than they feed, and give birth to their young in alternate years. With the return of southern spring, they swim again into high latitudes and take advantage of the rich plankton pasturage that follows the melting of the ice floes (Mackintosh, 1946).

Responsiveness to food and temperature must be thought of, nevertheless, not as an expression of simple cause and effect but rather as a congenital trait that has evolved from prolonged selection pressure. Migration has become so thoroughly keyed into the seasons that the calendar, rather than the thermometer or the actual state of the larder, marks arrival and departure.

Without such a general hypothesis regarding the instinctive character of migration, we should be at a loss to account for variant types, for example: (1) «partial migrants», among which only a proportion of the individuals from one breeding locality, or even from one brood, migrate; (2) species which migrate chiefly along east-west, rather than north-south lines; (3) species which, for reasons at least partly interpretable, follow extremely circuitous routes; (4) migrants to high latitudes, which «outstrip the spring» by crossing daily, for periods of a month or longer, isotherms that are progressively cooler; (5) striking instances in which insectivorous land birds, such as the European swift and the North American orchard oriole, depart from their summer territory before their preferred food has reached peak abundance. Examples such as the last may be correlated with the normal period of moult of the flight quills in the species concerned. Bird migration has an explicit linkage not only with food and climate («average weather») but also with the critical metabolic processes of moult and reproduction.

Migration is thus an ecological phenomenon with a genetic basis. Wherever there are marked seasonal changes, a selective advantage for most populations results from a shift in environment. The origin of migration is not to be sought in a particular past epoch, such as an Ice Age, because its dynamic nature is demonstrable today. The eastern North American song sparrow is a partial migrant throughout much of its range. In Ohio the sedentary proportion of the local population increases with each succession of mild winters. Several severe winters, on the other hand, are sufficient to tip the balance in favor of migratory members (Nice, 1937, 1943).

English mallards are sedentary representatives of a migratory species. A shipment of eggs of this duck was made

from England to Finland, where 62 of the hatched ducklings were banded. All of these migrated in autumn, and recoveries were made from points as distant as France and the Balkans. Half the ringed mallards returned next spring to nest in Finland (Valikangas, 1933). There could be no better proof that the migratory trait is carried in the germ plasm, but that a certain climatic threshold is required for activation.

The Technique of Migration Studies

Since the turn of the century, methods of investigation have been vastly improved by organized recording along routes, and by the marking of individual animals. In addition to the wellknown ringing or banding of birds and bats, tags have been applied to fish, shrimps, etc., butterflies have had their wings marked with a ticket-punch, ears of mammals have been tattooed, and metal disks have been shot into the blubber of whales. At least 5,000 marked whales are still at large in the southern ocean. Six million migratory birds have been equipped with rings bearing a number and the address of a responsible agency, and recoveries now total hundreds of thousands. Recently, various combinations of colored celluloid bands that permit sight recognition of an individual bird, or a member of a particular colony, have proved useful for discovering the migratory habits of such coastal travellers as the herring gull.

Bird-ringing has been coupled with the experimental transportation of birds over long distances, often into areas quite unknown to them, and has brought to light astonishing capabilities of orientation.

And finally, physiological research under laboratory conditions has furthered analysis of environmental factors, such as the effects of light upon the endocrine glands. Hormones secreted by the latter control, in turn, the total metabolism of the bird, including such discrete though correlated expressions as migration, reproduction, and moult.

The Pattern of Migratory Behavior

What are the factors, including the seasonal «releasers», that induce an individual animal to migrate? What produces the onset of «migration restlessness» which even captive birds exhibit at appropriate times? These influences are to be distinguished from the evolutionary, selective factors responsible for making migration a characteristic of a species.

Within the past two decades, research in many lands has given us at least the framework of an answer to such ques-

tions. Some of the pioneers in endocrine investigation with birds, such as Rowan (1929), now appear to have tied their inferences too closely to reproduction, specifically to the alternate enlargement and regression of the sex glands. For we know, however, that immature birds also migrate, in both directions, and in some cases for two or more years before their first breeding period. In this respect birds differ sharply from such vertebrates as amphibians. It has been shown, moreover, that northward or southward migration of adult birds may begin and continue after castration.

Later investigators have concluded that the essential conditions for migration involve more factors than a change in the secretory activity of one type of tissue. Bissonnette, who experimented with the effect of changes in the duration and intensity of artificial illumination upon both birds and mammals, attempted to integrate his own evidence with that of others (1937), and noted that the anterior part of the pituitary gland (known to be light-sensitive) exhibits an inherent cycle of secretory activity that affects both the thyroid and the gonads. He then elaborated an ingenious theory which linked up the active and «resting» phases of migration with the alternating functional and refractory states of the pituitary.

The current point of view is well stated in a series of papers by Wolfson (particularly 1945), who offers data on the relation between migration and the pituitary, the hypothalamus (the part of the brain-stem particularly concerned with bodily activities), and the periodical deposition of fat. Migration can not be activated, he finds, by transitory changes in the environment. It results from a metabolic response of the bird to progressive alteration in day-length over a relatively long period.

This hypothesis not only derives from the experimental findings, but has the added merit of fitting the respective average migratory and sedentary proclivities of birds of high latitudes, where the day length varies widely, and of the intertropical zone, where the change is negligible. It enables us also to devise migratory categories of «short-day» and «long-day» requirements. The Arctic fulmar migrates southward, as if grudgingly, only far enough to retain sufficient daylight for its feeding in the dark weeks between November and January. Its fellow seabird, the Arctic tern, crosses the equator as far as Antarctic latitudes and probably enjoys more daylight than any other creature.

The preparation for migration, according to Wolfson, is marked by increase in secretion of the pituitary, growth of

the sex glands, heavy deposition of visceral and subcutaneous fat, and concomitant increase in body weight. When this complex response reaches a state that fits the bird to meet the severe energy requirements of migration, the appropriate patterns of behavior are released as soon as an environmental factor «pulls the trigger».

That bird migration may be of more elaborate genesis than that of most animals is indicated by the relatively little comparable research undertaken with lower forms. Reinke and Chadwick (1939) found that newts in the terrestrial phase can be induced to seek the water in which they mate by the implantation of anterior pituitary tissue from the same species or from other vertebrates. This would suggest a simple «reproductive migration», though doubtless under natural conditions an external releaser would still be required.

Orientation

Direction-finding presents one of the most puzzling aspects of migration. It is an established fact that fish, birds, and marine mammals travel expeditiously for hundreds or even thousands of miles along courses, and toward goals, in some instances unknown to them. With equal sureness, they ultimately return to the starting place, for migration is now known to represent mostly travel between two fixed points.

Homing studies on Pacific salmon indicate a high degree of «memory» in adult fish for the localized spawning grounds in which they originated. The faculty presumably lies in responses to gradients of water composition and temperature, but the data are by no means sufficient to justify all the conclusions that have been drawn from them.

It is unfortunate that much interpretation of homing has been conditioned by the feats of the domestic pigeon, a bird which is, at best, only a man-made homer. The rock dove, its wild progenitor, is a non-migratory species with weak homing talents. Even after centuries of selective breeding, racing pigeons still depend for creditable performance upon long training and practice. Platt and Dare (1945) report that untrained homing pigeons possess absolutely no inherent ability to find their loft from strange territory at distances that countless wild species would cover by unhesitant bee-line flight. The pigeons have counterparts, of course, among non-migratory wild birds such as the house sparrow and the goshawk.

Examples of speed and precision in direction-finding by migratory birds, without the aid of features of landscape which they had previously known, abound in recent ornithological

literature. A large proportion of nesting starlings, swallows, storks, terns, petrels, and other species removed in various directions from their homes have promptly returned from distances up to more than 1000 miles. In some cases the best percentage of returns, and the fastest average rates of flight, have been achieved by birds released at the greater distances! When transportation from the nest has been conducted by a route forming two sides of a triangle, the homeward course, even of birds that had been narcotized or rotated in transit, has proved to be the direct line, and the elapsed time has been of the same order as for birds carried out by the shortest route.

Experiments by Lack and Lockley (1938), and Lockley (1939), with Manx shearwaters — oceanic birds which never voluntarily fly over land away from their breeding grounds and which, incidentally, do not occur in the Mediterranean Sea — showed that these birds found their way back to their Welsh island after being released at Venice, or at altitudes above 5000 feet in the Swiss Alps, distances from home, by way of the sea, of nearly 4000 miles.

Some birds that perform long migrations have extremely restricted ranges at both the nesting and wintering ends of their tracks. The jack-pine warbler *(Dendroica kirtlandi)* breeds only in three counties of northern Michigan and winters only in the southern Bahama Islands. Certain oceanic birds that have huge migratory ranges, while nesting only at small and remote islands, exhibit amazing navigational powers. Thus the greater shearwater *(Puffinus gravis)* breeds nowhere save at two islets of the Tristan da Cunha group in the South Atlantic, but during the southern-hemisphere winter it migrates into the northern hemisphere and makes a clockwise circuit of the North Atlantic, some members of the population reaching the Greenland coast. Examples ringed at their Tristan burrows have been captured by fishermen on the Grand Banks of Newfoundland.

Roberts (1940) records the return of 81 per cent of Wilson's petrels, banded at the nest in the West Antarctic Archipelago in December 1935, and recaptured in February 1937. Twenty-two examples were occupying the same burrows as previously, and at least 20 had the same mates (the mates of two had not been ringed). This petrel migrates into the northern oceans, making a round trip of not less than 7,000 miles and in most instances probably much more.

Direction-finding and homing are not synonymous. Homing is toward a known site, and is performed chiefly by

birds which have bred, or are breeding. Migration leads to an almost equally limited goal which, however, is in many instances *unknown* to the migrant, as in the autumn flights of young birds travelling by themselves. The young of some species (e.g. gannet, European stork) depart before the adults; those of others (e.g. New Zealand cuckoo) weeks after the adults. The intrinsic problems of homing and direction-finding are the same in so far as they relate to distant orientation. Visual observation is not sufficient to account for the ends achieved.

In general, two types of theories have been advanced to explain orientation. The first postulates sensory clues whereby the bird sets its course toward a particular goal. The second regards success as the result of random scattering, or of systematic exploration such as «spiralling». The latter hypothesis may be at once discarded, because the time-scale of homing excludes the leisure that chance or trial-and-error would demand. Rüppell (1937) found that the average time of return among the subjects of his experiments increased not in geometric ratio with flight distance but, rather, in arithmetic ratio. A bird released at 500 miles from its nest required five times (not 25 times) as long for return as one released at a distance of 100 miles.

The sensory-clue or landmark hypothesis helps only slightly more, even if «landmark» be extended to include prevailing cloudbanks, thermal gradients, color of ocean water, direction of sunrise, or other simple geographical, meteorological and ecological relationships in which, as suggested by Griffin (1944), birds may recognize significance. Currents of air or water would not be detectible without the aid of sensory stimuli from other points of reference. Orientation through response to a grid of the earth's magnetism is only one of a number of recurring «explanations» that have not thus far withstood the test of critical experiment. Neither has any receptor-organ been discovered other than the five familiar sensory systems. The only candid statement that can be made is that the means of orientation are as yet no more than dimly comprehended.

LITERATURE CITED

Schneirla, T. C.—1945. The army-ant behavior problem; nomadstatary relations in the swarmers and the problem of migration. Biological Bulletin, *88*: 166-193.

Mackintosh, N. A.—1946. The natural history of whalebone whales. Biological Reviews of the Cambridge Philosophical Society, *21*: 60-74.

Nice, M. M.—1937. Studies in the life history of the song sparrow I. Transactions of the Linnaean Society of New York, *4*: 247 pages.

1943. Studies in the life history of the song sparrow II: the behavior of song sparrow and other passerines. *Idem*. *6*: 252 pages.

Välikangas, Ilmari.—1933. Finnische Zugvögel aus englischen Vogeleiern. Vogelzug, *4*: 159-166.

Rowan, William. 1929.—Experiments in bird migration. I. Manipulation of the reproductive cycle: seasonal and histological changes in the gonads. Proceedings of the Boston Society of Natural History, *39*: 151-208.

Bissonnette, T. H.—1937. Photoperiodicity in birds. Wilson Bulletin, *49*: 241-270.

Wolfson, Albert.—1945. The role of the pituitary, fat deposition, and body weight in bird migration. Condor, *47*: 95-127.

Reinke, E. E., and **Chadwick, C. S.**—1939. Inducing the land stage of **Triturus viridescens** to assume water habitat by pituitary implantations. Proceedings of the Society for Experimental Biology and Medicine, *40*: 691-693.

Platt, C. S., and **Dare, R. S.**—1945. The homing instinct in pigeons. Science, *101*: 439-440.

Lack, David, and **Lockley, R. M.**—1938. Stokholm Bird Observatory homing experiments I, 1936-37. British Bird, *31*: 242-248.

Lockley, R. M.—1939. Further homing experiments with Manx shearwaters in 1939. The Countryman, *20*: 94-96, 129-135.

Robert, Brian.—1940.—The life cycle of Wilson's petrel. British Graham Land Expedition 1934-37, Scientific Reports. I: 141-194.

Rüppell, Werner. — 1937. Heimfinderversuche mit Staren, Rauchschwalben, Wendehälsen, Rotrückenwürgern und Habichten (1936). Journal für Ornithologie, *85*: 120-135.

Griffin, D. R.—1944. The sensory basis of bird navigation. Quarterly Review of Biology, *19*: 15-31.

Many of the foregoing papers contain extensive bibliographies.

An informing recent article on the general subject is the following three contributions by A. L. Thomson, the first two of which are fully documented:

1926. Problems of bird-migration. 350 pages.

1936. Recent progress in the study of bird-migration: a review of the literature, 1926-35. Ibis, *6*: 472-530.

1944. Bird migration: a short account. (Revised edition), 192 p.