

Movements and migration

The Principles of migration

We shall use the term migration here to refer to almost any pattern of movements by living things. The mass movement of herds of wildebeest across the plains of Africa, the seasonal migrations of swallows and of red admiral and monarch butterflies, the return of salmon to their natal stream. All invite two questions: why do animals migrate and how do they know the way? Taking the first question first, an answer can at least be given in abstract terms. Each kind of animal lives best in a particular environment. There must be enough of the right food, the temperature and habitat must be right, there must not be too many other animals that would parasitize it, or kill it for food. In some cases, the environment is so constant, or the animal can live in such a wide range of environments, that once an animal has found a suitable place to live in it will not need to move far to satisfy all its bodily wants. Snails of the species *Cepaea nemoralis*, for example, usually die less than a hundred yards away from where they hatched. However, environments are usually so variable that even if the conditions are good where the animal is now, they probably will not be in a month's time; it may then be better to be a hundred miles south. The abstract reason why species migrate is that environments change so that the best place to be varies with time. The pattern of animal movements should follow the pattern of environmental change. For instance, if environmental changes are capricious, the

animal's migration viewed in isolation will also be capricious.

The answers to the second question, of how animals find their way when migrating, can be more various. If the animal has a sufficient sensory range, it need only move towards areas that its sense organs reveal to offer better conditions. This kind of 'planned migration' is performed for example by wildebeest (Figure «1.1). Wildebeest (discussed on p 102 below) inhabit the plains of Africa, and are frequently on the move. But they do not move blindly, in the hope of coming to better pastures. Wildebeest eat grass, and grass grows after rain; they can sense where rain is falling by using their eyes and ears (but not their noses): they then migrate in that direction. Wildebeest movements follow, at a distance of a few days, the pattern of rainfall; but they only keep moving so long as rain is falling or has recently fallen within the area scanned by their senses.

Planned migration is well suited to the capricious pattern of local rainfall in East Africa. But other environmental changes are more predictable. The animal can anticipate them, rather than waiting for direct evidence. In temperate regions there are regular seasonal cycles; ultimately driven by the regular cycling of the Earth around the sun. Associated with the cycle of day-length and temperature are many other cyclic changes that matter to many animals: cycles of plant abundance; of leaves on trees, of the insects that live on plants. It is not surprising, therefore, that many animals perform regular seasonal migrations, northwards in the spring and southwards in the autumn.

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(in the northern hemisphere). The insects (mainly Lepidoptera) and birds that do so cannot directly sense the superior environment of the north (in the spring), but its superiority, on average, is guaranteed by the predictable changes of the seasons.

The seasonal migrator needs an accurate cue to anticipate the seasons, and at least a compass sense to guide it. They measure the seasons by the changing day length, as may be demonstrated by keeping migratory birds under artificial day length conditions: they then migrate at a time dictated by their experienced day length, rather than the time of year. The effect of day length on behaviour is mediated hormonally; the birds are prepared to migrate in the autumn by declining production of sex hormones at the end of the breeding season; they do not migrate if injected with sex hormones. Similarly, the release of sex hormones in the spring, which stimulates reproduction (p. 46), also stimulates northward migration, an association that led the biologist J. B. S. Haldane to remark that although 'we must be very careful in attributing human motives to animals, the emotion behind migration in breeding places is almost certainly more like human love than hunger or curiosity/ Seasonal migrators could in principle orient themselves by a simple sense of direction; all they need to do is obey some such rule as 'fly two hundred miles south' or a more complicated series of directions. They could obtain compass information from the sun and stars, and it is indeed known that some seasonal migrators follow stellar patterns; stellar orientation has been particularly well studied in the indigo bunting, a bird that inhabits North America. Probably most such birds possess more powerful navigational skills, such

as those we shall discuss shortly for pigeons, but it takes special experiments to demonstrate the fact.

Most insects are not powerful enough fliers to be able to carry out seasonal return migrations; but a few can. The monarch butterfly (*Danaus plexippus*) is one. It is a large insect, strikingly coloured in black and gold, which lives mainly in North America. In the summer the monarch is distributed from Mexico to Canada, but with falling temperatures it moves south, and in the winter, it is only found in Mexico and the southernmost United States (Figure 4.2). In the spring they migrate north again. Not all monarchs migrate south in the autumn; some hibernate in the north. Those that do migrate move at astonishingly high speeds, of up to 100 miles a day. If the winter is warm in Mexico they live as free individuals as in the summer, but when it turns cold they aggregate in dense groups, and remain still in order to con-

serve energy. For a cold blooded insect, the main reason for seasonal migration is probably the need to be in a warm enough place to allow an active life; a warm blooded bird does not have that problem.

We have considered why animals migrate; we might also remark on its ecological consequences. Migration can regulate the local density of animals. If the density of animals in an area increases to the point of overcrowding, there will be insufficient food to go round, and it might pay an animal to move away. If competition is too great in one place, it may be better to try another. For this reason, an increase in population density often precipitates a round of emigration. The migrations of lemmings are stimulated by overcrowding. So too are the movements of aphids (insects

that live on the sap of plants including greenfly) Most aphids can grow up either as a wingless stationary form or a winged migratory form; they are more likely to grow up with wings if the local population density is high. The regulation of population density can only be a consequence of migration, not the reason why natural selection causes the habit to evolve. Natural selection only favours habits that make organisms leave more offspring, the advantage of a habit must therefore *be* in the short-term. Population regulation, however, if it has any advantage at all, can only be a long-term one. It must therefore be a consequence of individual decisions to emigrate, taken on the grounds that conditions will be better elsewhere, not on the grounds that the population level must be kept down in order for the local resources to be conserved. Natural selection takes no account of long-term considerations.

Homing

Local landmarks and home cues:

The life-cycles of many animals require them to find their way back to a particular place. The task for a green turtle (Figure 4.3) to find a tiny island in the expanse of the Atlantic Ocean, or a salmon to find the exact river tributary in which it was born appear to us exceedingly difficult. Because the purpose of homing is often self-evident (in might, for instance, be a finding the right place to lay eggs), the question of how they find their way is usually more interesting. We might distinguish three possible answers. One is that animals memorize local landmarks and directions on their way out, and simply reverse the directions to find their way home; a second is that the

home site itself has some property that can be recognized at a distance. The third, which is most likely to be important in long distance homing, is that the animal has an internal 'map' sense, and can both estimate its own map reference, and knows that of the home site. We can consider reasonably clear cut examples of the use of local landmarks and of homo stimuli, but when we twine on to a possible map sense we shall move into one of the more unsettled areas of the science.

Let us consider first the homing problem of the bee-killing digger wasp *Philanthus triangulum*. Female wasps of this species dig burrows in the sand, to provide a nursery for their offspring. Each female digs several (about 6 or 7) cells off the side of her burrow, and lays an egg in each cell. When the egg hatches into a larva it will need food. That is where the bee-killing part of the wasp's name comes in. The mother wasp goes out of her burrow, catches and kills a bee (by stinging), and brings it back to the burrow. She then opens the entrance to the burrow and takes the bee down to one of the cells. She continues to catch and bring back bees, one at a time, until each larva has about two bees to eat. The mother wasp, therefore, does not merely dig a burrow, and later leave it never to return: she departs from and comes back to it many times. On every return she has to find her burrow, distinguishing it from its surroundings. It is not an easy task to find a particular burrow, because these wasps can nest in quite dense groups; there might be more than twenty burrows within a circle of five-yard radius. The problem of how the digger wasp locates her home has a special place in the history of ethology: it was one of the first questions about behaviour

mechanisms over to he asked, and exper imentally answered It was studied by Niko Tinbergen in 1020, on the heaths and sand dunes of Hulshort in Holland.

Tinbergen first confirmed, by individually marking all the nests and wasps in a particular area, that each wasp does indeed always return to her own burrow. He then performed some simple experiments to test whether the digger wasp recognized her own entrance by die distinctive array of odd objects (haphazardly fallen sticks, pine cones, stones etc.) around it. or by some stimulus emanating from the entrance itself. He placed around the entrance oi each of several chosen burrows a neat circle oi pine cones. He left them there for a few days. checking Out the wasps still kept returning to their burrows. He then wetted for the weeps to leave on bee hunting expedition and while they were away he moved the cones a yard or so away from the entrances (Figure 4.41 When the wasp returned they landed where the entrances should have been, in the centre of the circle of pine cunes. Evidently, they recognized the entrance by its surrounding landmarks, not by any stimulus from the entrance itself.

Learned local landmarks are a feasible means to navigation in a local, familiar area. But longer distance homing must require other technique. Let us now consider the techniques of the salmon. All sperm of salmon have similar life cycles. They are laid at egg in river tributaries all over the northern hemisphere. They live their first few months in the river, then migrate downstream to the sea. they spend two or three years in feeding and growing out at sea, during which they cover thousands of miles and when mature they migrate back to exactly the same river, and same tributary

as they were born in. How do they find their way home? the answer is thought to be mainly by smell. The attractive odour may come from either (or both) of two sources the young salmon which are still in the stream, not yet having migrated to the sea. and any other characteristic odours in the stream. Salmon have been shown to be capable of the necessary olfactory discrimination, but the most direct evidence that they use their sense of smell comes. From experiments, of the kind first performed by W.J. Wisby and A.D. Hasler, in which the salmon's olfactory sense was impaired. Wisby and Hasler