ANIMAL NAVIGATION

TALBOT H. WATERMAN

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Baby green turtle entering the surf.

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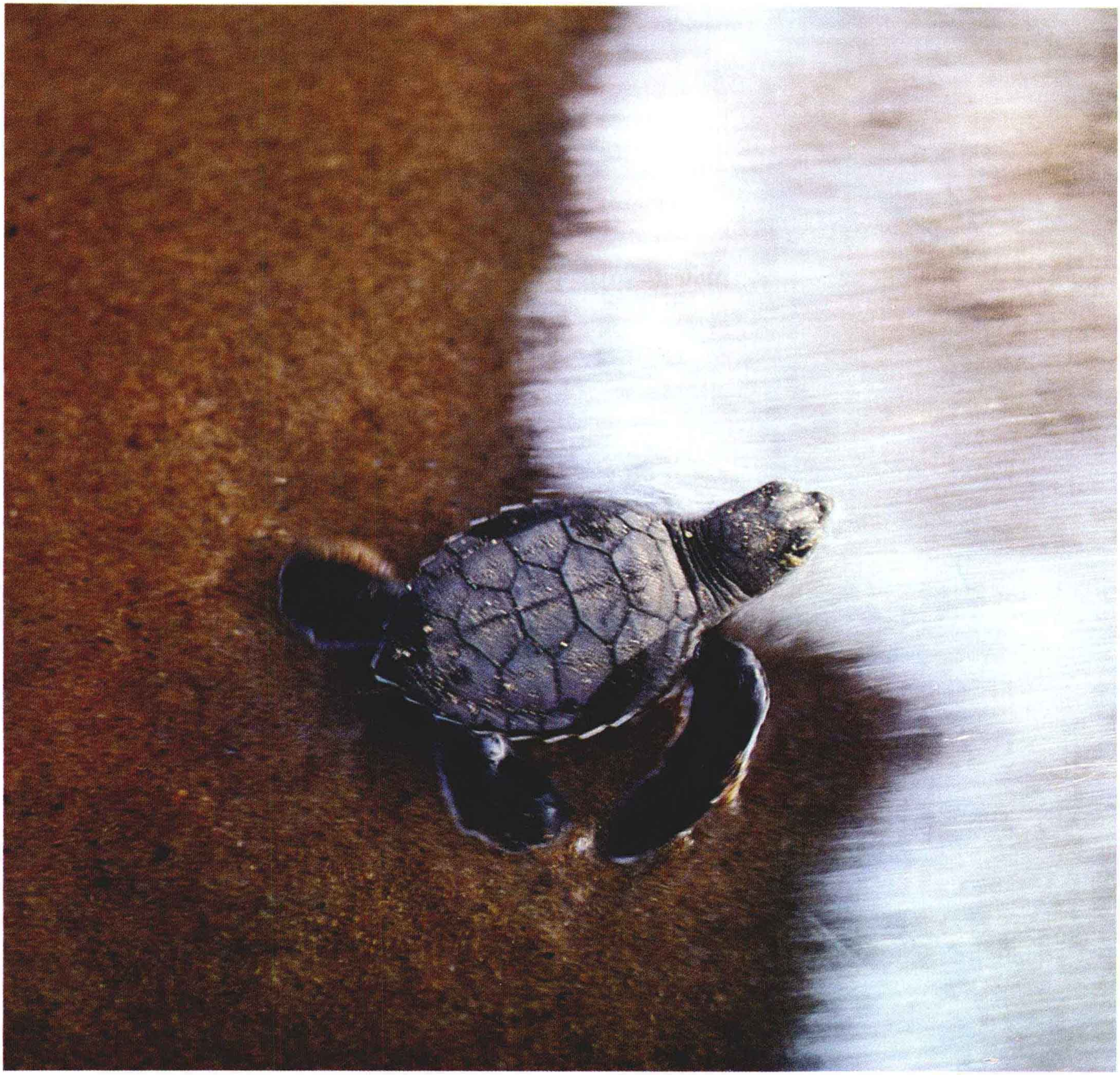


Preface

Because the roots of this book reach far back into the beginning of my scientific career, *Animal Navigation* reflects a major part of my academic and personal life. Visual orientation in a water mite was the topic of my senior honors research in college and was the subject of my first published paper. John H. Welsh, with whom I did my Ph. D. thesis, and Henry B. Bigelow, the first Director of the Woods Hole Oceanographic Institution, who was a no-nonsense inspiration in marine science, were germinal influences during my undergraduate and graduate years at Harvard. My scientific outlook was also significantly shaped by the psychophysicist S. S. Stevens, despite some resistance on my part at the time I worked with him at the Psychoacoustic Laboratory.

Further World War II operational research on radar at the Radiation Laboratory at MIT and in the Pacific reinforced and broadened my interest in biological navigation. Shortly thereafter as a junior faculty member at Yale, I was profoundly affected by a lecture given by Karl von Frisch in which he described his recent discovery that honey bees use the polarization of sky light in their orientation. Not long afterwards I wrote a review titled "Flight instruments in insects," inspired in part by my wartime concern with aircraft navigation and in part by the excitement I felt about von Frisch's research. Over the years the give and take of my university teaching, particularly in a perennial graduate course on animal orientation and navigation, also fostered and molded my interest. Even now, as Professor Emeritus, I conduct research on the orientation of marine animals to underwater polarized light, trying to discover if they can use it as bees and ants do for spatial orientation and direction finding. I am deeply indebted to many people and many pivotal experiences. Teachers, students, colleagues, associates, and friends have all contributed numerous ideas and queries for which I am most thankful. The various institutions and agencies that over the decades supported the underlying research and study were crucial from undergraduate days on. The Society of Fellows at Harvard, the Office of Naval Research, the National Geographic Society, the Woods Hole Oceanographic Institu-

tion, the National Science Foundation, and Yale and Harvard Universities should be specially mentioned.

Those who have collaborated most directly in the preparation of this book and in the procrustean task of editing it should be thanked particularly—Mabs Campbell, my long-time research and editorial assistant; Dan Maffia, for four fine paintings; and not least, several of the publisher's staff: Janet Wagner, for bountiful and often enhancing editorial advice; Phil McCaffrey, for assembling text and illustrations of high quality whose parts all know one another; Travis Amos, for compiling superb photographs; Nancy Field, for book design; Mike Suh and Anna Yip, for overseeing the art work; and Susan Stetzer, for coping with a whirlwind production schedule.

Talbot H. Waterman
New Haven

Animal Navigation

Contents

Introduction

Our everyday experience is full of animals and people on the move.

Mornings around sunrise sea gulls, alone or in small groups, fly unhurried past my windows. As I start my warm-up exercises and meditation, they are on their way from nighttime roosting areas along the Connecticut shore to daytime foraging and feeding grounds. While they fly 10 or more kilometers inland, past Konald's Pond, Lake Dawson, and beyond, I wonder idly how they know their way. Can they already see their destination when they fly up from their roost? Are they following West River to its source in Bethany Lake? Do they take a fix on West Rock from the harbor and then follow its steep scarp further inland? Or do they have a mysterious "sixth sense," some innate map and compass, which guides them? Have they already explored the area and learned the way? Clearly my early rising neighbors are commuting downtown at the same time by driving along a route made familiar through repeated use.

From my sixth-floor laboratory in Kline Biology Tower at Yale, I used to look down on a big hollow oak that is home and jungle gym for a troop of gray squirrels. This particular tree, one of many growing on what were once the broad sloping lawns of the Hillhouse mansion, has long been the hub of a local squirrel population. From its nest holes baby squirrels emerge each summer, learning to climb and run over its trunk and branches. Later they jump to neighboring trees, then venture farther and farther away from home until they develop their adult territories. But many of them return to this oak for shelter, for fellowship, and seasonally for breeding.

On warm summer days, the sunny window ledge of my laboratory usually has a bee-fly (a near perfect mimic for a bumblebee) poised on its outer edge. Scanning the bright southern sky for some time, the insect suddenly flies furiously into space.

Red-winged blackbirds *Agelaius phoeniceus*, like many bird migrators, gather in ever-increasing flocks before finally departing on their fall mass movement southward.

After a few seconds out of sight, it returns as swiftly to resume its panoramic watch. These forays continue at frequent intervals through much of the midday. According to colleagues knowledgeable about insects, these are mating flights in which the male fly waits on the ready until he spots a passing female of the species. Then he pursues, intercepts, and, if the foray is successful, copulates. My observation that the males returned with abdomens pumping, a little breathless from their flight, yet never brought back traces of captured prey certainly fits such an explanation. But only rarely was I able even to see that the fly was pursuing something, let alone be sure that its target was indeed an attractive female bee-fly!

It is tempting to tell, too, of the thousands of starlings that roosted nightly last fall in those same Hillhouse oaks. Each morning they dispersed widely to feed, returning again soon after sunset to spend the night in a dense jittery flock. Then they were gone for the winter. I could also recount the mile-long straggling flight of red-winged blackbirds that passed daily over the Tower at sunset for most of a week in November, heading easterly toward a roost apparently near East Rock or Sleeping Giant Mountain. No doubt they were either joining a huge flock mobilizing to head south or just waiting for the weather to urge them on to the rest of their long journey. Such anecdotes remind us that most animals (including humans) spend much of their time in transit—whether swimming, flying, walking, creeping, burrowing, jogging, running, galloping or jetting, from one place to another. All this movement depends mostly on the interaction of two factors. First, the earth is a mosaic of localized sharply different places: mountaintops, meadows, hot springs, glaciers, beaches, forests, deserts, deep seas and so on. Second, although many animals may prefer one of these habitats, they must move through the larger environmental patchwork to meet their complex needs. The mountain goat, for instance, may thrive in high alpine meadows in the summer but has to come down to lower levels in winter. Deer that browse in the fields at night hide in the forest during the day. The best place for an animal to feed is usually different from the best place for it to sleep, and the best place to build a nest is ordinarily still somewhere else. Furthermore, the suitability or availability of these special regions often changes regularly with the seasons, the time of day, the tides, and even the organism's age. Accordingly, a mobile animal's habitat typically consists of a number of subhabitats. Each of these has certain features that satisfy particular biological needs at a specific time or during a certain phase of the life cycle.

To move between subhabitats efficiently and safely animals must travel in the right direction, to the right distance, at the right time. How they are regularly able to reach these objectives is the subject of this book. *Navigation* enables animals to find their way from one place to another. It is a regulated, nonrandom activity that improves their chances for survival in the earth's spatial and temporal mosaic. In this book animal "objectives" and "goals" do not imply self-awareness or intentional planning on the organism's part. Rather the objectives and goals are considered to be the "set points" of the organism's programmed behavior much as the temperature

Because loons have weak lifting power for their flight and legs and feet that are set so far back on their bodies that the birds can scarcely walk, they cannot take off from land and need long expanses of water as well as high air speeds, perhaps 35 kilometers per hour, to become airborne. When the remote wilderness lakes in the northern United States and Canada—the usual summer habitat for the common loon *Gavia immer* in North America—are frozen over, these fish-eating divers must migrate seasonally to seek open water as well as available food.

dialed on a thermostat normally brings the system it controls to the heat level indicated. Obviously, animal navigation is far more complex than a simple temperature regulator. Yet the analogy serves because our main purpose is to determine how the system works rather than why or how a certain objective was set for it. For instance, the means whereby an arctic tern can navigate halfway around the world from the antarctic pack ice, say, to the coast of Greenland are surely a different matter from why it happens to breed in Greenland and to live during the nonbreeding season in Antarctica. For animals as for human pilots, finding the way is quite distinct from the urge or decision to move somewhere else. Animal navigation will accordingly be explained here mainly in terms of *how* it is done with only occasional attention, as in the last chapter, to *why*.

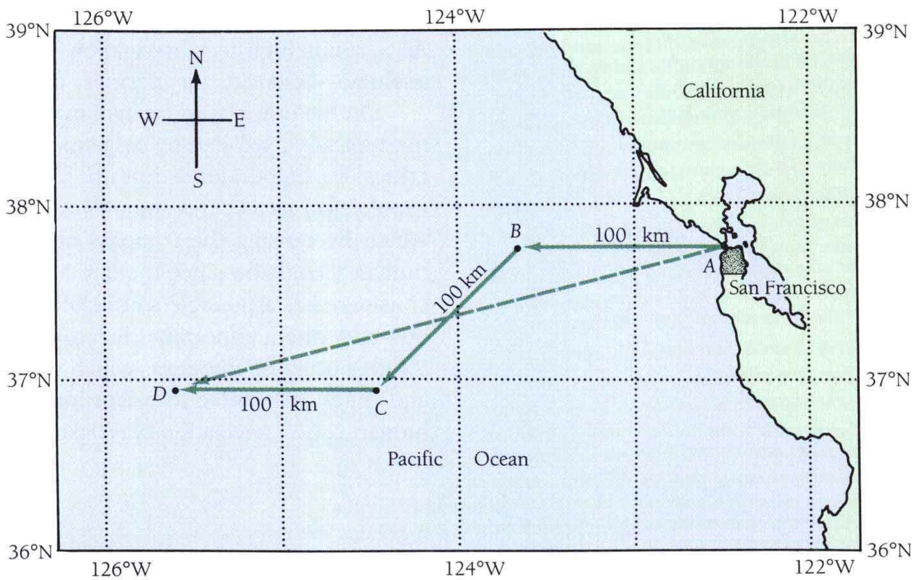
When distances are short and the animal can, for instance, see or hear its goal, a formal navigation program may in human terms seem trivial. Yet at night, in fog or whenever the goal is far away, navigation is surely needed. At certain times finding the way requires skill that seems to verge on clairvoyance. However, sophisticated *human navigators* ordinarily take a matter-of-fact approach to their job. Because we know exactly how human pilots navigate, reviewing their methods should be useful in trying to understand how animals reach their destinations. Human navigation is made up of four mutually supportive procedures. One or another of these may suffice under favorable circumstances. However, in a pinch, the navigator exploits every available means to reach his destination.

The first procedure is *piloting,* in which known natural landmarks or seamarks (like a submerged reef) as well as markers of human origin such as buoys, lighthouses, and airway beacons are used sequentially in coastal voyaging or overland flight in clear weather. Shorelines, rivers, and mountain ridges clearly serve certain animal navigators in the same way. Hawks and eagles migrating along mountain ridges and the gray whales' close following of the North American Pacific coastline are examples. Provided that visibility is good and familiar landmarks plentiful, human piloting in well-known territory is simple and readily learned. Charts and maps are usually important adjuncts to memory. They are essential in places not known to the pilot. Particularly on land, where there are well-posted roads or trails, we are all quite used to piloting when driving or hiking. Difficulties obviously arise when landmarks are either forgotten or hard to identify and signs are illegible or missing. If such clues are absent or unknown, piloting must be replaced by exploration. Then common sense as well as rules of thumb, like always head downhill or turn right at any fork, apply. Ordinarily after such path breaking, the ability to return home is critical.

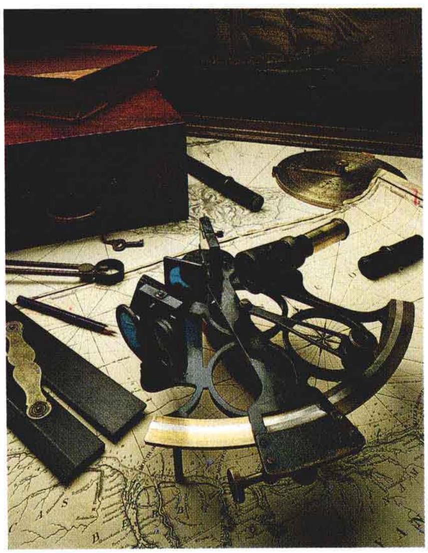
The second navigational procedure, *dead reckoning,* can be used without landmarks—on or under the open sea, in fog, in the air above the clouds—and in exploring the unknown. To use dead reckoning the navigator measures the direction

Migratory routes often follow coastlines like the one in this air view of the Peninsula de Quevedo on the Pacific coast of Mexico, just north of the Tropic of Cancer.

An example of dead reckoning. Suppose that a ship sails due west from San Francisco and the Golden Gate *A* for an estimated distance of 100 kilometers; then at *B* it changes course to southwest for another 100 kilometers; finally at *C* it again heads directly west for still another 100 kilometers to *D*. The navigator can readily calculate his ship's position at *D* as 280 kilometers from *A* in a direction nearly west by south. If the latitude and longitude of *A* are known, the location of *D* is easily determined. Usually, however, winds and currents cause errors, which must be corrected with other kinds of information.



Classic tools of a ship's navigator include charts, a compass, a chronometer, a sextant (center) sailing directions, astronomical tables, and various measuring and drafting instruments.



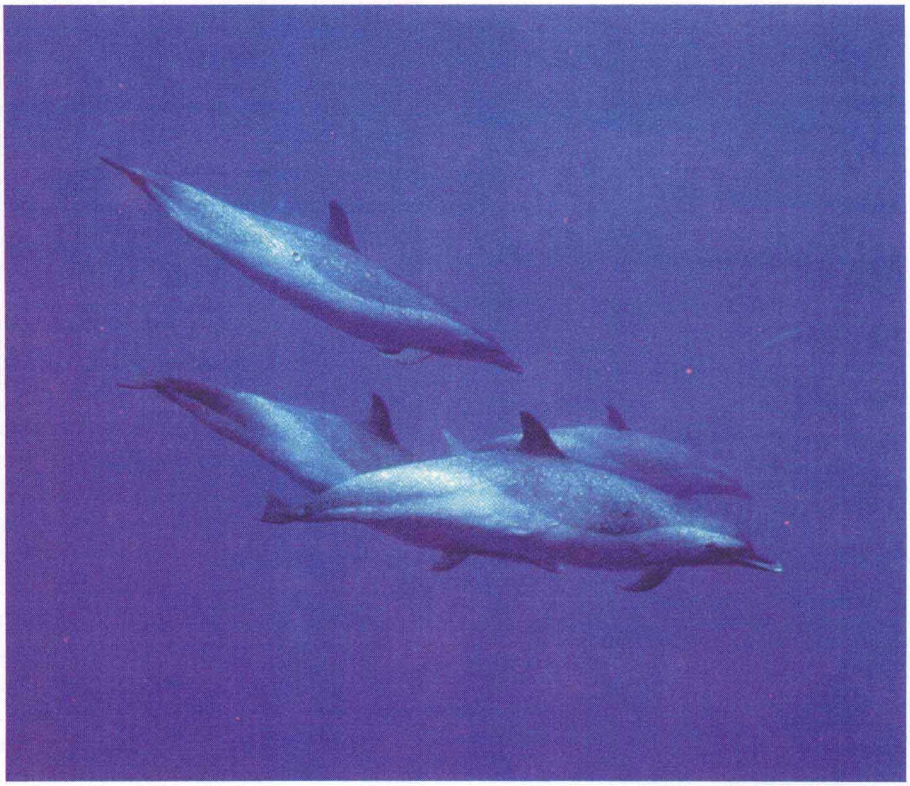
of travel and the distance covered on each leg of the course. While advancing, he repeatedly adds the measurements for a given segment of the journey to the preceding one to yield the current position relative to the starting point. This process is repeated until the destination is reached. Note that a compass and a clock, as well as ways of measuring speed and drift, are essential to the human pilot. Although they lack real instruments and graphic maps, animals are known to use dead reckoning often.

The third procedure is *celestial navigation* in which the sun, moon, planets, stars, or sky are used to obtain positional, directional, or temporal information. Locating north from the bearing of the polestar, fixing one's location by calculating its latitude and longitude from the sun or stars, and determining local noon from the moment the sun reaches its highest point in the midday sky are common human uses of celestial observations. An accurate clock, celestial charts and tables, as well as such instruments as a sextant, are typically needed for this kind of navigation. The sun's direction and other data derived from the sky help orient and time the movements of the honey bee and migratory birds as well as many other kinds of animals.

Finally the fourth human procedure is *electronic navigation*. This is widely used in direction finding, obstacle avoidance, runway location, latitude and longitude determination, and timekeeping. The great advantage of such systems is their independence of time of day and weather. Nowadays sophisticated methods, such as finding one's location by using computer-processed satellite signals, tend to overshadow the first three, much older, procedures even in international yacht races.

However, no animals can conceivably have even the simplest instruments required. As a result high-tech navigation of this sort is interesting to us now mainly by analogy—between, for instance, a ship's sonar and a porpoise's echolocation.

On the other hand, animal migrators clearly do use additional navigational aids not typically exploited by us. Some of these depend on certain senses, like olfaction, critical for bloodhounds but not for jet navigation. Others take advantage of several geophysical factors that animals can sense. For example, the earth's magnetic field, which by causing the compass needle to indicate north, has played a key role in human navigation since the late Middle Ages, has in more recent times often been considered as a possible source of information for animal path finding. Other obvious and often important directional signals may come from winds or currents. Swells on the open ocean, which often maintain a steady direction over large areas and times, may serve to orient long-range migrating fish and birds. (In traditional human canoe navigation wave patterns do indeed provide important data.) Other



As air-breathing mammals, porpoises are remarkably successful aquatic animals, fast swimming and wide ranging in the world's oceans. Here near Hawaii a group of spotted dolphins *Stenella attenuata* dive in pursuit of prey (fish or squid). Porpoises and dolphins skillfully use echolocation for short-range navigation, but their long-range methods are largely unknown.

less familiar geophysical clues for animals may include the Coriolis force due to the earth's rotation. This acts to deflect moving objects including animals—clockwise in the northern hemisphere and counterclockwise in the southern. Its strength decreases as one moves toward the poles. The earth's gravitational field, sustained electrical potentials in water (some due to fluid flow), local anomalies in the earth's magnetic field, the atmosphere's barometric pressure, and infrasound generated by storms or surf (of very low frequency and inaudible to us) may all assist animal navigation. Infrasound carries easily over long distances in the atmosphere and is readily detected by some birds, at least. The intriguing possibility that animals use these geophysical clues to navigate remains in many cases incompletely documented. Both the senses involved and the evidence for their application need intensive research. Undoubtedly some of the mysteries and controversies of animal migration could be dispelled by first identifying and then confirming the importance of these and still other subtle information sources that may remain to be discovered.

Having asked some pertinent questions, we may now recall our most basic definitions. How animals find their way from one place to another is what we mean by *animal navigation*. We should add to this "efficiently and safely" because their navigation is an adaptive process that increases a migrating organism's chances for survival and reproduction. *Migration* as used in this book means periodic cyclic movement from one part of an animal's habitat to another and back. Animals may migrate between two remote summer and winter living areas, like Alaska and Central America, or among a series of subhabitats. There are many patterns that we shall encounter. Because animals migrate, we know that they navigate. Solved navigational problems are evident in the routes and timing of migrations made by many insects, fishes, birds, and whales. The duration of the round trip, the use of one or more way stations, and the distance traveled all vary widely from species to species as does the biological reason for the journey. Typically though, migration is a seasonal, annual phenomenon closely related to reproduction, development, feeding, climate, and weather. But some species may complete only a single migratory cycle in a generation lasting a number of years; examples are the Pacific salmon and American eels, which die after spawning once. In contrast, some insects require more than one generation to complete a single seasonal circuit.

Usually migration implies rather long distances traveled, but what "long" means may be quite relative. For instance, a very long goal-oriented movement for a microscopic *Paramecium* would not have to reach more than one or two body lengths of a blue whale! Obviously the actual size of animals strongly affects their migratory range. Speed and efficiency of locomotion typically increase rapidly with size. The swimming speed a trout can sustain, for instance, varies with its length, multiplied by three or four. Thus a fish that is twice as long as another can swim six to eight times faster. Running and, to a lesser extent, flying speeds are also typically scaled (within limits) to animal size. Larger animals are consequently more likely to migrate globally than smaller ones are. The cost of locomotion—that is, the energy required