Chapter 1

Navigating—Problems and Strategies

■ Devil Birds of the Atlantic

It was a navigator's worst nightmare. Shortly after midnight on a cloudy September night in the middle of the North Atlantic, the ship was suddenly attacked. Out of nowhere the screeching and wailing ghosts of long-dead sailors swept through the rigging, terrifying the superstitious seamen and drowning the captain's shouted orders. The panicking crew knew instantly that they had trespassed on the infamous Isles of Devils, haunted by the souls of the thousands of crewmen who had perished on the treacherous shoals. But by the navigator's reckoning, they were far to the west of the legendary death trap.

Within minutes, though, over the din came the fatal sound of waves breaking on a lee shore to the east. Turning the ship and piling on sail was their final mistake: the keel ran hard into one of the lethal coral reefs that ring the islands. The ship sank almost immediately, joining countless others that had suffered the same fate in that graveyard of the Atlantic that is the Bermudas. What had gone wrong?

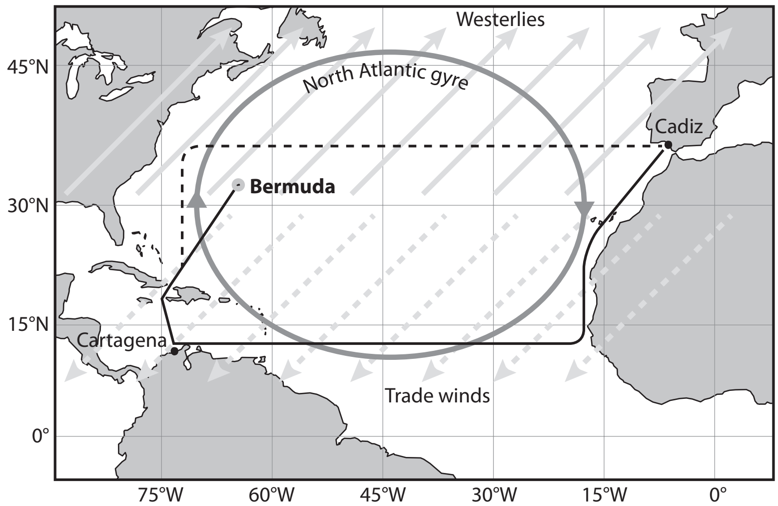
Long-distance navigation is a life or death challenge for many nonhuman animals as well; the difference is that *they* know what they are doing. Few sights are more impressive to earthbound people than an isolated formation of geese passing overhead on their way to distant summer or wintering grounds. Theirs is not a journey on a wing and a prayer: all but first-year birds have a detailed map of the route in their brains, complete with remembered landmarks for piloting. After dark in the spring and fall literally billions of songbirds traverse the skies each night unseen, often to destinations hundreds or thousands of miles away. Unlike waterfowl, these passerines are using multiple compasses and a mystical GPS sense to find their way. At least 30 species would have been passing overhead on that fatal night in the Atlantic, maintaining their steady course for 2300 miles from Nova Scotia to South America.

Animals were on the move in the surrounding waters of the North Atlantic as well, racing against time to reach new habitats as the seasons changed. Humpback whales migrate past Bermuda on thousand-mile journeys with maps and compasses adapted to the gloom of the ocean. Many fish and sea turtles are similarly equipped for equally monumental seasonal redeployments. Below them on the seafloor spiny lobsters prance in tandem lines on arduous journeys, knowing their location in the cold darkness to within a few feet.

On a more local scale, honey bees and many other insects on the Bermuda islands, as elsewhere, commute scores of times each day from home to sources of food, water, or building materials, using a series of backup compasses and learned landmarks. Relative to their small body size and myopic vision, these trips are nearly as epic as those of geese, and each journey is a life-or-death event. Nesting birds on this mid-Atlantic refuge log many hundreds of miles shuttling back and forth first to collect nest material and then food for their young; getting lost would mean starvation for the next generation. Mice do much the same on the ground, but must employ a different set of cues and processing strategies more suited to running mazes than finding distant continents. Monarch butterflies flutter 2000 miles south from the United States and Canada to a remote mountain peak in Mexico, orienting by the ever-moving sun and a mysterious sense of location.

Faced with what is to us an alien task in an unforgiving world, humans stand in awe of the judgment and precision with which animals use cues—often undetectable by us—that are frequently ambiguous and ephemeral. We must depend on luck as much as talent, trying with clumsy approximations to replicate the compass sense that animals use innately to work out the rules of piloting and mapping, and to pinpoint our position on the globe without the seemingly magical combination of sensory abilities and inborn processing circuits that for other species comes as standard equipment. The navigators whose ships came to grief on Bermuda's reefs were, in fact, employing an amalgamation of generally reliable animal strategies. What went wrong for that ill-fated ship beset by devils?

When Fernandino deVerar set sail in his well-armed, two-masted, 300-ton Portuguese merchant ship *San Antonio* in 1621, he understood the risks. He had sailed that spring from Cadiz in southwestern Spain for Cartagena in what is now northern Colombia with a load of goods for the American colonies. Like all human navigators of the time he was unable to judge his east–west position (the longitude) when out of sight of charted land, so his ship had sailed south with the northern coast of Africa clearly visible to larboard (the left, or port, side of the ship). He had abandoned this piloting strategy once his collection of instruments, charts, tables, and measurements of the sun's elevation combined to tell him he was 12° north of the equator—roughly the latitude of his destination 3000 miles on the other side of the Atlantic. Then deVerar had turned west and, using a magnetic compass, sailed along this latitude until he reached the Caribbean. This vector strategy is similar to the way many migrant songbirds navigate



Journey of the *San Antonio*. The ship left Cadiz with a following wind and sailed south along the African coast to the latitude of Cartagena. Then it used the trade winds and the North Atlantic gyre to propel it to the Caribbean. The return voyage was to take it north to the latitude of Cadiz, then east with the westerlies and gyre at its back to Cadiz (dashed line). Unable to measure its longitude, the vessel in fact drifted east and ran aground on the reefs of Bermuda. (The rectangular projection used here exaggerates east–west distances at higher latitudes.)

their first season, before they learn enough to plot routes that incorporate the subtle realities of spherical geometry.

Going south before "westing" to the New World allowed sailors to take advantage of the trade winds, which blow generally from the northeast in the northern tropics. The resulting "broad reach," with the breeze coming diagonally from behind, extracts the maximum force from the wind. The ocean current at this latitude, part of the North Atlantic gyre, also provides a welcome two-mile-an-hour push to the west. Hundreds of species of migrating birds, sea turtles, and fish also know how to take advantage of these winds and currents.

The problem for sailors came with the return journey, their ships laden with treasure looted from Mexico and Peru. September is the height of the hurricane season in the Atlantic; the *San Antonio*, one of many vessels waiting in Cartagena, did not load her share of the booty until late August. It was a rich haul: thousands of hides, 6000 pounds of indigo, 30,000 pounds of tobacco, 5000 pounds of sarsaparilla, and 5000 English pounds worth of gold and silver. But there was not a moment to lose before bad weather set in.

Unfortunately deVerar and his convoy could not simply sail back east; that would take them into the teeth of the wind and current. Without wings or fins to propel them, they instead had to return to the gyre and sail north amid often contrary winds, piloting their way through the islands of the West Indies. The captain's plan was to use his magnetic compass in a two-step strategy of vector navigation. The compass would allow him to bear north to the latitude of Cadiz and then (resetting his course to the east) let the westerlies and the gyre carry him across the Atlantic. As the *San Antonio* left the last of the well-charted Caribbean islands behind and plunged north toward her turning point at 36.5° north latitude, she necessarily lost track of her exact position.

The convoy depended on occasional sightings of the sun and stars for latitude; for longitude they had to rely on *dead reckoning*, a common procedure used by animals that we will look at in detail presently. This all-too-appropriately named strategy keeps track of approximate headings and speeds and times (with, in the case of humans, nothing more sophisticated than a compass, a knotted rope, and an hourglass), and then attempts to reconstruct location by integrating over the various legs of the journey. As with any bird or fish in the same situation, small errors in judging distance, direction, time, or velocity inevitably accumulate, making the resulting estimate ever less accurate. And once out of sight of land there is no way to factor in the drift induced by currents or wind. A sideways drift alters the actual direction traveled; a drift along the axis of travel—equivalent to a headwind or tailwind while flying—changes the distance covered.

The part of the gyre they were in as they left the Caribbean is notoriously unreliable. They might be in the center of the flow, being carried north or northeast at 3 mph; they might be a bit to the east in the Sargasso Sea, the huge calm eye of the gyre; or they might be in the Gulf Stream, which peels off unpredictably to the NE, warming Europe as it carries tropical waters to the British Isles. To make matters worse, the convoy was racing before a tropical storm, and had gone without a sighting of the sun or stars for some days.

By the first hours of September 12 deVerar's ship was at 32.3° latitude, about 250 miles south of their intended right turn. Unaware of the branch current that was propelling the ship and with no celestial sightings (the clouds hid the first-quarter moon, which in any event had set at midnight), the navigator's dead reckoning placed them about 50 miles south of his actual position—a harmless enough mistake on its own. The rest of the convoy, scatted by the storm, was about 20 miles behind and slightly to the west. Unfortunately, the *San Antonio* and the other ships also had drifted about 100 miles east of the northerly track they were trying to maintain, carried by a warm offshoot of the Gulf Stream. The tide was at its highest about 2 a.m., just covering the treacherous reefs.

Just ahead, the "devils" had taken wing about three hours earlier. Nocturnal gadfly petrels known as cahows spend their nights flying low over the water in search of squid, punctuating their hunting with loud, eerie screeching. The lights aboard the *San Antonio* had drawn them like moths as the ship pushed blindly NNE, just to the west of the islands that were home to the seabird colony. The terror inspired by the unearthly shrieking of the birds combined with the navigational incompetence of her human pilots and the shortcomings of their instruments to doom the ship.

San Antonio's track. This satellite view shows the chain of islands that make up Bermuda and (in light gray) the surrounding reefs, which are mainly to the west and north of the islands. The ship was sailing NNE, entering this picture in the lower-left corner and striking a submerged reef about two miles west of the mainland.

Unlike the sailors, the cahows are superb navigators. They seem to know their longitude to within a mile and their latitude with even better precision, clouds or no clouds. Their internal compasses are far more reliable than anything the hand of man could produce at the time. The islands were the birds' breeding grounds; this was their one landmark in a sea empty for hundreds of miles, a beacon of safety rather than danger. And the cahows are by no means exceptional. The ocean around Bermuda is full of equally adept navigators, many of which know just where they are at any given moment. Green and loggerhead sea turtles, white-tailed tropicbirds, American eels, yellow-fin tuna, and humpback whales—none of these animal navigators are in danger of losing track of their position for long. Only our species earns this dubious distinction.

An animal's ability to know its location and the direction of its goal is one of the greatest mysteries of science. Increasingly, though much remains to be discovered and understood, this ability seems less magical. Some of the mysteries are merely products of our opposing desires to romanticize behaviors on the one hand and oversimplify them on the other, and thus to look in the wrong places for answers. We also are prone to anthropomorphize, imagining that animals see challenges in the same way we do and use the same strategies to solve the problems they encounter. As a result, we have often overlooked some surprising alternative approaches that make complex tasks much simpler for well-programmed animals. In particular, we have assumed that our fellow creatures cannot measure orientation parameters any more accurately than human instrumentation, and ought in fact to do less well than our elaborate and expensive equipment.

Our plan is to look briefly at the range of orientation strategies evident in animals, from the simple to the astonishing. Because an essential component of many of these strategies is the ability to measure periods and intervals, we will examine time sense. The next most basic component is an array of alternative compasses to orient movement. We will then look at how time and compasses combine with memory to permit piloting and inertial navigation. This will lead us to the greatest challenge to human understanding, the map sense. With a fuller picture of how animals navigate, we will conclude with the imminent threats humans pose to navigators: habitat destruction and climate change.

As we will see, understanding animal navigation is often critical to conservation, and the recent gigantic steps in decoding the workings of the compass and map sense have come not a moment too soon. Consider the plight of the cahows, whose superb navigational skill and unearthly voices proved no defense against hungry colonists or their rats, cats, and rooting hogs.

Gurnet Rock, off Bermuda. It was on a desolate islet like this, half a mile to the west, that the last colony of cahows clung to life. (The exact location of the refuge island remains a secret.)

The wholesale slaughter of the birds continued despite one of the earliest efforts at conservation, a 17th-century edict by the governor against the "spoyle and havocke of the Cohowes." They were thought to be extinct on the mainland by the late 1620s, less than 20 years after the islands were first settled.

After more than three centuries with no confirmed sightings, however, 18 nesting pairs were discovered on a small, inhospitable islet on the southern fringe of Bermuda in 1951. None of their young survived that year, decimated by rough weather, competing tropicbirds, and scavenging rats. After an intensive breeding effort there are now 250 individuals, their survival dependent on dedicated conservationists who transfer the chicks painstakingly to handmade burrows on larger islands.

Our knowledge of the cahow's behavior, and particularly the way the chicks imprint on the location of their burrows and the coordinates of their particular tiny island, is still a bit sketchy. Each pair lays only one egg. Several nights after its parents leave for the open ocean the fledged but inexperienced chick walks out of its burrow to the edge of a nearby cliff, looks at the stars overhead, makes some mental measurements (probably of magnetic field strength and inclination), spreads its wings, and plunges into the dark to take up its destiny as a wandering seabird. Without specialized instruments, charts, or tables, the cahow depends day after day on its innate ability to orient and navigate the North Atlantic. Five years later each steers its way back to Bermuda to breed. How do they do it?

■ Getting Warmer

Cahows are, to be sure, pushing the limits of evolutionary technology. For most species of navigators and migrants the challenges are less extreme, though every bit as important. Sightless coral larvae spawned on the reefs just off Bermuda must make their way up near (but not too near) the surface at the right time of day to avoid predatory reef fish, feed for a few weeks, and then return to the reefs to find a suitable place to settle and start growing. Bacteria, protozoans, and plankton that inhabit the island soil and the inshore waters also move up and down, responding to cues that indicate danger or safety, food or toxins, forever improving on their location as best they can in a changing world. The bees tirelessly carrying pollen and nectar from the island's semitropical vegetation back to their hives are among the most elegant navigators on the planet.

To combat what he saw as an anti-intellectual wave of anthropomorphism in animal psychology, the 19th-century psychologist

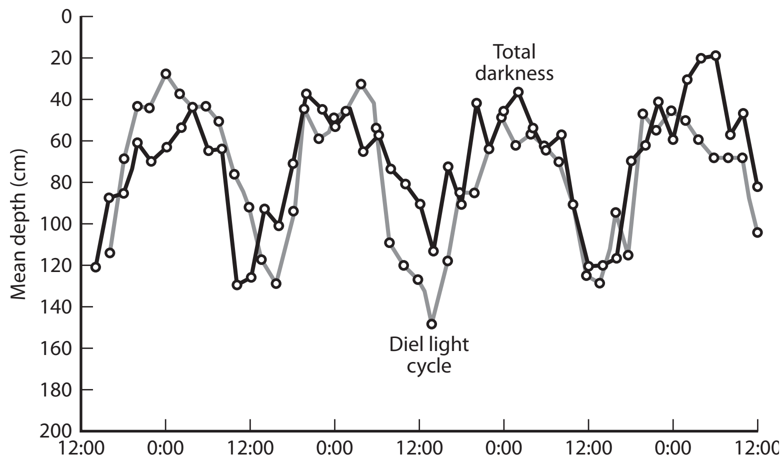
C. Lloyd Morgan asserted that when multiple theories compete, the explanation that introduces the fewest steps is likely to be the best. The sensible injunction to researchers to account for an animal's behavior in the simplest possible manner is known as Morgan's Canon. In the first half of the 20th century behaviorists even used this mantra to account for human behavior entirely in terms of conditioned responses to stimuli.

Because animals were seen as little more than machines, researchers invoked the canon to explain navigation and migration in terms of automatic responses to immediate environmental cues. Whether in bees or bacteria, petrels or protozoa, much of orientation and navigation is based ultimately on a limited set of sensory cues and processing tricks. But while these strategies are largely inborn, it does not follow that they are simple.

Zooplankton, the minute drifting organisms in the sea that ultimately feed nearly all of the ocean's fish, migrate down daily and back up at night. The logic of this redeployment is simple. Their prey—the photosynthetic bacteria, protists, and algae collectively known as *phytoplankton*, or drifting plants—are near the surface around the clock. But the many fish with excellent vision that eat the zooplankton are generally *diurnal*, active during the day. For copepods and other zooplankton, dining on phytoplankton at night and plunging into the relative safety of the depths during the day makes perfect sense.

The massive migration of zooplankton has been simplistically explained as an alternation between an aversion to light when the sun is available, and a balancing aversion to gravity when the sun is not present. In fact, however, the zooplankton begin their journeys *before* light levels change, actually anticipating dawn and dusk.

While much of animal (and human) behavior is in fact rooted in relatively simple responses, navigational abilities typically depend on sophisticated processing as well as multiple sensory and endogenous (internal) inputs. Even with microorganisms, for in-



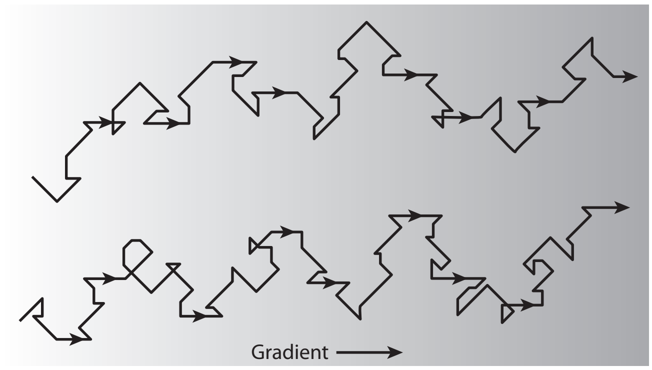
Vertical migration in zooplankton. Tiny crustaceans known as copepods migrate up to feed on phytoplankton (photosynthetic microorganisms) at night. During the day when the fish that feed on copepods are active, the crustaceans swim down to the darkness of the deep water. The copepods perform the same vertical redeployment in the laboratory in the absence of external cues. (Figure drawn from description of plankton minitowers appearing in Bochdansky and Bollens [2004].)

stance, something far more interesting than simple reactions is going on. Zooplankton moved from the ocean to a darkened aquarium still redeploy down in the daytime and up at night, at least for a few days. This surprising persistence of vertical movement is not based on some trick for sensing the sun through solid walls; instead the organisms have a 24-hour timer that has "learned" which are the daytime hours and which are associated with night. The rhythm persists in constant light or dark. The internal timer, not the appearance and disappearance of the cues, controls the creature's response preferences. Shift dawn artificially by a few hours and plankton experience jet lag, only slowly getting back into phase with the sun.

Movement directly toward a cue is called a *taxis*. *Phototaxis* (toward light) causes hatchling sea turtles on a beach to move toward the relatively bright horizon out to sea (as opposed to the darker horizon inland); negative phototaxis sends roaches scurrying away from light. Zooplankton employ negative phototaxis to orient down to safety in the daytime. A *negative geotaxis* (away from the earth) takes them back up at night. But taxis is just a word; the underlying behavior is not necessarily simple, nor consistent between creatures. Geotaxis in some bacteria, for instance, is based on magnetite grains: miniature magnets rotate the mud-loving organisms automatically and point them roughly down. Some single-celled algae have clumps of dense starch grains at one end weighing them down; other species have a low-density oily bubble that signals the way up. More complex animals—ourselves, for instance—devote an entire organ and many neurons to determining the direction of gravity. A reductionist might try to describe a human's erect stance as negatively geotactic, but we are none the wiser as a result.

Unlike the nearly universal orientation to gravity, most taxic behavior is based on comparing two or more measurements. The measurements can be made simultaneously or sequentially. Perhaps the simplest taxis known, and doubtless the oldest evolutionarily, is the positive *chemotaxis* that leads bacteria up a food gradient. The behavior is based on a sequential comparison overlaid on a biased random walk. Bacteria have to use time comparisons; they are too small to sense a difference between the concentration of a chemical at their front versus their back ends. To measure a gradient, these microorganisms must sample the sugar concentration at different places and remember whether the last measurement was better or worse than the current one. Most bacteria move by means of rotating flagella that act as propellers. Every few seconds the bacterium pauses and sets out in a nearly random new direction. They have a simple rule: if things are getting better, delay the next reorientation; if things are getting worse, try a new direction sooner.

This "getting-warmer" strategy requires at least brief memory. It is by no means restricted to microorganisms. A male moth look-

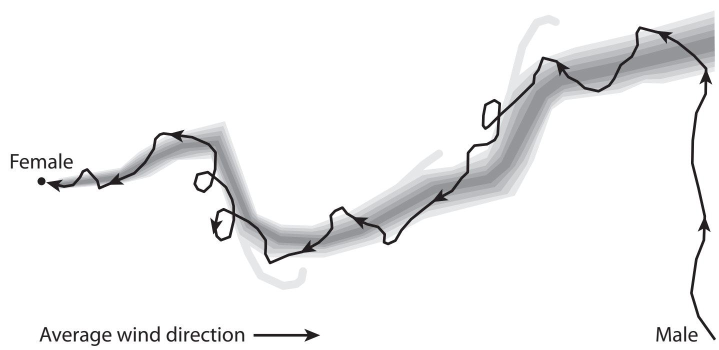


Bacterial chemotaxis. Two bacteria are shown moving up a gradient to the right. Each bacterium moves along a track but periodically stops and adopts a new direction. The length of each leg depends on whether the bacterium senses that the concentration is increasing or decreasing, and at what rate. Thus the bacterium persists in directions that take it up the gradient, but quickly abandons orientations that take it down.

ing for a mate locates the source more systematically, flying long transects across the wind searching for a trace of the sexual pheromone of his species. When his antennae sense the odor he turns upwind (positive *anemotaxis*). But even as he works his way up the scent trail he casts back and forth, finding first the right-hand edge of the odor plume, and then the left. This makes sense because the wind direction may have changed gradually (producing a curved plume) or rapidly (generating a nearly discontinuous one). As with bacteria, the moth's tracking behavior depends on successive measurements of odor concentration. We do something similar when we try to locate the source of an odor or the location of a heat-producing object.

More common to our human experience, however, is the simultaneous-comparison approach. Although low-frequency localization depends on analyzing the time delay between our ears, we localize high-frequency sound by comparing the intensity in the left ear versus that in the right. A positive *phonotaxis* (toward sound), as we observe when female crickets or frogs move toward singing males, or the negative phonotaxis of moths trying to avoid the sonar clicks of hunting bats, involves orienting so as to equalize the intensity or time of arrival of cues that are being measured simultaneously by the two organs. A marine or terrestrial flatworm displaying positive phototaxis is doing the same thing, equalizing the light intensity reaching its two simple eyes. If the light is brighter on the right the animal turns right until the left eye is equally stimulated, and thus tracks its way toward the sun.

These appealingly simple taxis-based behaviors cannot, however, explain most aspects of animal orientation. The more that is known about orientation behavior, the clearer it becomes that animals are using much more sophisticated processing to maneuver around their worlds. A sea turtle in the Atlantic can steer a steady course toward magnetic east when in a particular range of latitudes, while a truly taxic turtle would have to choose between north (positive *magnetotaxis*) and south. An ant making its way to



Positive anemotaxis. A female moth at the far left releases a pheromone into the breeze, which moves generally but irregularly to the right. At the far right a male moth is flying a crosswind transect until he detects the odor. He then turns into the wind, retaining some of his crosswind momentum. When he exits the odor plume he turns back and flies crosswind until he picks up the trail again, reversing course when he cannot locate the scent within a few seconds.

Table 1.1. Common Orientation and Navigation Strategies

1. Taxis	Orienting directly toward or away from a cue
2. Compass orientation	Maintaining a constant bearing relative to a cue, or a constant absolute direction if compensating for cue movement
3. Vector navigation	Using a sequence of compass bearings to steer a course; generally independent of landmarks
4. Piloting	Navigating relative to familiar landmarks; may or may not involve compasses
5. Inertial navigation	Dead reckoning; keeping track of each leg of a journey to compute location later; generally independent of landmarks
6. True navigation	Navigating with an apparent knowledge of the location of a distant goal; generally independent of landmarks

and from a familiar food source may need to keep a particular tree 135° to the left on the way out and 135° to the right while returning home. Simple taxes alone cannot account for such behavior.

Even with animals whose lives seem simple, then, there is more to navigation than taxes. And when we scale up to the challenges faced by insects, birds, whales, and humans, the need for systems of increasing sophistication to meet the demands of almost infinitely complex problems becomes inevitable. Humans have developed clumsy ad hoc strategies for navigating, and we will use these as models to understand what animals are doing with far greater ease and elegance.

The first analogy we need to call on is the compass, which humans use to maintain a constant bearing in the world. Because the main animal compass—the sun—moves through the sky, humans and animals alike need some way to measure time to move beyond simple taxes. Memory adds more power to the navigational system: sequential compass bearings linked to timing systems can provide the vectors that guide migrating songbirds. Like humans, animals too can memorize landmarks in earth, air, sea, or sky to provide piloting information. Many animals also can keep track of the distances and directions on the outward legs of a journey to compute location through dead reckoning. Then, for those creatures lucky enough to know where they are on the face of the globe, "true" navigation can take them to the actual location of a distant goal. Each layer of processing enhances the survival prospects of animals that must travel to feed or reproduce.

In the chapters to come, we will discuss each system and the creatures that employ it in an effort to understand what senses and abilities they call upon, and how they manage such incredible feats.

Chapter 2

When and Where

Taxes are powerful forces that drive much of behavior, particularly of microorganisms. But a monarch butterfly heading south toward an isolated mountain peak in Mexico a thousand miles away can do much more. It will steer to the right of the sun at 9 a.m., toward the sun at noon, well to the left of the sun at 3 p.m., and so on, always heading due south. This remarkable behavior is commonplace among animals, and is even more elaborate than it sounds. The exact direction of south relative to the sun depends not just on the time of day, but on the date and latitude as well, complications that appear to pose no great difficulty for either insects or nonhuman vertebrates. Nor does compass orientation necessarily depend on a particular cue. Animals employ a similar and equally flexible compass-bearing ability when they use stars, polarized light, magnetic fields, and visual landmarks—even when they compensate at the same time for crosswinds or currents. Our goal in this chapter is to take a preliminary look at the range of navigational and mapping strategies available to animals.

Taxis-based orientation is the simplest strategy, a special case in which the goal happens to lie directly toward or away from a cue, as is often the situation when orienting to gravity or away from danger. For the monarch, whose wintering spot may be in any of an