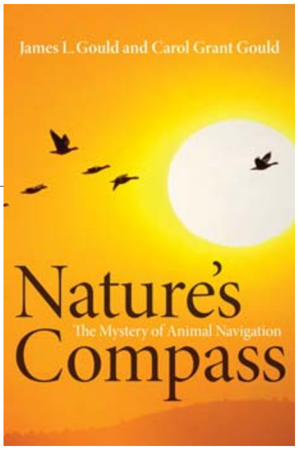


Migration and the Future: Conservation and Extinction

by James L. Gould and Carol Grant Gould

Why do animals migrate? For the southern right whales we studied as graduate students, the answer is clear; during the winter the Antarctic ice sheet expands, covering the summer feeding grounds. Though the rich concentration of krill is still there, air-breathing mammals can no longer safely feed. And because whales are warm blooded, lingering in frigid water waiting for the return of spring is metabolically expensive. Instead, the right whales make annual pilgrimages to traditional coastal sites in the temperate zone 2000 miles to the north.

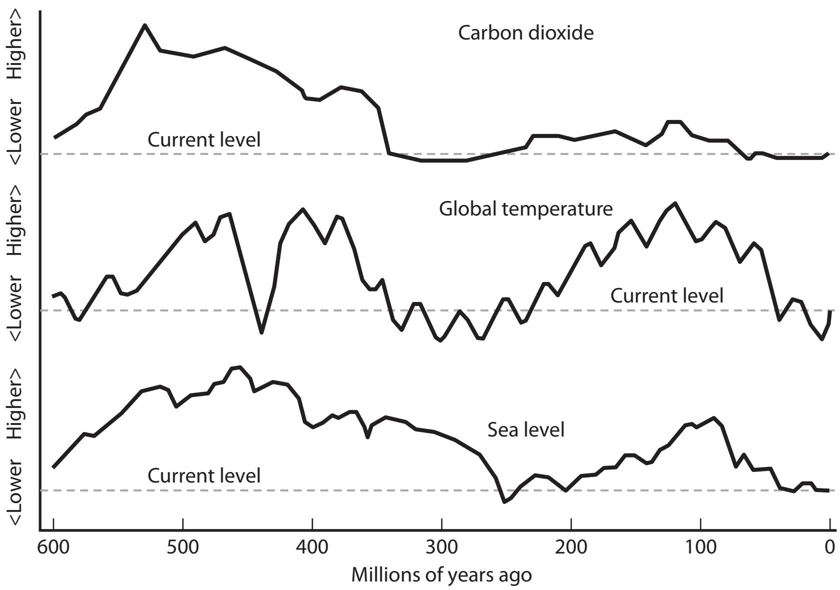
For the group of about 60 whales we worked with, the winter refuge is Golfo San José on the Patagonian coast of Argentina. There they give birth and mate, relatively safe in protected bays from families of killer whales on the hunt. Like all migrants, right whales are sensitive to habitat and climate changes, as well as to human activity. These gentle creatures have been hunted nearly to extinction, and the remainder have been exiled from bays with shipping or industrial development. Rising ocean temperatures are pushing surviving populations of whales, as well as other sea creatures, to alter the timing of their age-old migrations. Given that 12% of bird species (including 45% of seabirds), most large whales, and all sea turtles are endangered, we must wonder how well migrants deal with these challenges, and what their long-term prospects look like.

■ Evolution of Migration

Migration evolved because its benefits outweigh the associated costs. The logic of natural selection dictates that a bird that breeds in the Arctic and overwinters in the tropics must be producing more surviving offspring on average, despite the costs in time and energy of flying hundreds or thousands of miles north to breed. Otherwise such a expensive system would not persist. In fact long-distance migrants have been doing especially well in the recent past; although they produce smaller clutch sizes and fewer broods, they have on average the same number of successful young as residents and short-distance migrants. Predation and starvation of fledglings in the tropics and temperate zone must be very high compared to the situation farther north, where the ephemeral bursts of spring growth make food briefly plentiful, while the cruel winters severely cull or eliminate predator populations. And not having to work as hard at parenting, adults live longer.

Though habitat and climate change are the focus of conservationist concern for migrants, these are precisely the factors that appear to have selected for migration in the first place. Change, of course, is inevitable; to accommodate it an animal can alter its mix of genes or its location (or, most often, both). The degree of change animals have faced through evolutionary history (600 million years [MY] for vertebrates, 200 MY for birds) is enormous. Average global temperatures have ranged from below freezing to above 100°F—and these are just averages. During ice ages the poles were even colder, while the tropics experienced still hotter weather during some of the interglacial interludes. During periods when all the polar ice has melted ocean levels have been 250 feet higher than they are at present; in times of global freezing the sea level has been almost 450 feet lower (though this has not happened for 700 MY). Vegetation has tracked this change in climate as the boundaries between tropical, temperate, and boreal forests moved thousands of miles in latitude. Animals had to relocate or go extinct. One obvious solution was to migrate, which allows animals to take advantage of the annual global differences in weather.

But it's not quite that simple. The usual picture of an all-or-nothing, species-wide choice of strategy is misleading; most species of birds, for instance, have a continuum of options. Some of the finches we see in the summer in Princeton have flown north



Climate variability in the past. Over the 600 million years that vertebrates have existed the earth has undergone major swings in climate and other characteristics important to migrants. Although in the simplest case carbon dioxide levels should control temperature, and temperature should control sea level (through the accumulation or melting of ice), note that the detailed correlation is not particularly strong. By historical standards, the planet has relatively little carbon dioxide in the atmosphere at the moment, is much cooler than average, and is experiencing a period of relatively low sea level.

from winter quarters on the Gulf of Mexico, but others have spent the cold months locally; some (not many, but their numbers are increasing) vacationed in between. In fact, the majority of bird species (55–60%) have a mix of individuals that have adopted either the resident strategy or the migratory alternative. Even among the permanent residents, though, migratory restlessness is evident in the spring and fall as some inner programming prompts the animals to prepare for journeys they will never undertake.

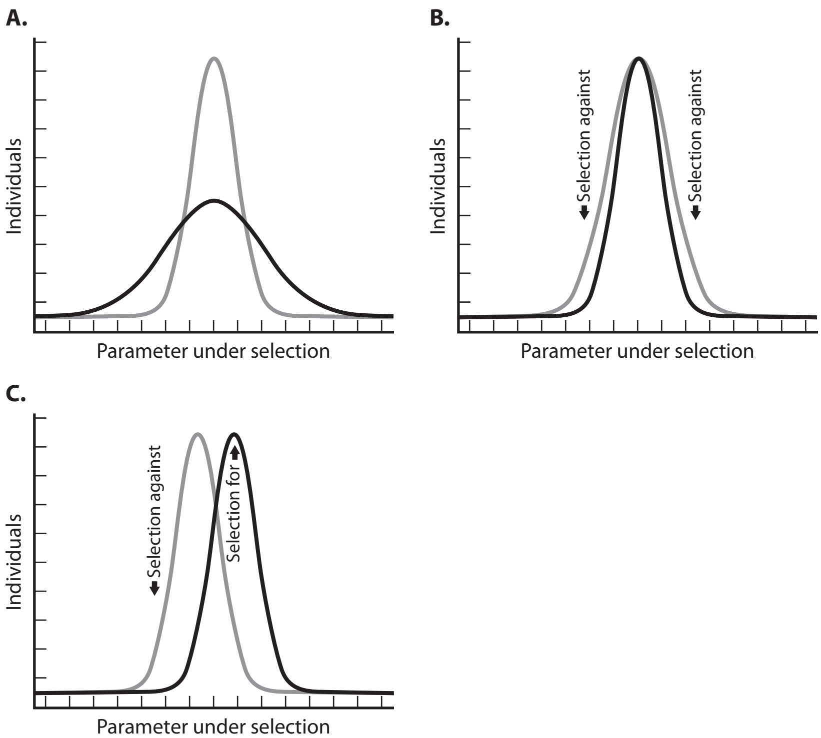
Birds within a given species typically differ in many relevant traits. There may be variations in the timing of spring and autumn migration (or the corresponding restlessness). The default direction for a young bird's first fall journey may vary with the population. There may be differences in the preferred distance (or amount of time) to fly, the ideal stopping latitude both for spring and fall, the preferred speed, and the number or duration, or both, of stopovers. The weighting of any cues that identify a suitable place to end the journey or pause along the way also may vary between populations and individuals. Each of these parameters is to a large extent genetic. But equally innate is a specific degree of *phenotypic plasticity*, a capacity for day-to-day change that confers an ability to alter behavior in response to current or past contingencies such as a bout of unusually warm weather or unfavorable winds.

Thus two sparrows under the same conditions may have different departure dates. A cross between them will produce offspring with an intermediate date, showing that this departure time is genetically encoded. And yet both will respond to a week of unusually warm weather in the late winter by starting their northward migration a day or two earlier, employing their neural weather algorithm to produce an adaptive one-time phenotypic adjustment.

Phenotypic fine tuning is generally stronger in resident populations, even compared to migrants of the same species. It is typically greater in short-distance migrants (seasonal journeys less than 200 miles) than in long-range species. But it can differ between groups; great tits in England adjust their egg-laying dates over a relatively wide range to match spring temperatures, while those in the Netherlands seem on average to ignore the weather. Even in the Dutch population, however, there is considerable genetic variation for the degree of plasticity, variation upon which selection can operate should a systematic advantage of one strategy over the other lead to greater relative reproductive fitness.

For evolution to occur though natural selection, migratory parameters must vary among individuals. Variation has to be heritable, and different variants need to have differential reproductive success. The variation in these traits is clear in migrating birds, but the *degree* of variation differs dramatically between species. A narrow range of genetic alternatives typically reflects a specialist species that has perfected an optimal strategy from which it barely strays. Low variation also is characteristic of small populations or species that have been through a "bottleneck" event in which population size (and the corresponding genetic variability) was severely pruned. The North American whooping crane population, for instance, numbered only 21 individuals in 1941, but has recovered to about 400 wild birds after intense conservation efforts. On average, we would expect species with low variability or low phenotypic plasticity to do less well in the face of environmental change.

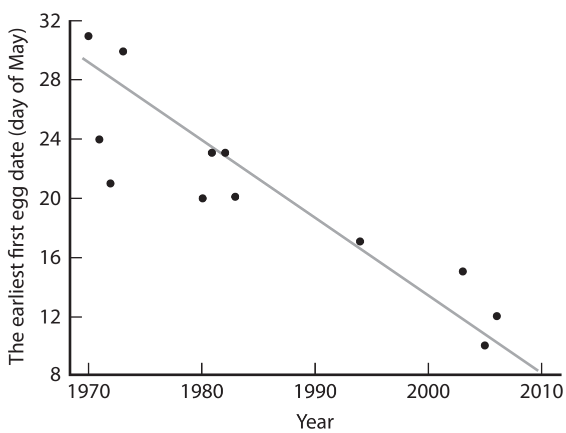
Selection affects the spread and centering of this variability in two major ways. Most commonly, normalizing selection trims the extremes of the distribution. Cliff swallows are a good example of normalizing selection. In Nebraska these birds arrive over a two-week period in the spring; the date of their first arrival has drifted earlier by about three days per decade in recent years. A severe cold snap in 1996, however, killed off the early arrivers. Because this trait is genetic, no birds arrived early in the subsequent year. Selection occurs at the other end of the flight-time distribution as well: in good years late-arriving swallows find the best nesting sites and most-fit mates already taken, and thus experience severely re-



Evolution of traits. (A) Species differ with regard to the amount of variation in the genome for parameters such as starting date, speed of travel, vector of first fall migration, and so on. Specialists and species with a small population size tend to have less variation (the narrow curve). (B) Most selection is normalizing, cropping off the ends of the distribution, thus narrowing the curve. (C) As conditions change, selection generally becomes directional, operating against one extreme or in favor of the other end, or both, shifting the distribution.

duced reproductive success. Bad weather typically removes less symmetrical individuals as well (which are presumably less fit), as well as unusually large and small members of the population. But if selection systematically favors one extreme or punishes the other (or, quite often, both), the mean value of the parameter will move in a consistent direction.

Because the start of the growing season above 45°N latitude has advanced 12–19 days in the last 50 years, both phenotypic compensation and selection for earlier or faster migration seem likely to be taking place. And in fact a variety of species have already accommodated the warming trend in higher northern latitudes. In the Finger Lakes region of New York State, for example, 26 of the 34 species of short-distance migrants breeding in the area arrived significantly earlier in the last half of the 20th century compared with the first half—all by at least a week, but in several cases by a month or more. The pattern is the same in Europe; reed warblers, for instance, have advanced their egg laying by about 20 days over the last 40 years. The capacity for change is even greater than this. Breeding experiments that push selection pressure artificially high can move up the departure date by a week or delay it by a fortnight in just two years without any need for phenotypic plasticity to accelerate the shift. Indeed, both breeding results and analyses of related populations with different migratory patterns show that all components of the navigational repertoire seem quick to respond to selection.

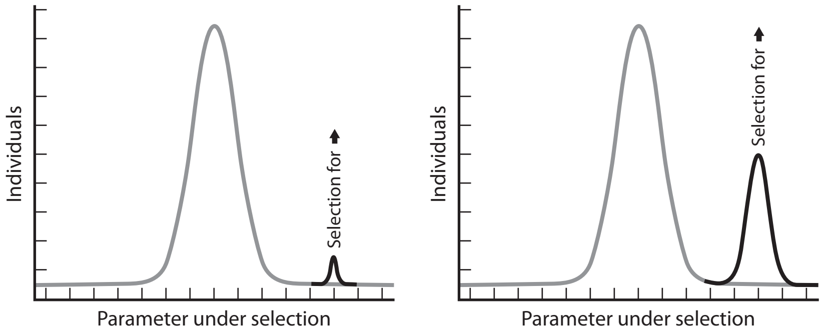


Laying dates for reed warblers. Reed warblers begin nesting almost three weeks earlier now than they did 40 years ago.

When three or more genes are at work in controlling the expression of a trait (which is the usual situation for any but the simplest factors), much of the genetic variation is normally hidden by the additive way in which the genes combine with one another. If, for instance, you were to flip a coin six times, you would get all heads only once in 64 tries; similarly, the most extreme combinations of genes in offspring are rarely seen. It is this reservoir of covert variability that allows selection to work so quickly.

The house finch population in North America is a dramatic example of hidden migratory potential. The natural range of this species until the 20th century was the American Southwest and western Mexico, where only 2–3% are migratory; the rest were year-round residents. In the 1940s California house finches were widely marketed in New York City and on Long Island as cage birds (so-called "Hollywood" finches). Apparently this practice ended with the threat of prosecution, though accounts differ as to which law was invoked. Most of the caged birds were released into the wild and can now be found throughout the United States, where they have largely displaced the native purple finch. The interesting thing is that in the harsh winters of the eastern and midwestern United States, 40–80% of the finches (depending on the exact location) are now migratory. Selection strongly favored the rare combination of genes that impelled the birds to fly south for the winter, and the species responded quickly.

Although directional selection is the most common agent of evolution, another powerful mechanism is a combination of chance and inbreeding. Suppose some outlier in the distribution—individuals with a highly unusual innate set of initial migration bearings or flight distances—were to stumble upon a favorable breeding habitat. They would enjoy enhanced reproductive success, and moreover mainly breed with other animals sharing the same unusual genetic proclivities. An entirely new migratory population could then evolve though what is commonly called a *founder effect*.

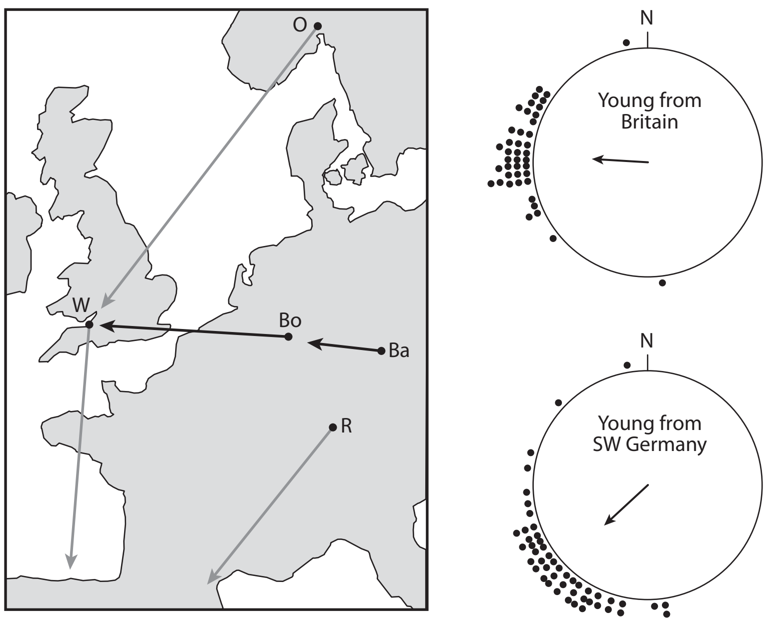


Evolution of a new population. Selection need not operate gradually. If a few individuals in one tail of the parameter distribution discover a new, highly favorable habitat, and if as a consequence they are reproductively isolated from the rest of the species, they may inbreed and create a genetically distinct population.

In fact this pattern of navigational innovation, essential for the spread of migratory species, has been observed or inferred numerous times. One particularly clear case, investigated in remarkable detail by Peter Berthold and his colleagues at the Max Planck Institute for Ornithology, involves the blackcap, a species of warbler. Blackcaps breed across northern Europe and typically winter in Spain. Each population has an average innate default departure vector appropriate to its summer location, and an equally innate sense of how far to travel. Within the population different individuals vary to some degree in their distance and direction proclivities. At least for flight duration the genetic basis of the variation is now understood; it depends on the number of two-base repeats in a gene unmemorably called *ADCYAPI*, which affects circadian rhythms and energy use.

Blackcaps hardly ever overwintered in the United Kingdom prior to 1950, even though Great Britain is on the route for the Norwegian population. But beginning about half a century ago, a group of warblers started spending the cold months in England and Wales. Cage-reared birds from Wales tell us that the innate first-fall vector is aimed west rather than SW (the typical direction for most other populations of these warblers). This suggested that the spring breeding area must be in Germany or Austria. Genetic analyses show that, in fact, nearly 10% of the blackcaps in these regions are now traveling to the United Kingdom for the winter. Crossing the two populations produces birds that prefer to fly WSW (into oblivion in the North Atlantic).

The likely scenario is that a few warblers from the western extreme of the vector distribution and the short end of the range of flight duration variation found the United Kingdom, did well, and returned to breed. They maintain the requisite genetic isolation by



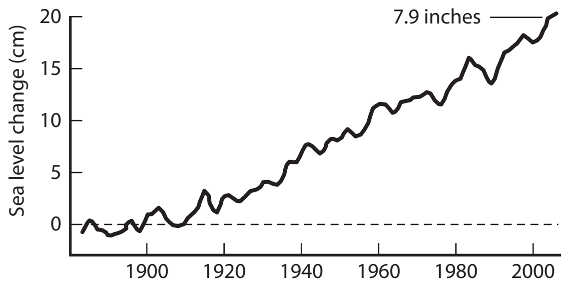
Rapid evolution of a new migration strategy in warblers. Blackcaps generally migrate SW in the fall and typically winter in Spain. One population (O) migrates through the United Kingdom en route. Since 1950 a population breeding in Germany has begun migrating west and wintering in Wales and southern England. The vector preference is strictly genetic: the bearings shown here represent hand-reared birds in their first autumn.

virtue of arriving back at the breeding ground early (a consequence of their much reduced route), completing their courtship and pairing before the Spanish contingents return.

■ Climate and Habitat Change

The threat of climate change and the ensuing change in global habitats have been concerns for decades. Discussion of their catastrophic potential reached a peak in the early 1970s when the National Academy of Sciences reported a "widely held consensus" that a major change was inevitable, and might already have begun. The overhyped worry then, however, was a repeat of the ice age of 20,000 years ago, which buried New York City under a thousand feet of glacial mass. This experience suggests that current furor over global warming merits some degree of initial skepticism. The situation is not helped by the political overtones and intellectual intolerance the debate has taken on, nor by the relatively uninformed use of often questionable or irrelevant data. For instance, hardly anything in the well-meaning film starring Al Gore, *An Inconvenient Truth* (2006), is wholly true.

Fortunately, there are two clear sources of data unaffected by political predispositions. The first we've already encountered: birds are migrating and nesting sooner, responding to the earlier growing season. Obviously these animals believe the planet is warming, and are betting their lives on this conclusion. The second is the ocean. Sea level changes in consequence of two main factors. First, the volume of water increases with temperature as a simple result of thermal expansion; second, it rises when terrestrial ice melts and the water makes its way to the ocean. Both phenomena are obvious consequences of global warming, though expansion is the dominant process at the moment. The oceans are, in essence, a huge, volume-based thermometer, and sea level has been increasing steadily. Whether this is mainly the result of human activity



Recent trends in sea level. Sea level has risen about eight inches in the last century, primarily as a result of the thermal expansion of increasingly warm ocean water.

raises another set of loaded questions; either way it's potentially a huge challenge for the earth's flora and fauna.

What exactly can long-distance migrants expect from this change in average global temperature? The earth's great biomes are on the move. The tundra, which as we have seen supports large populations of migrants with its boom-and-bust cycles of growth, remains characteristically treeless because its spongy surface retains water that cannot drain away through the underlying permafrost. As temperatures rise the permafrost recedes, opening the moss-dominated tundra to the incursion of forest. Assuming no abatement of warming, even conservative estimates put the treeline boundary between boreal forest and tundra up to 250 miles farther north within the next two centuries, with as much as 40% of the tundra changing into evergreen-dominated taiga in the process. Much of the current taiga, in turn, will be encroached upon by temperate forest flora, which will eventually be under pressure at its southern boundary from tropical species.

Because it is the tundra that supports so many of the long-distance migrants, and particularly birds, it follows that although the growing season will lengthen, the habitat area will shrink enormously. Unless the extended summer allows for a round of second nesting, it's hard to see how the earlier spring will benefit the birds.

In any event, most long-distance migrants seem to be advancing the start of their spring migration departures only minimally. The tropics, where they spend the winter, provide few cues to signal the onset of spring thousands of miles to the north. Long-distance migrants must depend on their innate programming to tell them when to leave, and thus miss out on the sort of genetic variability and phenotypic response that power the adaptability we see in short-range migrants. On the other hand, records show that long-distance migrants are traveling faster on their way to high latitudes, probably because they do not need to wait for their climate-dependent food supply en route to catch up. For shorebirds there is another potential difficulty: the rising sea level will probably consume wetlands faster than succession can create new ones suitable for foraging and breeding. Swamp and marshland take a long time to develop into the richly productive habitats the birds depend on.

For residents and short-distance migrants the picture is slightly different. For one thing, in the Northern Hemisphere the boundary between residents and migrants has been moving north, having shifted more than 25 miles poleward in the past 30 years. Correspondingly, short-distance migrants like blackcaps are tending to truncate their southward journeys in the fall, overwintering farther north as well. And the proportion of birds rearing a second or even a third brood in the spring and summer has increased sharply. Here in Princeton a second nesting by house wrens was unusual 40 years ago; today even a third round of reproduction is commonplace. In the United Kingdom some overachieving sparrows are now rearing four broods each year. The greater phenotypic plasticity and range of hidden genetic variation in residents and short-distance migrants enables them to accommodate the change, and even profit by it. It remains to be seen whether this innate adaptability is sufficient to keep pace with the relatively rapid rate of climate change currently under way.

But while many species have the inherent capacity to accommodate climate change, the more serious threat for most is habitat destruction. More than 40% of endangered birds are in that category because of habitat loss somewhere in their range. For birds adapted to reproduce in grasslands, the worldwide loss of 25% of this habitat to crops is a serious blow. Birds overwintering in the tropics face a 5% loss of rain forest per decade. Depending on your preferred definition, forests worldwide cover only 50–65% of their former expanse, removing not only breeding habitat essential for some residents and migrants, but places for long-distance migrants to stop and feed on the way to their more distant targets. Even where forests have declined less they are increasingly fragmented, a process that creates a distinctly different forest-edge habitat at the expense of a mid- and deep-forest ecology, areas that support distinctly different species. Predators and nest parasites are especially common on forest edges, and human development is parceling what were vast sweeps of deep secure forest environment into small patches, surrounded by perilous edge.

By far the biggest victims of habitat destruction are the shorebirds: the rich wetlands environment that is life to them and so many other creatures is valuable coastal real estate to humans. The "reclamation" of marshes and mangroves, the damming of streams, and pollution of bays and rivers by cities has reduced shorebird habitat drastically.

While we have focused on avian migrants, the situation is equally challenging for other long-distance travelers. Monarch butterflies are steadily losing their relatively small wintering habitat in the mountains west of Mexico City to illegal logging. Sea turtles are losing their nesting habitats on beaches to development, and risk being caught by long-line fishing or trawling while at sea. Salmon are losing their eggs and fry to sediment-heavy runoff from forest logging while adults are exiled from their native streams by dams and introduced sport fish. Wild salmon are overfished, and are increasingly diseased from parasites picked up from fish farms they pass on their way to the sea. At home or on the move, the combination of climate change and habitat loss is threatening migrants to an unprecedented degree. In the disturbing words of conservationist David Wilcove in his prescient book *No Way Home* (2008), a migrating animal "travels without any knowledge of what may have happened to its breeding grounds, its wintering grounds, or any of the places in between since the last time it made the journey. . . . Migration is an act of faith after all, a hardwired belief that there is somewhere to go to and a way to get back."

Against this set of challenges we are fortunate to have an increasing understanding of the ways animals navigate. Whooping cranes are recovering in large part because we now know about their strip-map approach to learning and remembering their migratory route. As a result young whoopers can be reared in an incubator anywhere on earth, imprinted on an ultralight aircraft, and then led along an arbitrary route complete with stopovers to a protected wintering ground. They, in their turn, will lead the next generation through the same journey. Similarly, the "devil bird" cahow is being rescued from the brink of extinction because conservationists on Bermuda understand the phenomenon of site imprinting. Cahow chicks, abandoned by their parents, emerge from their burrows and memorize the magnetic parameters of their nest site on the night they fledge. Thus they can be moved to a safer nesting site any time up to the day before they take wing, and will return to that same spot when they are ready to breed five years later.

But things are not always this straightforward. For instance, conservationists would like to take advantage of magnetic nest-site imprinting in sea turtles by moving the eggs to new beaches before hatching, thus reestablishing extinct populations. But this needs to be done quite late in the developmental period: sex in turtles depends on incubation temperature, and is calibrated by stabilizing selection to the conditions of the natal beach to yield a 50:50 mix. Thus when biologists attempted to reintroduce green sea turtles to Bermuda from the Caribbean, the lower sand temperatures on the Isles of Devils resulted in thousands of all-male hatchlings—turtles that we observe returning each year in a futile search for mates.

In addition to the power our understanding of strip maps and true maps confers, the beacon-based system of salmon allows conservationists to reintroduce these migrants to streams they have "forgotten," or to establish new populations in promising, unpolluted locales. The process begins with imprinting fry raised in hatcheries with an artificial odor on the first day of the smolt stage, then releasing them into the brackish waters near the mouth of the river system in question to memorize the map coordinates. The target stream then needs to be baited with the artificial odor the appropriate number of years later to guide returning adults. Afterward the artificial odor is no longer needed; the natural aromas of the rivulet will be memorized by the new generation of smolts six months or more later before they head downstream.

Increasingly researchers are making use of technological solutions originally developed to solve the problems posed by our own innate navigational shortcomings—the problems that doomed the *San Antonio*'s crew. Miniaturized GPS trackers, for instance, in addition to getting clueless motorists to their destinations, can reconstruct the journeys of many species of migratory animals, revealing how their onboard compass and map senses are guiding their travels as well as their choice of stopovers and termination point. This information provides insights into migratory pathways and the cues animals use, both in terms of their sensory equipment and neural programming.

Often these results tell conservationists what *won't* work. Recall that most migrating birds (waterfowl excepted) set off that first autumn along an innately specified vector. Only genetic variation and selection can do much to alter their instinctive headlong rush into the unknown. Given that we cannot put every endangered migrant on emergency conservational life support, some sort of triage is inevitable. For many species, variation and selection provide the best chance these victims of human population growth have for long-term survival.

A wider understanding and appreciation among the peoples of the several independent nations crossed by a migrant's journey will be essential in preserving the habitats these animals need, habitats that may only be used a few weeks each year. Expecting people to stop using the planet and its resources—to forego growing needed crops, for instance, to make life easier for transient grassland species—is useless. Preventing short-term climate change is an equally fantastic dream. But seeking international cooperation in highly targeted and well-financed ways to accommodate migrating species is in many cases a realistic goal, while we work out the ways to shape or at least ameliorate our planet's destiny.

We understand enough—or perhaps just know enough to realize how to fill in the gaps in our understanding—to help at least some of these species survive. What's mainly lacking is the irrational, optimistic zeal necessary to make conservation work—irrational in the sense that we must assume with no very good reason that we can decode mysteries and use those discoveries to solve real-world problems. We need to tell the fascinating story of navigation and migration to those in and along the travel corridors, communicating the awe and wonder that fuels the research of most serious biologists.

This should not be impossible. Whether it's their ability to judge time and distance, use vectors and beacons, create cognitive maps, take compass bearings from cues indecipherable to us, or draw on an inborn map sense to position themselves on the planet, there are enough intriguing mysteries in animal navigation to engage the imagination and creative energies of new legions of conservationists around the globe.