



MIGRATION

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GLOSSARY

circannual rhythms Endogenous, or internal, rhythmic cycles of one year in duration that govern the onset and cessation of migratory behaviors.

compass orientation Navigation in a particular direction without reference to landmarks or sites of origin or destination. Migrants are known to use compass information from magnetic fields, chemical gradients, and visual features such as the stars, sun, and planes of light polarization.

diadromy Migrations that take individuals between fresh and salt-water habitats, a common phenomenon for many migratory fish species.

partial migration The case where intrapopulational variation in migratory behavior leads some individuals to migrate while others within the same population may only migrate locally or remain sedentary.

zugenruhe Restlessness exhibited by some migratory

species, especially birds, if not allowed to migrate during their usual migratory period. It reflects an underlying physiological transition to a migratory state.

MIGRATION DESCRIBES the movement of individuals between spatially separate ecological communities, typically on a seasonal or annual schedule. Several characteristics of migrations distinguish them from other forms of animal ranging behavior, including more persistent movements, of greater duration, that follow a more direct path with fewer turnings. Furthermore, migrants do not respond to resources along their path, but show a heightened response to the same resources near the migratory journey's end. This latter feature distinguishes migrations from typical foraging and dispersal movements. Behavioral specializations may include specific activity patterns particular to departure and arrival, and unique patterns of energy allocation to support long-distance movements. The ecological consequences of migration are that they take a species from one community of organisms to another and they partition life histories so that specific phases or events occur in different ecological communities.

I. INTRODUCTION

Migrations capture the human imagination like few other animal behaviors. The single-minded struggle of

the salmon fighting its way upstream, the barely visible formation of geese piercing the sky overhead, and the thundering line of wildebeest snaking across the open savanna—all speak of ancient rhythms that drive life on our planet. The often great distances moved and the large numbers of individuals involved make animal migrations a conspicuous and essential aspect of many regions' biodiversities. Animals migrate for many reasons but in general do so to avoid temporarily unfavorable conditions or to locate particularly favorable areas that can meet specific biological needs, such as reproduction. However, it is somewhat ironic that migrations might actually increase a species' risk rather than reduce it. Protecting migratory species requires preservation not only of their final destinations but their migratory routes and stopover points as well. In effect, migration inextricably links the fates of biotas across the length and breadth of the globe. No natural phenomenon makes the point better that biodiversity on local and global scales shares the same actors and the same processes that drive them. In this chapter we explore the nature, scope, and patterning of animal migrations as a prelude to discussing how human-caused changes in the environment are likely to impact migratory species. We not only address direct effects on migratory species behavior, ecology, population dynamics, and evolutionary potential, but we also consider indirect impacts on the ecological communities and regional biodiversities that disruption of migrations can produce.

II. WHAT IS MIGRATION?

Definitions of "migration" abound in the scientific literature, many of which capture the nature of the behavior for specific taxa but fail to generalize across taxa. Commonly cited elements include long distances traveled and movements from one place to another, then back again. But what is "long"? Dark-eyed juncos (*Junco hyemalis*) and Blackburnian warblers (*Dendroica fusca*) are both small passerine birds that migrate with the seasons; both breed at higher latitudes in northeastern Canada (among other sites) yet juncos may migrate only a few hundred kilometers to their overwintering range while Blackburnian warblers fly several thousand kilometers to overwinter in the Andean forests of Ecuador. The lengths of these respective trips differ by an order of magnitude, yet in examining the ecology and behavior of each species, we might well consider both to constitute migrations. For example, both involve moving between distinct ecological communities on a consistently timed, seasonal basis. Similarly, "typical" migrants, like

most birds, travel the same circuit each year. Others, however, may only complete a single circuit in their lifetime (e.g., salmon) or only *part* of a circuit before they die, such as insects in which successive generations continue the journey their predecessors began. Should we exclude such species from the "migratory" category despite other aspects of behavior, physiology, and life history held in common with typical migrants?

From a biodiversity perspective, migration drives a species' life history and pattern of resource use, and it ties together ecological communities in different regions. Thus, defining migration in ecological terms of a species' use of space over time is imperative to understanding its functional impacts on biodiversity. However, one also needs to ask, does biodiversity refer to just the specific organisms found within a region, or does it encompass the specialized behaviors such organisms display? Ecological consequences aside, are sedentary populations of Canada geese interchangeable with migratory ones when summing up a region's biodiversity? If migratory and nonmigratory races or subpopulations—whether genetically or phenotypically different—each represent unique components of biodiversity, then we must also define "migration" in terms of the behavioral mechanisms distinguishing them.

The combined ecological and behavioral dimensions of migration have plagued attempts to come up with a single definition suitable from both perspectives. Ecological definitions have included "the act of moving from one spatial unit to another" by Baker (1978) and "the persisting change that is left over when all other, minor excursions are removed" by Taylor and Taylor. Both capture the essential idea of migrations extending the ecological space used by individuals, although ambiguity over what constitutes a spatial unit or minor excursion renders each too imprecise to be of much use in distinguishing migratory from nonmigratory species.

Dingle (1996) has taken Kennedy's lead to propose a definition of migration that emphasizes the differences between migrations and other forms of animal movement. He uses clear behavioral terms to distinguish migrants from nonmigrants, yet he uses each species as its own reference for differentiating movements with different ecological consequences. Generally put, nonmigratory (ranging) movements are driven by the immediate need to acquire or safeguard resources, and they cease when suitable resources are encountered or are adequately defended. The length and timing of foraging and territorial defense movements will vary daily, or on even shorter time scales, depending on the frequency of encountering resources or potential threats. Commuting daily between refugia and feeding

locations, such as the diel movements of zooplankton and other aquatic animals, is similarly directed by resources and is responsive to their location and abundance. Even dispersal to establish a new home range or to leave a natal group usually ceases as soon as a suitable new home range is found. In contrast, once they set out, migrants will ignore many of the resources they encounter, or use them briefly to refuel, and only become responsive again to resource abundance and quality after all or a critical part of their journey has been completed. Migratory movements thus entail specific changes in behavior and physiology that distinguish them from nonmigratory movements, even those that are circular in nature. Defining migrations relative to a species' other forms of movement results in a more generally applicable definition and one that encompasses the diversity of the migratory behaviors animals display.

Specifically, five mechanistic attributes distinguish migratory behavior: movements are (a) more persistent and of greater duration than ranging movements and (b) follow a more direct path with fewer turnings. There is (c) an initial suppression of responses to resource-derived stimuli, but often a heightened response to such stimuli near the migratory journey's end. Migrants may also have (d) specific activity patterns particular to departure and arrival and (e) unique patterns of energy allocation to support long-distance movements. Of course, not all migrants will show all five characteristics, but as a group these traits circumscribe the suite of distinct and specialized behaviors entailed in migration. To these behavioral attributes we add two functional hallmarks of migrations: (f) they take a species from one community of organisms to another, and (g) they partition life histories so that specific phases or events occur in different ecological communities.

Two common uses of the term "migration" will not be considered in this chapter: (a) migration in the paleontological sense of species shifting their historical distributions with climate change or geological events and (b) migration as geneticists use the term to refer to gene flow between populations.

III. MIGRATORY PATTERNS: A TAXONOMIC SURVEY

The diversity of migratory behavior in animals overwhelms attempts to neatly summarize its character and function. Generally, animals migrate to escape unfavorable conditions or to exploit favorable ones, yet defining

"favorable" or "unfavorable" is often specific to the taxon examined and the life-history function at hand. Polar and cold temperate habitats tend to have more migrant species than tropical ones because they vary so strongly in productivity and habitability, although this tendency differs widely among the major taxonomic groups. Migration distance and duration similarly vary to a great degree, even within groups of species that migrate for the same reason. Differences in physiology account in part for this variability, since larger body sizes can store relatively more energy to fuel longer trips and lower the weight specific cost of transport while certain forms of locomotion, such as flying or swimming, are more efficient than others. In addition to physiology, physical forces such as winds and currents act in concert with habitat topography to further shape the migratory route and schedule. Biogeographic history may even play a role in these features of migration since routes may be hard-wired genetically and slow to adapt, or learned and dependent on knowledge within lineages. Indeed, migrations present a truly fascinating mix of evolutionary puzzles in behavior, ecology, physiology, and biogeography (see Dingle, 1996, for an excellent introduction to these). The broad surveys that follow provide an overview of migration prevalence, function, and character for the major taxa with specific emphasis on the biodiversity of migrants per taxonomic group and region.

A. Birds

Birds epitomize the act of migration for many people. Whether one lives in the temperate zone or tropics, New World or Old, Southern or Northern Hemisphere, migratory species constitute a significant and conspicuous fraction of the avifauna. At the most northern and southern latitudes, close to 100% of bird species migrate out of the region for part of the year. For example, 135 species breed in the arctic zone, yet all migrate south to spend most of their year elsewhere. In more temperate regions, a majority of species, and nearly all insectivores, migrate to more tropical latitudes after breeding. Approximately 200 species migrate from North America to the West Indies, Central, and South America each year, while many more make shorter distance migrations into the southern United States and Mexico. In Europe, 177 species, or 40% of the region's avifauna, migrate from temperate breeding grounds to overwinter in Africa; 104 species from western, central, and eastern Asia join them there. Moreau has estimated that 5 billion individuals make this migratory journey south to Africa alone; the comparable number for the entire

globe is surely several times this. Seasonal fluctuations in temperature ultimately drive food production cycles at higher latitudes, setting the schedule for migratory movements, but in tropical climates distinct wet and dry seasons may function in an identical manner. Substantial numbers of birds follow regular migratory routes that track resources such as fruiting or flowering trees, seeding grasses, or invertebrate flushes brought about by rains. Indeed, this form of short-distance movement may be the most common type of migration in birds. For example, out of 1450 breeding species in Africa, 532 species have been classified as intra-African migrants.

Bird migration is clearly a ubiquitous feature of our planet's biodiversity, yet migrant species are not distributed equally around the globe. In particular, birds that migrate in excess of 1000 km—moderate and long-distance migrants—are more prevalent as breeders in the northern hemisphere. This is largely due to the much greater land area at higher latitudes in the Northern than in the Southern Hemisphere. For example, only 20 species among the hundreds that breed in the temperate regions of southern Africa migrate as far north as the equator, while a much larger number and proportion of Palearctic species overwinter in the same equatorial region (noted earlier). Similarly, only 8% of the nearly 600 species breeding in Australia and Tasmania migrate in and out of the temperate zone. In the New World, 31 species of shorebird (e.g., plovers, sandpipers, curlews) breed at higher latitudes in the Northern Hemisphere and migrate thousands of kilometers to spend their nonbreeding seasons in the Southern Hemisphere, yet not a single shorebird species that breeds in the south even migrates as far north as the equator during its nonbreeding season. Although the actual bases for these fascinating patterns remain relatively unexplored, they suggest a greater sensitivity of northern avifaunas to factors that threaten moderate and long-distance migrants off their breeding grounds.

Long-distance migrants accomplish truly stunning feats. Blackpoll warblers (*Dendroica striata*), weighing only 10 to 20 gm, embark from Cape Cod on a nonstop, 86 hr, 3500 km flight 2000 m above the waves of the Atlantic to the northeastern coast of South America. Tundra-breeding shorebirds such as the Pacific golden plover (*Pluvialis fulva*) make nonstop 5000 to 7000 km journeys to wintering grounds in the South Pacific. Arctic terns (*Sterna paradisaea*) have the longest migration of any bird, and perhaps any animal, traveling an annual circuit that can exceed 40,000 km. They breed in the boreal summer along the northern edges of the Old and New World continents, then migrate along

the western edges of North America, South America, Europe, and Africa to feed in the rich waters off Antarctica's pack ice during the austral summer. Close to 8 months of each year are spent in transit between these two endpoints.

The Arctic tern's migratory journey seems extraordinary but it typifies why many birds migrate. In doing so, they exploit highly seasonal flushes of food resources, especially to meet the increased demands of breeding. High variability in food supply at higher latitudes, especially in insects and other invertebrates, makes it difficult for species to reside permanently in the habitat. However, the very predictable nature of these fluctuations allows mobile species to rely on them for part of their annual cycle. The absence of resident competitors may make these ephemeral resources even more abundant and accessible to migrants. Thus, the typical migratory movement for birds involves making an annual round trip between seasonally resource-rich breeding sites and nonbreeding areas where resource abundance may be lower but less variable over time.

Seasonal resource variability explains why many birds migrate, but what determines how far they go and where their final destinations lie? Proximal determinants of migration distance and route include weather patterns, history, the distribution of resources along the way, and the character of the landscape. The north-south orientation of mountain ranges in North, Central, and South America tend to funnel migrants along corridors also running north-south, whereas Eurasia mountain ranges run east-west, forcing many Palearctic migrants to make large westerly movements before they are able to fly south. The importance of trade winds or winds generated by weather fronts to migratory journeys can be seen in the often very different routes followed when moving north versus south (e.g., Arctic tern study by Alerstam). The migratory path of the white-rumped sandpiper (*Calidris fuscicollis*) extends the length of the Western Hemisphere and appears carefully choreographed to coincide with seasonal pulses of invertebrate prey along the route. History too seems to shape migratory paths and destinations as suggested by the very indirect route (via the eastern Mediterranean) taken by red-backed shrikes (*Lanius collurio*) migrating from the Iberian Peninsula to their nonbreeding range in Central Africa.

Habitat suitability is a more ultimate determinant of migration distance and destination. Species with very specific habitat requirements may have limited options for suitable nonbreeding areas. For example, the upland sandpiper (*Bartramia longicauda*) breeds in North American grasslands and must travel 10,000 km to over-

winter in the pampas of Argentina—the only similar Southern Hemisphere grassland habitat in the New World. Many tundra-breeding shorebirds migrate to the southern coastlines of South America, Africa, Southeast Asia, and Australia where extensive intertidal mudflats and rocky beaches provide abundant invertebrate prey. Most neotropical migrants—the warblers, flycatchers, vireos, swifts, hummingbirds, swallows, tanager, orioles, and raptors—migrate more moderate distances to forest and scrub habitats in Central America, the West Indies, and northern South America. In addition to the general structure of the habitat, competition with resident forest species and other migrants certainly influences where migrants settle during their nonbreeding seasons.

Often the question of how far migrants move depends on which population one examines. Many migratory birds conduct “partial” migrations where some individuals migrate while others remain as year-round residents on the breeding grounds or move only short distances (e.g., European blackbird, *Turdus merula*). Different age and sex classes may pursue different migratory strategies, as in the dark-eyed junco of the eastern United States. Alternatively, all individuals may migrate but different populations travel different distances. A common pattern in this case is for higher latitude breeding populations to migrate the longest distances, “leap-frogging” beyond the migratory movements of lower latitude populations (e.g., fox sparrow, *Passerella iliaca*). Some sanderling (*Calidris alba*) populations migrate only a short distance from their tundra breeding grounds to overwinter in the northwestern United States while others travel 7500 km to nonbreeding areas in Chile. Apparently, the much greater energetic and exposure costs of migrating to South America are offset by much richer food resources and a more hospitable climate, so that the payoffs for each strategy are equivalent, and both short- and long-distance migrants persist.

The presence of both migratory and nonmigratory strategies in the same species underlines the opportunistic and flexible nature of bird migration. As environmental changes occur or as a species expands its range, migratory behavior can often adapt to fit the new circumstances. The European starling (*Sturnus vulgaris*) is a widespread, permanent resident of Britain today, yet in the 18th century starlings regularly migrated out of Britain to overwinter in warmer regions of Europe. Long-term climate change has presumably made Britain a more hospitable place for starlings to spend their winters. Conversely, several species resident year-round in Europe have extended their breeding ranges north

over the past century. These more northerly populations have developed full migrations to southern Europe for overwintering. Migrants may also establish nonmigratory populations along traditional migratory routes as resources become more abundant or habitats are altered, for example, the barn swallow (*Hirundo rustica*) in Argentina and the Canada goose (*Branta canadensis*) in eastern North America. With industrial parks in North America supporting extensive expanses of grassy lawns some Canada geese cannot only forage sufficiently well at temperate latitudes during the winter, but high levels of vegetative production during the spring and summer enable them to stay and breed.

A fascinating form of bird migration not related directly to food abundance is molt migration. It is particularly common among waterfowl that molt all their flight feathers simultaneously and thereby lose the ability to fly. To escape predation, they may migrate to coastal areas, large lakes, or far off-shore until their new feathers have grown in.

B. Mammals

Small (<5 kg), nonvolant mammals represent a large fraction of our planet's mammalian biodiversity—rodents alone account for 40% of all mammal species—yet very few species are known to migrate. Rather than leave highly seasonal habitats when resource abundances decline, many small mammals hibernate or reduce activity levels and wait for conditions to improve. Species known to migrate include lemmings in the arctic tundra and a variety of rats, mice, and shrews living on the Kafue River flats of Zambia studied by Sheppe. In both cases, these small mammals move several kilometers to escape flooding conditions as snow melts (lemmings) or rivers flood (Kafue mammals).

Migration occurs more commonly among a second, highly diverse mammal group, the bats (25% of all mammals). The ability to fly and travel large distances more efficiently than via terrestrial forms of locomotion must account in large part for this difference between bats and other small mammals. Fruit-eating bats in West Africa migrate 1500 km annually, following the movement of rains and the consequent pattern of fruit abundance. As in birds, different sex and age classes may migrate different distances; juveniles migrate further, perhaps trading-off reproduction for more abundant food and greater survivorship. Similar migrations tracking fruit, nectar, and insect abundances have also been found in Australia and the New World tropics.

Insectivorous bats breeding in the temperate regions of North America and Europe commonly migrate,

showing two distinct patterns of movement. Like many birds in these regions, species such as the Mexican free-tailed bat (*Tadarida brasiliensis*) and the hoary bat (*Lasiurus cinereus*) travel a maximum of 800 to 1700 km south to overwinter in warmer sites where their insect food can still be found. These individuals do not hibernate, but other individuals of the same species may make only part of the southward journey to hibernate at sites along the migratory route. The second migratory pattern involves movements of shorter distances (10–200 km), and more variable orientation, from summer ranges to particular winter hibernation roosts. For example, as Griffin discovered, the little brown myotis (*Myotis lucifugus*) hibernates in a few select caves and mine tunnels in northern New England, yet migrates usually less than 100 km back to summer ranges both north and south of these wintering sites. Seasonality determines the timing of migration in these species but the very specific requirements of hibernation, such as temperature stability, humidity, and protection from predators, drive migration distance and direction. It is not uncommon for 75 to 95% of the population in a large geographical area, or even an entire species, to migrate and hibernate in only a few caves. Both migratory patterns are particularly common among species that roost in trees during the summer, presumably because trees make very poor, exposed winter hibernation sites.

Among terrestrial mammals, migrations are most common, and most spectacular, in the ungulates, or hoofed mammals. In the Serengeti ecosystem of Kenya and Tanzania, more than 1 million wildebeest (*Connochaetes taurinus*) and several hundred thousand plains zebra (*Equus burchelli*) and Thomson's gazelle (*Gazella thomsonii*) migrate seasonally along a several hundred kilometer annual circuit. A spatially varying seasonal rainfall pattern, and the consequent growth in grass that it generates—the primary food of all three species—determines the migration's timing and route, although drinking water availability and salinity may also play important roles. Plains zebra and wildebeest populations elsewhere in Africa make similar migrations between wet and dry season grazing areas, but in smaller numbers. These species are not obligatory migrants, however, since resident, nonmigratory individuals can be found in most populations. Other ungulate migrations driven in part by seasonal food availability include the movements of caribou and reindeer (*Rangifer tarandus*) in the Holarctic region from tundra in the summer to taiga during winter. The more wooded taiga also provides greater protection from harsh winter conditions; eastern North American populations of "woodland" caribou do not migrate at all.

Ungulates in temperate regions often migrate altitudinally with the seasons, moving to lower altitudes in winter to avoid harsh weather, low food abundance, and low food accessibility due to deep snow. Such species include bighorn sheep (*Ovis canadensis*), elk (*Cervus elaphus*), mule deer (*Odocoileus hemionus*), and feral horses (*Equus caballus*) in the Nearctic and chamois (*Rupicapra rupicapra*) in the Palearctic. Migratory distances in these species are usually short. An interesting exception is the mule deer, where each individual or family has a definite summer and winter range yet the migratory route is often not the most direct link between them. Individuals have been observed to travel 150 km in straight-line distance, crossing six mountain ranges in a winding route to do so. Tradition appears to have a tremendous effect on defining seasonal ranges and migratory routes in this species.

For marine mammals, annual migrations are the rule rather than the exception. The baleen whales, or mysticetes, migrate the longest distances, some moving thousands of kilometers from tropical to polar waters and then back again each year. Northern and Southern Hemisphere populations both migrate in this way, but their opposite schedules prevent overlap in the tropics. Food availability and quality at higher latitudes drive the timing of these movements. During the polar summer, long day-lengths lead to phytoplankton blooms which, in turn, generate huge abundances of the zooplankton, such as krill, that baleen whales specialize on when feeding. The lipid content of krill and small fish prey, or energy per mouthful from the whale's perspective, also rises during the summer months. Indeed, polar waters provide such an amazingly rich food source that many species forego feeding the rest of the year, consuming enough during a 3-month summer binge to not only maintain themselves for the remaining 9 months but to complete a hemispheric round-trip and breed. Species such as the fin whale (*Balaenoptera physalus*) both mate and give birth 11 months later in warm, low latitude waters. Lactation lasts for 6 to 7 months and the calf is weaned on the summer feeding grounds; fat reserves for lactation just after birth may constitute 50 to 75% of a female's body mass. Lower thermoregulatory costs in warm water presumably allow the binge-migrate-and-fast strategies of baleen whales to be successful, especially since warm, tropical waters may also provide a thermal environment more conducive to calf growth.

Odontocetes, or toothed whales such as dolphins, pilot whales and beaked whales, may show regular seasonal movements between breeding and nonbreeding grounds, but long-distance migrations rarely occur. Most toothed whales feed on single food items like fish

and squid and, as a consequence, must feed every day to maintain themselves. Many have large feeding ranges through which they travel 20 to 60 km per day. Short-distance migrations typically occur when food abundance in an area changes seasonally, such as when fish schools move off-shore or concentrate in river mouths. Some Arctic odontocetes, such as the narwhal (*Monodon monoceros*) and beluga (*Delphinapterus leucas*), migrate short distances seasonally as the polar pack ice retreats and opens up calving grounds in warmer-water estuaries. When the ice returns, they move back with its advancing edge to deeper, ice-free waters. Only the sperm whale—the largest odontocete—migrates distances comparable to those seen in the baleen whales. Adult males move two to three times the distances of females, reaching richer feeding areas at higher latitudes in order to achieve and maintain their much larger body sizes.

Among pinnipeds, 44% of phocid (true or hair seals) species migrate seasonally while only 14% of otariids (fur seals, sea lions) do so. This difference may arise from the phocid's greater reliance on seasonally changing pack ice, rather than solid land, as a substrate for giving birth, raising young, and molting. For example, harp (*Phoca groenlandica*) and hooded seals (*Cystophora cristata*) whelp on pack ice in March near Newfoundland, among other sites, then migrate north with the retreating pack ice to feed. Annual round-trips may cover 4000 km, although there is much variation in migratory distance and route among individuals and populations throughout the North Atlantic. Northern elephant seals hold the current record for the longest migration of any mammal: 18 to 21,000 km annually as they move twice between Californian islands used for breeding (January–February) and molting (July–August) to higher-latitude feeding areas rich in cephalopod prey. Northern fur seals, perhaps the only true migrants among the otariids, migrate in the opposite direction of most phocids, breeding at higher latitudes in the summer months and migrating south to temperate waters to overwinter.

Although clearly not mammals, sea turtles closely resemble pinnipeds in their migratory behavior. Adults migrate to specific island or continental beaches where eggs are laid. Hatchlings venture immediately to the sea where they may spend 30 or more years before maturing and returning to the same beach to complete the cycle.

Tropical marine mammals, such as dugongs and manatees, are generally nonmigratory, although the West Indian manatee (*Trichechus manatus*) population in Florida may move several hundred kilometers north in summer to exploit new feeding areas, retreating back

to warmer waters in the winter. Their need for warm water in which to overwinter has in some cases made them dependent on the warm-water discharges of coastal power plants.

C. Fish and Other Aquatic Species

Fish show a range of migratory patterns, both among different species and different populations of the same species. Migration is relatively common in this group, particularly as a means of linking rich feeding habitats with specialized spawning grounds that provide refuge for eggs and young fish. For diadromous species—the most studied and conspicuous migratory fishes—this journey requires moving from marine to freshwater environments in order to breed (anadromous: e.g., salmonids, shad, sticklebacks, lampreys) or, more rarely, the converse (catadromous: e.g., freshwater eels, southern trout, southern smelt). Anadromous species predominate in cold-temperate and subpolar waters in both hemispheres, while catadromous species more commonly occur in warm-temperate and subtropical waters. The benefits of moving from lower to higher productivity habitats to feed and grow may account for this pattern since marine productivity is higher at high latitudes while freshwater productivity is higher at low latitudes. Anadromous species constitute a higher proportion of total coastal fish diversity in the Pacific than they do in the Atlantic, largely due to the Atlantic's much higher coastal fish diversity overall.

As with marine mammals (e.g., baleen whales), migrant fishes with separate feeding and spawning areas must feed intensively and store sufficient energy reserves for both migration and spawning. Although many species migrate only a few kilometers between feeding and breeding sites, some fish migrations are truly remarkable in length (also discussed later). Upstream distances in diadromous species include 300 to 400 km in lampreys, 500 km in shad, and well over 1000 km in some salmon and sturgeons. Sockeye salmon migrating upstream expend 70% of their available energy in reaching the spawning grounds and the rest on spawning itself; not surprisingly, both sexes die shortly thereafter. The combined toll of fasting, migrating upstream, and spawning results in semelparity for most diadromous species, but some species, such as the Atlantic salmon (*Salmo salar*) and northern populations of American shad (*Alosa sapidissima*) may migrate and spawn more than once. The dramatic physiological transition required to move between freshwater and marine environments may also be a factor in the prevalence of semelparity among diadromous species.

Salmonid migrations typify anadromous life cycles,

but they also illustrate the very flexible migratory strategies of fish. Pacific salmon (*Oncorhynchus* spp.) spawn in streams at cold-temperate and subpolar latitudes on both sides of the Pacific. After hatching, they either (a) travel immediately downstream to the ocean or, (b) before migrating to the ocean, move downstream to lakes where they spend the next 2 to 4 years, or (c) remain in their hatching stream for one or more years. Once in the ocean, some species migrate the breadth of the Pacific to reach feeding areas while others remain closer to their spawning streams; accordingly, the time spent feeding and growing in the marine environment varies among species but is generally 2 or more years. The same species may have several distinct upstream migrations throughout the year. Further variation on this pattern is shown by individuals (e.g., sockeye salmon: *O. nerka*) that never migrate to the ocean but remain in lakes and move upstream to spawn with ocean-returning migrants. In contrast to other anadromous fish, such as shad and lampreys, salmonid ancestors resided year-round in freshwater and evolved the ability to migrate to marine habitats, perhaps accounting for the great variety of migratory strategies now seen in this group.

The best known catadromous migrants are the freshwater eels (*Anguilla* spp.). They occur throughout the world, including North America and Europe where most studies of their life cycles have been conducted. In North America, adult eels live in rivers and brackish estuaries from the Gulf of Mexico to Labrador, migrating into the Atlantic to spawn. The actual spawning sites still remain a mystery, but small larvae (leptocephali—once thought to be a separate species with no affinity to eels) have been found in the Sargasso Sea, suggesting spawning is here or very nearby. Over the first year, currents carry the leptocephali toward inshore habitats where they metamorphose into glass eels and leave the marine environment. After several years in fresh water, they are ready to migrate, spawn, and complete the cycle, dying after they spawn. Interestingly, adult females are found at greater distances from the spawning grounds—further up rivers, in lakes, and at higher latitudes—than adult males and should thus have greater costs of migration. Females also grow larger at maturity suggesting very different life history strategies for the two sexes.

Oceanodromous species, or those that migrate throughout the marine environment alone, often travel complex migratory circuits between sites optimal for different stages of the annual or life cycle. Ocean currents and coastal topography shape these movements, and those of prey items, adding further complexity to

the annual migratory pattern. For example, Atlantic herring (*Clupea harengus*) have numerous northern subpopulations, each with distinct spawning and feeding grounds and each following its own migratory route and schedule without intermingling to any great extent. Immature fish have separate migrations, moving inshore during warmer months and offshore to deeper waters during winter. Upon reaching maturity, they follow the migratory circuit of their parents. Other oceanic long-distance migrants include cod (*Gadhus morhua*) and plaice (*Pleuronectes platessa*) at higher latitudes and several tuna species in temperate and tropical waters. In most cases, these migration circuits are on the order of 1000 to 3000 km in diameter. Littoral migrations also occur commonly among oceanodromous species, but they are generally much shorter. Those species moving to track food resources usually move offshore in winter, while species migrating inshore during winter may do so to spawn in relatively predator-free habitats.

Species living solely in freshwater (i.e., potamodromous) commonly migrate from deep to shallow waters in order to spawn. A large variety of potamodromous fish migrate throughout the world's lakes and rivers, including freshwater rays, sturgeons, suckers, minnows, pikes, sunfishes, darters, perches, and catfishes. Shallower, upstream habitats may exclude certain predators or have water characteristics (e.g., oxygen, temperature, or silt levels) more suitable to the development and growth of eggs and young fish. The South American characin, *Prochilodus mariae*, has both non-migratory, lake-breeding and migratory, stream-breeding individuals within the same population. The observation that lake breeders expend five times more energy on egg production than stream breeders suggests that stream habitats provide sufficient benefits in offspring survival to compensate for the high energetic costs of migration.

Beyond fish and marine mammals, migration in aquatic animals is less common—or perhaps just understudied. Spiny lobsters in the family Palinuridae demonstrate a very curious migratory behavior, queuing up in long lines of up to 50 individuals that snake their way along the ocean bottom towards deeper, more sheltered habitat. These movements, as much as 30 to 50 km in length over several days, usually occur seasonally in response to a greater incidence of polar storm fronts, which bring colder water temperatures and greater wave disturbance to the shallow water habitats the lobsters feed in during warmer months. Migration thus allows spiny lobsters to exploit a resource-rich, yet seasonally stressful, habitat.

Plankton show distinct migrations in the water column driven by the seasonal availability of nutrients. During months of high productivity, plankton migrate to surface waters; as productivity declines, they return to lower depths and often enter into a state of diapause. Since changes in light work in concert with endogenous rhythms to set the schedule for these movements, the maximum depth reached during the nonproductive season will depend on how far light penetrates the water. In the Northeast Atlantic, typical maximum depths are 1200 meters. Seasonal planktonic migrations are most prevalent at higher latitudes and in regions where currents cause seasonal upwellings of nutrients. (Many planktonic species demonstrate diel vertical “migrations” in the water column, but because these constitute daily ranging movements rather than migrations by the definition given earlier, we do not consider them further.)

D. Amphibians and Reptiles

Amphibian life cycles often require a return to water to reproduce, resulting in migrations from feeding areas or refugia to seasonal ponds, streams, and other water sources. However, salamanders and anurans are not known for their great mobility and consequently most species do not travel far from where they were born. Red-bellied newts (*Taricha rivularis*) may hold the distance record for their migrations of 1 km from feeding range to breeding site. Similar migrations in anurans may extend several kilometers. Still, migrating anurans are remarkable for their fidelity to specific breeding sites and the precision with which individuals are able to return to the same few meters of shoreline each year.

Lizards very rarely migrate, but those that do also move to seek out suitable nesting sites. Green iguanas and a few related species that nest on islands may move as much as several kilometers to lay eggs at specific sites; the scarcity of appropriate soil in their island habitat presumably drives these migrations. The red-sided garter snake (*Thamnophis sirtalis parietalis*) migrates to winter hibernacula, such as limestone sinkholes, aggregating in the thousands to buffer the harsh winter conditions of Manitoba.

E. Insects and Other Terrestrial Invertebrates

Our current state of knowledge regarding insect migrations contains a number of spectacular examples but gives the overall impression that the phenomenon is

not common in this group despite its huge contribution to our planet's biodiversity. Well-known examples include the Eurasian milkweed bug (*Lygaeus equestris*) and the North American ladybird beetle (*Coleomegilla maculata*), which perform seasonal movements from summer feeding and breeding sites to more protected areas a few kilometers away. There they diapause and last out the winter surviving on stored fat. Individuals may coalesce at specific sites and form spectacular aggregations. As in other migratory species we have considered, migration allows both species to exploit rich, but seasonally variable, habitats. Because many insects have highly specialized feeding and breeding requirements, even small seasonal variations in temperature, moisture, and light levels may be sufficient to trigger migrations to sites where individuals can wait for local conditions to improve (i.e., diapause). The general migration pattern illustrated by ladybirds and milkweed bugs may thus be widespread among both temperate and tropical species. However, small insects are likely to migrate only short distances and be overlooked and understudied, especially if migrations occur without individuals aggregating into conspicuous groups.

An alternative migration pattern takes individuals from habitats declining in quality to richer sites that allowing feeding and breeding to continue. Among the noctuid, or armyworm, moths—a group found throughout the world—several species follow annual round-trip migratory circuits of several hundred kilometers that take them to successively higher latitudes or to habitats recently freshened by rain with host vegetation more suitable for breeding. In many cases, these species have become significant agricultural pests having a life history ideally suited to quickly exploiting ephemeral but rich food sources. Interestingly, single generations may complete only part of the migratory circuit, raising fascinating questions regarding the evolutionary genetics of migration timing and navigation. Perhaps the most famous migrant of this type is the monarch butterfly, *Danaus plexippus*, of North America. Monarch larvae feed on milkweeds and the timing of migration coincides with seasonal milkweed growth. In autumn, adult butterflies from as far north as eastern Canada migrate more than 1000 km south to overwinter in huge aggregations at only a few critical sites in the mountains of central Mexico. In spring, these same adults migrate 200 to 300 km to the northern edge of the Gulf of Mexico where they breed and die. Successive generations then move north tracking the milkweed growing season.

When large-scale migrations occur in insects, they are truly astounding behaviors if one considers the size

of the travelers and the distances covered. Because insects have only limited capacity for fuel storage, they depend more greatly than other migrants on winds to propel and direct their movements. North American aphids, for example, fly for 2 to 24 hours and travel from 50 to 1100 km before setting down. Differing wind speeds at different altitudes account for the variation in flight time and distance moved, but aphids probably exert some control over these features by choosing an altitude at which to fly.

In response to deteriorating local conditions, either due to seasonal reductions in food or increased densities, some insects develop long-winged (i.e., macropterous) forms able to travel relatively large distances to find more suitable habitat. Examples include planthoppers and aphids. These irruptive movements also occur in other taxa, such as birds, but they resemble dispersal processes more than the migrations we have so far considered.

Terrestrial crustaceans, such as hermit crabs and ghost crabs, must migrate from nonbreeding, feeding habitats to high-salinity water in order to breed. These movements occur seasonally, especially in response to tidal cycles, and may require movements from 10 to 3000 m each way.

IV. ATTRIBUTES OF MIGRANTS AFFECTING SUSCEPTIBILITY TO HUMAN DISTURBANCE

As we have seen, migrations appear to serve a few common functions. In general, they enable species to temporarily avoid harsh conditions or to meet important biological needs that are separated by great distance. Not surprisingly, there are certain attributes of migrants that affect their susceptibility to human disturbance.

First, migratory species often use a variety of habitats, leaving them vulnerable to multiple points of disturbance. Often harm is felt mostly at one destination. Bachman's warbler (*Vermivora bachmanii*), for example, was driven to extinction by the destruction of its overwintering habitats in the tropics. For others, however, such as many Neotropical migrant birds, the impacts of human activities are felt at both endpoints of their migrations. Globe-trotting species like the white-rumped sandpiper typify the precarious dependence of migrants on habitat health across a tremendous geographic scale. But harm need not be limited to the endpoints of a migrant's journey. Any diminution in

quality of refueling sites along the way could winnow a population and limit its ability to replenish its numbers before the next cycle of migration. And given that migratory trajectories for many species are shaped by the vagaries of prevailing winds or currents, conservation strategies entailing the protection of all stopover areas becomes almost impossible. Even where resting points are protected, unintended consequences associated with the normal nonintrusive behavior of naturalists can put migrants at risk. Steady viewing by bird-watchers at refuges along coastal fly routes has been known to force birds to move too far offshore where they can no longer feed on inshore marine invertebrates exposed at low tides.

Sea turtles probably illustrate best the effects of migratory species being vulnerable at many life-history stages to the excesses of human behavior. Not only are their eggs sought after and easily harvested by indigenous peoples, the beaches themselves are often degraded by the activities of affluent humans. Entire breeding populations are eliminated when beach habitats are developed or severely compromised in their abilities to launch young when dune buggies destroy nests or excessive night lighting disrupts the water-seeking behavior of newly hatched young. In addition, for those young that mature to subadults and return to the breeding grounds, nets of fishermen, particularly shrimpers, provide the *coup de gras* to the species by drastically reducing the pool of future breeders. In fact, it has been shown for that the most vulnerable period in the life cycle is not the nestling, but rather the subadult, stage. Although protecting beaches and increasing the number of functioning beaches gives the species a head start by diversifying recruitment sites, sea turtles are most vulnerable to extinction if the number of subadults is reduced. It is at this point in the species' life history where a long life of breeding commences and reproductive value is highest. Only by insisting that shrimpers insert turtle excluder devices (TEDs) in nets so that the turtles can escape before drowning will there be any hope that those migratory species already endangered will survive.

Second, migratory species often aggregate when traveling. While this behavior might reduce each individual's risk of falling prey to nonhuman predators, both aquatic and terrestrial species in groups are easy targets for the advanced harvesting gear employed by commercial fishers and hunters. In prehistoric times, hunters stampeded herd animals off cliffs and into canyons where massive kills occurred. Such actions have been implicated in the extinction of many of the North American megafauna. Today even the smaller, more elusive

and difficult to capture prey are at risk. Many marine fisheries involving migratory schooling fishes, such as those of cod and haddock, have been overfished. And despite moratoria, many are not recovering.

Third, since many migratory species move according to very precise schedules, any delays caused by human alteration of the habitat or disruption of normal movements could lead to a cascade of effects, jeopardizing a species' ability to replenish its population numbers reduced by ordinary mortality. As noted earlier, migrating shorebirds if forced to linger longer at refueling refuges, could have breeding seasons shortened sufficiently to lose the ability to lay one or more clutches. And since selection favors renesting because nest predation rates are already high, any force constraining such efforts could severely limit a species' recruitment potential.

Despite these attributes that threaten species survival there are some beneficial traits exhibited by migrants. By occupying, at least temporarily, many different habitats, migrants can spread risks and thus can escape catastrophes that befall one location. Unless all individuals in a species simultaneously occupy the same habitat, survivors from habitats not impacted by the catastrophe can serve as sources for increasing species numbers. Migratory species are also more likely to find and colonize new habitats as they are opened up by climate change or other human-induced and natural changes in the environment.

V. ECOLOGICAL CONSEQUENCES OF HUMAN DISTURBANCE ON MIGRANTS

As humans fragment landscapes, many migratory species will find themselves in peril. For species that must move from one region to another in order to meet a variety of biological needs, any barrier disrupting these movements could lead to local extinctions. In southern Africa, fences are being built either to prevent mixing of wildlife and livestock and the concomitant transmission of disease (ensuring that exported beef is disease free) or to prevent wildlife from gaining a competitive edge over livestock when both compete for critical resources such as food near water. Without access to these resources at the time of year most critical for developing juveniles, any migratory population's recruitment will be severely curtailed. Many local populations will either go locally extinct or will be transformed from "sources" of new emigrating individuals to "sinks" where excess individuals from healthy populations find

refuge. Even for populations that still boast numbers in the hundreds of thousands, such as the plains zebra or even African elephants (*Loxodonta africana*), fragmentation of the large populations is well underway. With human populations expanding into habitats only marginally suited for horticulture, the cry for fencing areas to prevent crops being consumed by migrating herbivores is increasing.

When the movements of these populations are disrupted, a cascade of indirect effects on both the recycling of nutrients in ecosystems and the structuring of animal communities are likely to occur. Since migratory species represent some of the largest aggregations and highest densities of individuals seen in the animal world, any disruption to migration is likely to reduce local density. Thus it is quite possible that the important impact on the structure of vegetation, or more generally the recycling of nutrients, will be altered. It has even been proposed that the overharvesting of sperm whales and the removal of their large carcasses from the ecosystem have impacted the community stability of the deep-sea communities associated with deep-sea vents. By preventing carcasses from falling to the ocean floor, an important source of renewing "island" resources has been eliminated, thus making it more difficult for species tightly associated with vents to hop from one vent to another. With respect to structuring communities, if plains zebras are unable to move in large numbers across the landscape from the tops of catenas where they forage during the rains to the wetter valleys where they move when the rains cease, then their facilitative effect on diversifying the herbivore community will be reduced. Typically, plains zebra move to the wetter valleys and graze down the tougher, fibrous forage that dominates these areas making the greener and more nutritious forage available for the ruminants that require such higher quality vegetation. Thus by disrupting the movements of such a "keystone" species, the diversity of large grazers could be reduced. Furthermore, exclosure experiments suggest that the grazing community could shift from one dominated by large ungulates to one populated by small rodents and lagomorphs. Since rodents often come in contact with people and harbor human diseases, the cascade of effects could be quite profound.

Perhaps one of the greatest impacts of disrupting movements will be seen via the effects that elephants have on the landscape. As populations become restricted to reserves if their numbers are allowed to increase, then their ability to transform a mosaic landscape of trees and grasslands into one of mostly grasslands will mean the disappearance of resident for-

est and woodland dwelling species of colobine monkeys and antelopes.

Even for those subdivided populations that can adapt to the nonmigratory habit—and in certain places such as the Ngorongoro Crater in Tanzania, resident and migratory populations of zebra, Thompson's gazelle, and wildebeest coexist—genetic effective population sizes will shrink and the loss of heterozygosity could leave the population vulnerable to the emergence of novel diseases or the devastating effects of inbreeding. The trend to isolate migratory wildlife into reserves that are too small, although serving as an immediate panacea to human population expansion and development, could have adverse long-term consequences for the health and survival of species unless they are designed to be of appropriate size or have appropriate corridors for migration included in their design. The creation of multinational parks in South Africa, Mozambique, and Zimbabwe that include important mixes of habitats required by a wide variety of migratory species is on the drawing board and offers some hope that subdivision and isolation of populations will be reduced.

Migratory species are also likely to be directly affected by global climate change. It has been suggested that the arctic tundra as a habitat might disappear. If the upper 2 to 3 m of permafrost, which helps bind the tundra together, were to disappear, then the tundra as a habitat would vanish. The effects would drastically reduce populations of caribou that traverse large distances across it as they move from summer breeding to more protective wintering feeding sites. Such transformations of animal communities have occurred in the past when climates have dramatically changed and migratory species were excluded from important parts of their ranges. For example, much of the Canadian-Alaskan megafauna vanished 10 to 20 million years ago when the forests closed and sedge and other patchy but nutrient-rich herbaceous species disappeared. But the scope of these impacts are likely to be greater in the near future because both the magnitude and rate of change associated with the climate effect is increasing and is being coupled with widespread land-use changes that are occurring in areas where the migrants will be forced to move.

VI. EVOLUTIONARY CONSEQUENCES OF HUMAN IMPACTS ON MIGRANTS

While it is clear that human behavior disrupting migrations will have ecological consequences, the effects on

the evolutionary potential, or even the future characteristics, of species are also likely to be large. Nowhere is this impact more evident than in North America where the range of the bighorn sheep has been severely reduced and fragmented. Bighorn migrate seasonally from meadows to mountaintops to avoid harsh climate and in search of grass that changes seasonally in quality at each location. As human populations have expanded, populations have been isolated into refuges, numbers are shrinking, and genetic diversity is being lost. In addition, hunting for trophy males is removing just those individuals with the best and most diverse genotypes. As a result, the ability of the isolated populations to remain genetically diverse enough to forestall problems associated with inbreeding or to avoid the ravages that would occur if a novel disease appeared has been severely compromised.

Migratory Atlantic salmon (*Salmo salar*) provide perhaps the clearest example of where human activities are causing a species to change under our own eyes. Atlantic salmon typically are born in fresh water and develop for 1 to 2 years before smolting and heading to sea to grow and fatten by feasting on a rich supply of marine invertebrates. Once they attain a certain size, they become sexually mature and return to rivers. There they travel long distances upstream until they reach clear and cool breeding grounds. Some individuals, however, never head to the sea. Instead, they remain in their natal streams and mature sexually at young ages and at small sizes. Such individuals are called parr and they never go through the smolting process that adapts them to a marine lifestyle. Under pristine environmental conditions, the fraction of the population that becomes parr is small since the reproductive gains of such a strategy are low. When competing for mates with larger more aggressive males, parr fare poorly. What matings they obtain are derived by "sneaking" among a mating pair and releasing milt at just the right time. Such events are rare and the mixing of milt is poor so such sneak matings result in few young being sired by parr. But the survival prospects of parr are high since they do not incur the risks of going to sea and, moreover, they begin breeding at a very early age. Thus over a lifetime, reproductive success is modest. But as human fishing increases and the netting of the older larger salmon intensifies, the *relative* lifetime reproductive success of parr is improving. Since the costs of migrating to sea and back again have increased dramatically, the long life span of parr gives them a relative advantage. And given that competition with the larger males for mates is also declining, the chances of parr securing matings are also improving. Thus it is not

surprising that the composition of the population is changing as parr increase markedly in abundance. The impact on the long-term stability of the population is unclear. But the long-term impact on the species appearance is clear, just as it is for yet another fishing industry that will go into decline as the large fish disappear.

See Also the Following Articles

ARCTIC ECOSYSTEMS • BIRDS, BIODIVERSITY • DISPERSAL
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