recording of local environmental parameters offer to provide complementary streams of extremely valuable information that will allow researchers to obtain an increasingly accurate picture of how migrating animals make movement decisions, and to do so across species boundaries. It is vital, therefore, that we bring together researchers from diverse disciplines to gather and integrate the knowledge that will prove essential if we are to conserve migratory populations in the face of increasing anthropogenic pressures.

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Primer

Conservation of migratory species

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Were you to find yourself somehow transported to the American Midwest in the 18th century, one feature that might strike you would be a curiously shifting cloud approaching from the northeast. As it drew closer, you might begin to discern some sound, "[like] an army of horses laden with sleigh bells" in the words of a Potawatomi Native American. However, not until it was nearly upon you would it become apparent that this cloud was made up of billions of individual birds. This was the autumn migration of the passenger pigeon (*Ectopistes migratorius*), the most abundant bird to ever be found in North America and perhaps in the world (Figure 1). By some estimates, the number of passenger pigeons in North America at the time of European colonization was greater than the combined number of all birds of all species found on the continent today. Yet, by the beginning of the 20th century, passenger pigeons had effectively been eradicated, in large part due to the extraordinary keenness with which they were hunted. By 1914, 5 billion birds were gone and the last passenger pigeon, Martha, died in the Cincinnati Zoo. Passenger pigeons represented an extraordinary example of one of Earth's great natural phenomena: the annual migration of organisms. They also highlight the potential vulnerability of migratory species. These seasonal movements are not only awe-inspiring; they are also critical for the health of countless species and ecosystems.

Human understanding of animal migration has been developing remarkably slowly. As late as the 17th century, many hypotheses about migration, such as the belief that birds undertook yearly migrations to the moon, reflected human creativity more than any empirical evidence. Our understanding of migration has improved substantially over the past century, particularly with the advent of tracking technologies. However, there remains much to discover about migration. Even the movement patterns of Earth's largest animal, the blue whale (*Balaenoptera musculus*), remain poorly understood. Unfortunately, just as we are coming to appreciate the scale and significance of animal migrations, many migratory species are experiencing substantial population declines as a result of habitat loss, overexploitation, climate change and other anthropogenic stressors. Some conservation strategies give hope for optimism, but far more conservation work is necessary to protect Earth's great travelers.

The migratory lifestyle

Migration is a temporally repeated movement undertaken by part or all of a species' population. It differs from other forms of movement in several important aspects. Unlike nomadic movement patterns, migration is repeated over a regular time interval, at least at the population level, and is often linked to seasonal patterns in temperature or precipitation. Additionally, while many non-migratory species may move substantially over the course of days or weeks within a well-defined home range, migration represents a purposeful departure from an established territory. The abandonment of familiar surroundings and the greatly amplified energetic cost mean that migration is often risky and marked by higher rates of mortality.

Migratory behavior is found across all types of animal and comes in a number of different forms. Migratory distances, for example, can vary enormously. The most substantial migration yet recorded is that of Arctic terns (*Sterna paradisaea*), with some individuals travelling over 80,000 kilometers in a single year. On the more modest end of the spectrum is the cricket frog (*Acris crepitans*), which may venture only a dozen meters or so from its native pond before returning to breed.

The number of times one individual in a given species migrates varies as well. Most avian or mammalian migrants will travel twice per year,

Figure 1. A taxidermied passenger pigeon.
Passenger pigeons (*Ectopistes migratorius*) were once abundant migrant birds, but were hunted to extinction in the early 20th century. Photo: © Jim, the Photographer/Flickr.

once in the spring and once in the fall, and they will continue this pattern annually throughout their lives. Other taxa, like spawning salmon, will only migrate once during their life in order to reproduce. In some migratory species, no single individual will live to complete the entire journey. For example, monarch butterflies (*Danaus plexippus*) in North America depart from the mountains of Mexico in February, spend the summer in the United States and Canada, and return to Mexico the next winter. During this time, 3–4 generations of monarchs will come and go, each completing one segment of the journey before producing offspring to take up the next leg in a grand international, inter-generational relay (for more on monarch migration, see the review by Reppert and colleagues in this special issue).

For many animal species, migration is essential for survival. Oceanic fish that spawn in inland rivers hatch physiologically adapted to fresh water and would not survive if their eggs were laid in a marine environment. However, the conservation of migratory species is of importance beyond the species' own well-being. Because they often travel great distances and interact with many different habitats along the way, migrants are excellent dispersal vectors for seeds, fungal spores and other less mobile organisms. Some species of bird consume higher-than-normal levels of seeds during migration, and many species of plant respond by timing their seed production to coincide with bird migrations. *Lindera* plants in North America, for example, time their fall fruiting to when many opportunistically frugivorous birds, such as hermit thrushes, are passing through. The long-distance transport of seeds by migrating animals allows plants to disperse across latitudinal ranges, helping them to cope with a warming climate. Animal migrations can also act to move vital nutrients from one habitat to another. Millions of salmon leave the ocean each year and travel up freshwater streams to breed. In doing so, they act as a vitally important food source for many upland species of animals. Additionally, after the salmon spawn and die, their decaying carcasses deposit hundreds of millions of tons of nutrients, which are taken up by plants and invertebrates throughout the rivers and surrounding forests. More than 6000 wildebeest dying during their migration every year contribute even more biomass and nutrients to the Mara River.

Many migratory species have important functions for human society as well. In addition to ecosystem services, such as pollination and pest control, the rise of ecotourism, often with the express purpose of seeing migratory animals, has grown into a multi-billion-dollar industry. In 2008, for instance, 13 million tourists took whale-watching trips, spending a collective $2.1 billion. In many developing nations, ecotourism is the fastest growing sector of the economy.

In some cases, a migratory lifestyle may help buffer a species against negative anthropogenic factors. Migratory species often have a greater dispersal capability than sedentary species and this can allow them to find new habitats should their previous home range become degraded or lost altogether. For example, approximately 17% of migratory bird species are extinct, threatened or near threatened with extinction, compared to 28% for sedentary and resident bird species (Figure 2). However, migratory species can face unique challenges as a result of traveling. The most notable is the migrants' reliance on multiple, often geographically distant habitats. This means successful conservation of migrant species must include the protection of all parts of a species' migratory range. Some areas may only be used for a brief period during migration as a temporary resting spot to find

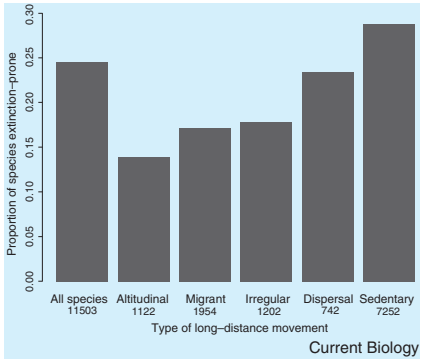

Figure 2. Proportion of world's bird species extinct, threatened or near threatened with extinction based on pattern of movement.
Numbers below movement types indicate total number of species in that group based on the taxonomy of the IOC World Bird List (www.worldbirdnames.org). To compare the increases in the numbers and proportions of extinction-prone species in the past decade, see Şekercioğlu (2007) Curr. Biol. *17*, R283–R286.

Figure 3. Migrating zombie crabs.
Migrating zombie crabs (*Gecarcinus ruricola*) in Cuba must cross several roads during the course of their short migrations and millions are killed each year.

food and shelter. Because of this brevity, conservation of these areas has been traditionally overlooked. However, without these sources of food and rest, many species would be unable to complete their epic treks. Additionally, the different habitats that migrants require often span several political entities. This means inter-governmental cooperation is an important, but often challenging, aspect of migrant conservation. The protection of just one population of great reed warblers (*Acrocephalus arundinaceus*), for instance, can entail coordinated efforts between the governments of at least 17 nations, including Turkey, Syria, Iran, Iraq, Saudi Arabia, Yemen, Sudan, South Sudan, Eritrea, Ethiopia, and Somalia, and across many conflict zones. In order to address the principal threats faced by migratory animals, these hurdles of geographic distance and international coordination must be overcome. In fact, the catastrophic level of hunting of migratory birds, including millions of songbirds, across the Mediterranean basin, North Africa and the Middle East is one of the biggest threats to migratory species worldwide.

Threats to migratory species

On a broad scale, the principal threats facing migratory animals are the same as for sedentary species, especially over-exploitation, habitat loss and climate change. However, the mechanisms by which these stressors imperil migrants differ between species and they can often interact to exacerbate conservation issues.

In the past, overexploitation has been the largest driver of wildlife loss, for migrants and non-migrants alike. Passenger pigeons, as noted earlier, disappeared completely in early 20th century due in part to uncontrolled hunting. Even some extant migratory species are only a shadow of their former populations. Before European settlers hunted their way across North America, there were perhaps as many as 35 million pronghorn (*Antilocapra americana*) and 50 million American bison in the wild. These species used to make long journeys across the prairies and served a key role in the health of prairie habitat. By the mid 19th century, both populations had dwindled to only a few thousand individuals. Today these species have recovered somewhat but they no longer engage in long-distance migration. Migratory animals are at a particular disadvantage when it comes to hunting. Because they repeatedly use the same migratory routes, it is much easier for hunters, both legal and illegal, to predict where game will be. In addition, migration may carry a population out of a protected area and into regions where hunting pressures are far greater.

Many migratory species are under extreme threat from habitat loss, particularly those that congregate in small areas. In China, thousands of Siberian cranes (*Leucogeranus leucogeranus*), the vast majority of the global population, spend the winter at or near Poyang Lake. Drought and water management in the region have already degraded the cranes' critical riparian habitat, forcing them to forage in suboptimal areas. Now, a proposed dam at the outlet of the lake threatens to further diminish the quality of the restricted area these birds rely on.

While habitat loss can negatively affect migratory species by eliminating important areas on which the animals depend, migratory animals also face an additional and unique threat: the impediment of movement along migratory routes. Roads, fences, dams and urban sprawl can create insurmountable obstacles for migrating animals that are already under severe energetic pressure as a result of their lifestyle. Runs of Pacific salmon (*Oncorhynchus* sp.) are about 5% of their historic levels due in large part to widespread damming of rivers in the western U.S. Similarly, crabs on Christmas Island and Cuba must cross several roads during the course of their short migrations and millions are killed each year (Figure 3). This has been enough to cause some breeding populations to vanish.

Climate change is becoming increasingly threatening. Climate change imperils migrants in a number of different ways. First, as many species change their phenology in response to a rapidly changing climate, mismatches in ecological synchronization are all but inevitable. For instance, pied flycatchers (*Ficedula hypoleuca*), which winter in sub-Saharan Africa and breed in Europe, have been unable to advance their spring migratory schedule at the same pace at which their insect prey have begun hatching earlier in northern latitudes. The result has been a dramatic decline in pied flycatcher populations.

Likewise, warming oceans may be causing declines in populations of plankton prey on which whales and other species rely. Gray whales (*Eschrichtius robustus*) migrating in the eastern Pacific have lower than normal fat reserves, imperiling their ability to undergo such arduous treks. Climate change also has the potential to severely alter precipitation patterns, diminishing the suitability of current migratory ranges. Gazelle, wildebeest and zebra in east Africa migrate in vast numbers, with millions of individuals traveling across the savanna (Figure 4). Their movements are tied to seasonal rainfalls and resulting vegetation. If precipitation patterns change such that this seasonal productivity is much reduced, then the great African ungulate migrations may disappear.

Overexploitation, habitat loss, and climate change do not act in isolation to imperil migratory species. Often, they synergize in catastrophic ways. Many species of turtle, for instance, are common victims of commercial fishing bycatch with hundreds of thousands of individuals inadvertently killed each year. Those that survive still have to deal with the beaches on which they breed being threatened by development and rising sea levels. The increases in energy expenditure during migration may make species particularly vulnerable to these threats.

Reasons for optimism

Though the overall trajectory for migratory populations has been discouraging, there are some hopeful examples of conservation success. Governmental regulation banning or reducing hunting has allowed many once scarce species to rebound. In the 19th century, whales were hunted to the brink of extinction. After the International Whaling Commission banned commercial whaling in the 1980s, many species have made a steady, if slow, recovery.

Protected areas may help alleviate the pressures of habitat loss, especially when designed to help facilitate movement. Increasing effort is being placed on habitat connectivity and reducing potential migratory barriers. Connected urban parks permit migrants to move through developed areas, and wildlife overpasses allow animals to cross highways safely. In Europe, volunteer organizations even help shuttle migrating common toads (*Bufo bufo*) across roads.

Every year, billions of organisms take to the air, to the sea and to waving grasslands on their grand migrations. They travel over mountains and across deserts, from wetland to scrubland to tundra. Some will traverse oceans, and others, small mountain ponds. An Arctic tern may see the North Pole in July and the South Pole in January, while a single Atlantic krill in the same period will travel a few hundred feet up a water column. Animal migration ties the world together in a way that no other natural phenomenon does. In the last few centuries, humanity has increased both the research and admiration of these inspiring migrations, as well as the rate at which we are threatening their populations. Coordinated efforts between scientists, citizens, and decision-makers can reverse negative trends in migrant species. However, continually building pressures require much greater efforts and coordination to preserve Earth's migrations.

Figure 4. A herd of Blue Wildebeest (*Connochaetes taurinus*) migrating through the Serengeti National Park, Tanzania.
Every year, nearly two million Blue Wildebeest undergo massive migrations from southern Tanzania to southern Kenya. They appear to make these movements based on seasonal patterns of rainfall and subsequent plant growth. These migrations are crucial to ensure that calving mothers have enough food for their offspring but fences, roads, and other barriers to movement make these journeys increasingly difficult.

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