

CLIMATE CHANGE AND ANIMAL MIGRATION

BY

THOMAS T. MOORE*

Animal migrations are important to the healthy function of many ecosystems. When biotic and abiotic cues are altered by climate change, migrations may be disrupted. Climate change has the potential to disrupt these migrations by altering habitat, changing resource availability, increasing habitat disturbance, changing phenology, and stopping migration. The act of migration (i.e., potentially travelling long distances) causes species to confront a wide range of climatic changes that make adaptation especially difficult. Future research goals should strive to obtain long-term data on migrations and better understand how—and whether—migratory species adapt to changes in climate. Future management techniques should strive to maximize the ability of the target species to adapt to climate change by providing species with more options (e.g., protecting alternative migration corridors) to react to changes in their habitat.

I.	INTRODUCTION	394
II.	CLIMATE CHANGE EFFECTS ON ANIMAL MIGRATION	396
	A. <i>Habitat Alteration</i>	396
	B. <i>Changes in Resource Availability</i>	397
	C. <i>Increases in Disturbance</i>	398
	D. <i>Changes in Phenology</i>	401
	E. <i>Migration Cessation</i>	403
	F. <i>Spatial Variability in Climate Change Effects</i>	404
III.	CONCLUSION	404

* Associate Instructor, PhD Candidate, Environmental Science, Indiana University School of Public and Environmental Affairs; M.A. Forestry, Tottori University, Japan, 2007; B.A. Biology, Murray State University, 2001. I would like to thank Michael Moore, Thomas Hill, Sabra Moore, and Vicky Meretsky for their insightful comments on earlier drafts. I also wish to thank Tokiko for her support, patience, and hard work, without which I could not have completed this project.

I. INTRODUCTION

Migrations are recurrent movements between habitats that often take advantage of seasonally productive habitat during the breeding season.¹ Migrations span a range of movements from long, cross-continental movements to comparatively short movements of a few hundred meters. Animal migrations are essential to the healthy function of many ecosystems by facilitating dispersal of plant species, cycling resources between locations, and allowing life to persist in some of the most extreme locations on earth.² Conditions in areas such as savannah, boreal forest, and alpine regions can be extremely harsh for much of the year, but do have brief periods of high resource productivity.³ Through migrations, species can take advantage of these productive periods while escaping the harsh periods.⁴ However, climate change may alter the dynamics of the habitats and processes on which migration depends. Due to their interactions with their environment, migrating species can be especially sensitive to climate change.⁵ While there has been much work on the effect of climate change on biological systems in general,⁶ few studies have attempted to gather that information and apply it to how climate change will affect migrations.

Climate change is predicted to have many varied impacts on species around the world.⁷ In this Introduction, I will discuss how climate change is predicted to impact biological systems in general. In the following Parts, I will provide more detail on how those impacts are most likely to be significant to animal migrations. Finally, in the Conclusion I will describe what scientific research and management techniques are needed to confront these effects.

¹ See D. Aidley, *Questions About Migration*, in ANIMAL MIGRATION 1–6 (D. J. Aidley ed., Cambridge Univ. Press 1981) (choosing a definition of migration that focuses on the change of habitat and the corresponding change in conditions of the animal's life and discussing factors that initiate migration); Rebecca A. Bartel et al., *Monarch Butterfly Migration and Parasite Transmission in Eastern North America* ECOLOGY SOC'Y AM. (forthcoming 2011) (manuscript at 3) available at <http://www.esajournals.org/doi/pdf/10.1890/10-0489.1>; T. R. E. Southwood, *Migration of Terrestrial Arthropods in Relation to Habitat*, 37 BIOLOGICAL REVIEWS 171, 174 (1962).

² Heather Reynolds & Keith Clay, *Migratory Species and Ecological Processes*, 41 ENVTL. L. 371, 374–378 (2011).

³ See W. J. Chen et al., *Effects of Climatic Variability on the Annual Carbon Sequestration by a Boreal Aspen Forest*, 5 GLOBAL CHANGE BIOLOGY 41, 51 (1999).

⁴ D.J. Aidley, *Questions About Migration*, in 13 SOCIETY FOR EXPERIMENTAL BIOLOGY SEMINAR SERIES: ANIMAL MIGRATION 1, 5–6 (D.J. Aidley ed., 1981); see Vicky J. Meretsky, Jonathon W. Atwell, & Jeffrey B. Hyman, *Migration and Conservation: Frameworks, Gaps, and Synergies in Science, Law, and Management*, 41 ENVTL. L. 447, 458 (2011).

⁵ D. Harvell et al., *Climate Change and Wildlife Diseases: When Does the Host Matter the Most?*, 90 ECOLOGY 912, 916 (2009).

⁶ See, e.g., Camille Parmesan & Gary Yohe, *A Globally Coherent Fingerprint of Climate Change Impacts Across Natural Systems*, 421 NATURE 37, 37–41 (2003).

⁷ See *id.* at 37; Gian-Reto Walther et al., *Ecological Responses to Recent Climate Change*, 416 NATURE 389, 389 (2002).

The most well-known impact of climate change is an increase in temperature.⁸ The temperature mean and variability are predicted to rise, so the average temperature will be hotter while temperature extremes also become more severe.⁹ In addition, precipitation patterns are calculated to change around the world, with much more rainfall in some regions while other areas will receive much less.¹⁰ Projecting exactly how precipitation patterns will change in the future is exceptionally difficult, with similar global circulation models¹¹ predicting different results.¹² Through the interaction of temperature and precipitation changes, water availability is predicted to decrease—even if it rains more—because evapotranspiration¹³ will increase with increased temperatures.¹⁴ In addition, glaciers and alpine snow pack will melt at accelerated rates, decreasing the sources of water that have sustained mountain streams and lower elevation rivers for thousands of years.¹⁵

The spatial variability¹⁶ of climate change impacts will be large. This is one reason why climate change is so difficult to manage for and predict. Some areas will become drier, others will become wetter.¹⁷ Some areas will become much hotter, while others may change only a little. However, evidence shows that colder regions (i.e., montane and poleward regions)

⁸ See Walther, *supra* note 7, at 389.

⁹ INTERGOVERNMENTAL PANEL ON CLIMATE CHANGE, CLIMATE CHANGE 2007: IMPACTS, ADAPTATION AND VULNERABILITY 41 (Martin Parry et al. eds., 2007); see also Camille Parmesan, *Ecological and Evolutionary Responses to Recent Climate Change*, 37 ANN. REV. ECOLOGY, EVOLUTION & SYSTEMATICS 637 (2006) (discussing the impact of gradual temperature change and increasing frequency of extreme events on species in various regions); Stefan Rahmstorf et al., *Recent Climate Observations Compared to Projections*, 316 SCIENCE 709, 709 (2007) (comparing climate data to Intergovernmental Panel on Climate Change projections).

¹⁰ J. Sillmann & E. Roeckner, *Indices for Extreme Events in Projections of Anthropogenic Climate Change*, 86 CLIMATIC CHANGE 83, 101 (2008).

¹¹ Also known as a global climate model, it is a complex computer simulation that is used to predict future climatic conditions for an (often large) area.

¹² D. A. Stainforth et al., *Uncertainty in Predictions of the Climate Response to Rising Levels of Greenhouse Gases*, 433 NATURE 403, 405 (2005).

¹³ Evapotranspiration is a contraction of the words evaporation and transpiration. The term is used to describe the amount of water that is lost into the atmosphere from the soil (evaporation) and lost from the surfaces of plants (transpiration). WEBSTER'S THIRD NEW INTERNATIONAL DICTIONARY 787 (2002).

¹⁴ INTERGOVERNMENTAL PANEL ON CLIMATE CHANGE, *supra* note 9, at 90–92; see Wolfram Schlenker, W. Michael Hanemann & Anthony C. Fisher, *Water Availability, Degree Days, and the Potential Impact of Climate Change on Irrigated Agriculture in California*, 81 CLIMATIC CHANGE 19, 32–33 (2007) (describing hydrological studies indicating how increased annual precipitation may actually result in decreased seasonal runoff).

¹⁵ INTERGOVERNMENTAL PANEL ON CLIMATE CHANGE, *supra* note 9, at 83–88; see, e.g., Ryan J. MacDonald et al., *Assessing the Potential Impacts of Climate Change on Mountain Snowpack in the St. Mary River Watershed, Montana*, 11 J. HYDROMETEOROLOGY (forthcoming 2011) (manuscript at 3, 15–17), available at <http://journals.ametsoc.org/doi/abs/10.1175/2010JHM1294.1>; T. P. Barnett, J. C. Adam & D. P. Lettenmaier, *Potential Impacts of a Warming Climate on Water Availability in Snow-Dominated Regions*, 438 NATURE 303, 306 (2005).

¹⁶ Difference in impacts across distance.

¹⁷ See INTERGOVERNMENTAL PANEL ON CLIMATE CHANGE, *supra* note 9, at 152 tbl.2.2.

have been most strongly affected by climate change and will likely continue to be.¹⁸

The result of all these impacts will be a likely reduction in primary productivity¹⁹ and the creation of “novel ecosystems” unlike anything in recorded history.²⁰ Diets will shift as the quality and type of food is altered. There will be other changes in community interactions as species composition and habitat types are transformed in reaction to climate change.

II. CLIMATE CHANGE EFFECTS ON ANIMAL MIGRATION

Climate change will affect all species, and migratory species will be confronted with many of the same climate change driven issues that non-migratory species must confront. However, due to their reliance on migration, migratory species may feel the effects of climate change in novel ways. When biotic or abiotic²¹ cues are altered by climate change in a way that organisms cannot correctly interpret or adapt to, migrations will be disrupted. As a corollary, since migratory species track seasonally available resources,²² if climate changes in such a way that resources—such as food or water—become reliably available throughout the year in one location, a species might cease migration and remain with the resources. In the following Parts, I will describe some of the ways migrants’ biotic and abiotic cues are being altered by climate change.

A. Habitat Alteration

Climate change is predicted to alter habitat around the world.²³ Significant changes in habitat, either along the travel corridor or at the

¹⁸ See *id.* at 674–76; see, e.g., F. Richard Hauer et al., *Assessment of Climate Change and Freshwater Ecosystems of the Rocky Mountains, USA and Canada*, 11 *HYDROLOGICAL PROCESSES* 903 (1997), available at http://www.tufts.edu/as/wright_center/iecws/materials/reading_list/2008_reading_list/assessment.pdf (assessing the impact of climate change on montane lakes and rivers).

¹⁹ Generally, primary productivity refers to how much life an area can support. It is often measured by the amount of new plant material that is created within a period of time. See CHARLES C. GRIER ET AL., U.S. DEP’T OF AGRIC., *PRODUCTIVITY OF FORESTS OF THE UNITED STATES AND ITS RELATION TO SOIL AND SITE MANAGEMENT PRACTICES: A REVIEW 1* (1989) (defining primary productivity as the measure of plant material produced by a forest per unit area per year); see also JEFF ARDRON ET AL., *DEFINING ECOLOGICALLY OR BIOLOGICALLY SIGNIFICANT AREAS IN THE OPEN OCEANS AND DEEP SEAS: ANALYSIS, TOOLS, RESOURCES, AND ILLUSTRATIONS* 50–52 (2009) (analyzing primary productivity by measuring phytoplankton production in the Pacific Ocean).

²⁰ Richard J. Hobbs et al., *Novel Ecosystems: Theoretical and Management Aspects of the New Ecological World Order*, 15 *GLOBAL ECOLOGY & BIOGEOGRAPHY* 1, 2 (2006).

²¹ The term biotic refers to living organisms, e.g., plants, other individuals of the same species. Abiotic refers to non-living things, e.g., temperature, day-length.

²² David C. Schneider & Brian A. Harrington, *Timing of Shorebird Migration in Relation to Prey Depletion*, 98 *AUK* 801, 809 (1981).

²³ David Bickford et al., *Impacts of Climate Change on the Amphibians and Reptiles of Southeast Asia*, 19 *BIODIVERSITY & CONSERVATION* 1043, 1052 (2010); Lucy A. Hawkes et al., *Climate Change and Marine Turtles*, 7 *ENDANGERED SPECIES RES.* 137, 145 (2009); Joshua J.

destinations, could disrupt migration and lead to a decline in the migrant population. For example, migratory shorebirds that use coastal wetlands as stopover sites rely on these sites to rest and eat, gathering energy for their continued journey.²⁴ Rising ocean levels may inundate these areas, increasing the distance shorebirds must travel between stopover sites.²⁵ Stopover sites are critical to shorebird migration success, but coastal wetlands are predicted to decrease in the future by as much as seventy percent in some areas due to climate change.²⁶ If stopover sites are lost, shorebirds may not have enough energy to travel to another available site.

As water availability decreases, migration may become more dangerous for terrestrial migrants as well. Amphibians, such as spadefoot toads and crested newts, move between pools of water to reach breeding and non-breeding habitat, relying on these movements to complete their life cycle.²⁷ As precipitation decreases, these bodies of water may decrease in size and number, making the necessary movement farther.²⁸ Amphibians cannot withstand extended periods without water, so there may be a point at which amphibian populations can no longer reach the next body of water, increasing death along the route or stopping movement completely. However, as mentioned earlier, future precipitation patterns are not clear, so there may also be areas where increasing precipitation creates larger or more numerous bodies of water. Whether these pools will be located within the range of a migration depends on the location of the population.

B. Changes in Resource Availability

As habitat is modified by climate change, habitat productivity will also change. For example, climate change may disrupt the growing season by changing temperature or precipitation beyond acceptable ranges for a particular species. This could reduce productivity and cause a decrease in available resources, such as the food and shelter necessary for survival. One of the most important factors allowing species to migrate long distances is

Lawler et al., *Projected Climate-Induced Faunal Change in the Western Hemisphere*, 90 *ECOLOGY* 588, 594 (2009).

²⁴ Kobi Merom et al., *Philopatry to Stopover Site and Body Condition of Transient Reed Warblers During Autumn Migration Through Israel*, 102 *CONDOR* 441, 443 (2000).

²⁵ H. Galbraith et al., *Global Climate Change and Sea Level Rise: Potential Losses of Intertidal Habitat for Shorebirds*, 25 *WATERBIRDS* 173, 174 (2002).

²⁶ *Id.* at 177.

²⁷ See, e.g., KENTWOOD DAVID WELLS, *THE ECOLOGY AND BEHAVIOR OF AMPHIBIANS* 244 (2007) (describing the movements of juvenile frogs between ponds); A. Meyer-Aurich et al., *Developing Agricultural Land Use Strategies Appropriate to Nature Conservation Goals and Environmental Protection*, 41 *LANDSCAPE & URB. PLAN.* 119, 123 (1998).

²⁸ Nicholas Ray, Anthony Lehmann & Pierre Joly, *Modeling Spatial Distribution of Amphibian Populations: A GIS Approach Based on Habitat Matrix Permeability*, 11 *BIODIVERSITY & CONSERVATION* 2143, 2144 (2002), available at http://www.unige.ch/ia/climate/grasp/downloads/ray_bc2002.pdf.

the availability of resource-rich areas to provide enough energy for completing the migration.²⁹

Conversely, some migratory species may benefit from climate change induced habitat modification. For example, high latitude ecosystems, such as boreal forests, are predicted to become more productive, at least temporarily.³⁰ As the temperature rises, the growing season may be extended in these colder regions allowing for greater productivity. Generally, however, the greater productivity may eventually be constrained by limits in other soil nutrients, such as nitrogen³¹ and increases in disturbance that accompany climate change may also limit increases in productivity.³²

C. Increases in Disturbance

If climate change proceeds as predicted, disturbances such as fires, drought, and floods will increase in number and magnitude, leading to further habitat alteration.³³ Long distance migrants, because of the long distances traveled, will therefore have a greater chance to come into contact with areas of fire, drought, or flood. These natural disturbances could also disrupt migrations by disturbing the landscape, which could cause a loss of shelter for migrants or a loss of the habitat productivity that migrants depend on for successful migration. However, new flooded areas may provide additional stopover sites for wetland and aquatic species and fires could provide a rich insect resource.

In addition, biological disturbances such as invasive species, pests, and pathogens are also predicted to increase as a result of climate change.³⁴ Areas that were previously inhospitable may become newly accessible to pests, predators, and pathogens due to changes in climate. Pests, such as the pine beetle, have already dramatically expanded their range in high elevation regions of North America.³⁵ In the past, the cold winters of these regions kept pine beetle populations low, but recent mild winters have allowed them

²⁹ See, e.g., Myrlyn Owen & Jeffrey M. Black, *Factors Affecting the Survival of Barnacle Geese on Migration from the Breeding Grounds*, 58 J. ANIMAL ECOLOGY 603, 615 (1989) (noting a strong relationship between losses of goslings on migration and food availability in feeding areas).

³⁰ A. R. Keyser et al., *Simulating the Effects of Climate Change on the Carbon Balance of North American High-Latitude Forests*, 6 GLOBAL CHANGE BIOLOGY (SUPPLEMENT 1) 185, 186 (2000).

³¹ Peter B. Reich et al., *Nitrogen Limitation Constrains Sustainability of Ecosystem Response to CO₂*, 440 NATURE 922, 924 (2006).

³² See Jonathan T. Overpeck, David Rind & Richard Goldberg, *Climate-Induced Changes in Forest Disturbance and Vegetation*, 343 NATURE 51 (1990).

³³ Aiguo Dai, *Drought Under Global Warming: A Review*, 2 WILEY INTERDISC. REVIEWS: CLIMATE CHANGE 45, 60 (2011); Maarten K. van Aalst, *The Impacts of Climate Change on the Risk of Natural Disasters*, 30 DISASTERS 5, 5 (2006).

³⁴ Matthew P. Ayres & María J. Lombardero, *Assessing the Consequences of Global Change for Forest Disturbance from Herbivores and Pathogens*, 262 SCI. TOTAL ENV'T 263, 264 (2000).

³⁵ W. A. Kurz et al., *Mountain Pine Beetle and Forest Carbon Feedback to Climate Change*, 452 NATURE 987, 987(2008).

to increase population size by extending breeding time.³⁶ This has led to dramatically increased tree mortality and changed forests into barren landscapes with defoliated, dead trees where there were once vibrant ecosystems.³⁷ This could negatively impact species that migrate in these areas by decreasing available food and shelter.

Some alpine birds migrate during the breeding season to avoid predation of their young. For example, in Costa Rica tropical birds that move to higher elevations to breed face a lower risk of predation than those that stay at lower elevations year-round.³⁸ This strategy to avoid predators may experience less success if climate change permits predators to shift their territory to higher altitudes. Climate change may increase disturbance by allowing an expanded range of predators and increasing predation on altitudinal migrants. While some migrants may then shift to even higher altitudes to keep ahead of the predators, eventually they will reach the tops of the mountains and there will be no further habitat to continue this avoidance strategy.

Whereas climate change will increase disturbances to migrants, migrants themselves may also cause disturbances to other species and ecosystems as a vector bringing disease from distant locations.³⁹ The spread of the West Nile virus in the Eastern United States and Lyme disease have been attributed to migrating birds.⁴⁰ Climate change may increase susceptibility of local species to disease brought by migrants by creating conditions less hostile to new pathogens. Moreover, local species may already be stressed by climate change, lowering their immune system resistance.⁴¹ However, it is possible that long-distance migration may actually decrease the spread of some pathogens as it allows individuals to escape areas of high disease concentration and may cause higher mortality in infected individuals (through the added stress of the act of migration), limiting their ability to spread the disease.⁴²

In addition to vectoring new diseases, migrants responding to climate change may cause disturbances if they shift migration corridors into new areas. A migration corridor shift could potentially disperse novel seed types,

³⁶ Kenneth F. Raffa et al., *Cross-Scale Drivers of Natural Disturbances Prone to Anthropogenic Amplification: The Dynamics of Bark Beetle Eruptions*, 58 *BIOSCIENCE* 501, 511 (2008).

³⁷ Craig D. Allen et al., *A Global Overview of Drought and Heat-Induced Tree Mortality Reveals Emerging Climate Change Risks for Forests*, 259 *FOREST ECOLOGY & MGMT.* 660, 669–70 (2010).

³⁸ W. Alice Boyle, *Can Variation in Risk of Nest Predation Explain Altitudinal Migration in Tropical Birds?*, 155 *OECOLOGIA* 397, 401 (2008).

³⁹ Elsa Jourdain et al., *Bird Migration Routes and Risk for Pathogen Dispersion into Western Mediterranean Wetlands*, 13 *EMERGING INFECTIOUS DISEASES* 365, 365 (2007); Robert P. Smith et al., *Role of Bird Migration in the Long-Distance Dispersal of Ixodes dammini, the Vector of Lyme Disease*, 174 *J. INFECTIOUS DISEASES* 221, 221 (1996); see also Reynolds & Clay, *supra* note 2, at 377–78.

⁴⁰ K. D. Reed et al., *Birds, Migration and Emerging Zoonoses: West Nile Virus, Lyme Disease, Influenza A and Enteropathogens*, 1 *CLINICAL MED. & RES.* 5, 8–9 (2003).

⁴¹ C. Drew Harvell et al., *Climate Warming and Disease Risks for Terrestrial and Marine Biota*, 296 *SCIENCE* 2158, 2158, 2161 (2002).

⁴² S. Altizer et al., *Animal Migration and Infectious Disease Risk*, 331 *SCIENCE* 296, 296 (2011).

alter species composition, and introduce invasive species.⁴³ However, in cases where migration corridors shift within a few hundred kilometers of the original route, the chance of introducing invasive species is reduced in comparison to large, cross-continental corridor shifts (i.e., the closer the new corridor is to the original corridor, the more the chance of introducing an invasive species is reduced).⁴⁴ On the other hand, because of climate change induced disturbance, resident species may have a decreased ability to fend off invasive species.⁴⁵

Migrants shifting into new areas may also cause disturbances as a new source of competition for resident species. If resident species and migrants share similar resource requirements, this could lead to increased competition and a potential decrease in resident species population. In extreme cases, migrants could overbrowse vegetation, damaging the habitat's ability to recover from migrants' feeding, decreasing the productivity of the area, and affecting a wide range of species. This could occur if migrations shift into areas that are more environmentally sensitive than traditional routes. Migrating species could also be a new source of predation. A shifted bird migration corridor, for example, could lead to an influx of new predators on insects that could have a substantial impact on the insect population of the region and any species that depends on them for food.

Finally, a shift in migration patterns due to climate change could disrupt local economies that depend on income from ecotourists and hunters that come to view or hunt migrating species.⁴⁶ This may especially be a problem in areas where wetland availability is predicted to decrease, such as the Great Lakes or central United States.⁴⁷ If the habitat of waterfowl (e.g., wetlands) is disrupted, migration corridors may also change to enable movement to regions with greater availability of wetlands, modifying long established patterns that wildlife enthusiasts have relied on to encounter migratory species, and shifting the areas that are popular with tourists.

⁴³ See Jessica J. Hellmann et al., *Five Potential Consequences of Climate Change for Invasive Species*, 22 CONSERVATION BIOLOGY 534, 539 (2008); Mason W. Kulbaba, Jacques C. Tardif & Richard J. Staniforth, *Morphological and Ecological Relationships Between Burrs and Furs*, 161 AM. MIDLAND NATURALIST 380, 380 (2009); Ran Nathan et al., *Mechanisms of Long-Distance Seed Dispersal*, 23 TRENDS ECOLOGY & EVOLUTION 638, 642 (2008).

⁴⁴ See Sharon Y. Strauss, Campbell O. Webb & Nicolas Salamin, *Exotic Taxa Less Related to Native Species Are More Invasive*, 103 PROC. NAT'L ACAD. SCI. 5841, 5841 (2006); Jillian M. Mueller & Jessica J. Hellmann, *An Assessment of Invasion Risk from Assisted Migration*, 22 CONSERVATION BIOLOGY 562, 564-65 (2008).

⁴⁵ See Angela T. Moles, Monica A. M. Gruber & Stephen P. Bonser, *A New Framework for Predicting Invasive Plant Species*, 96 J. ECOLOGY 13, 14 (2008) (discussing the increased likelihood of incursion by invasive species in areas with changing environmental conditions).

⁴⁶ See Hellmann et al., *supra* note 43, at 537.

⁴⁷ Geoffrey Wall, *Implications of Global Climate Change for Tourism and Recreation in Wetland Areas*, 40 CLIMATIC CHANGE 371, 376 (1998).

D. Changes in Phenology

Phenology is the timing of recurrent biological events, the causes of that timing, and the interrelation of these events among the same or different species.⁴⁸ Examples of phenological events include dates of flowering, leaf drop, time of hibernation, or mating season.⁴⁹ These events and relationships are an essential part of any ecological community because they are critical to reproduction and resource use. However, predictable phenological events are especially critical for migratory species because of the extra resources and body stores that are necessary for a successful migration.⁵⁰

Climate change will modify seasonality, resulting in many changes in the phenology of plants and animals, as they respond to the changing environment. As climatic conditions change, species will vary in the rate and direction of phenological change—some species may track the changes, others may shift timing too much, while still others may not adapt at all.⁵¹ Individuals may even react differently within the same species.⁵² This has the potential to impact many migrations by changing trophic interactions⁵³ when methods of reproduction and resource use become out of sequence and long established patterns are disrupted.

Phenological mismatches are already affecting migratory species.⁵⁴ A well-studied example is an oak-Winter-moth-great-tit system. Winter moth (*Operophtera brumata*) caterpillars need young leaves to develop.⁵⁵ If caterpillars hatch too early, there is not enough food.⁵⁶ If they hatch too late, there are too many tannins in the leaves for the caterpillars to get much energy from the leaves.⁵⁷ A similar dynamic occurs for great tit (*Parus*

⁴⁸ Franz Badeck et al., *Responses of Spring Phenology to Climate Change*, 162 NEW PHYTOLOGIST 295, 295 (2004).

⁴⁹ Inés Ibáñez et al., *Forecasting Phenology Under Global Warming*, 365 PHIL. TRANSACTIONS ROYAL SOC'Y B 3247, 3252 (2010) (describing the first flowering dates and leaf fall); David W. Inouye et al., *Climate Change is Affecting Altitudinal Migrants and Hibernating Species*, 97 PROC. NAT'L ACAD. SCI. 1630, 1630 (2000) (discussing such phenological activities as hibernation and reproduction in the context of climate change).

⁵⁰ See Owen & Black, *supra* note 29, at 615; Stuart Bearhop et al., *Stable Isotope Ratios Indicate That Body Condition in Migrating Passerines is Influenced by Winter Habitat*, 271 PROC. ROYAL SOC'Y B (SUPPLEMENT 4) S215, S217 (2004).

⁵¹ Marcel E. Visser & Christiaan Both, *Shifts in Phenology Due to Global Climate Change: The Need for a Yardstick*, 272 PROC. ROYAL SOC'Y B 2561, 2561 (2005).

⁵² *Id.* at 2566.

⁵³ The interactions between organisms in a food web. See A. G. Rossberg et al., *How Trophic Interaction Strength Depends on Traits: A Conceptual Framework for Representing Multidimensional Trophic Niche Spaces*, 3 THEORETICAL ECOLOGY 13, 13–14 (2010).

⁵⁴ See David W. Inouye et al., *supra* note 49, at 1632; Josep Peñuelas et al., *Changed Plant and Animal Life Cycles from 1952 to 2000 in the Mediterranean Region*, 8 GLOBAL CHANGE BIOLOGY 531, 543 (2002).

⁵⁵ ROBERT D. CHILDS & DEBORAH C. SWANSON, UNIV. OF MASS. EXTENSION, THE WINTER MOTH (2004), available at http://www.umassgreeninfo.org/fact_sheets/defoliators/winter_moth.pdf.

⁵⁶ Marcel E. Visser & Leonard J. M. Holleman, *Warmer Springs Disrupt the Synchrony of Oak and Winter Moth Phenology*, 268 PROC. ROYAL SOC'Y B 289, 289 (2001).

⁵⁷ *Id.*

major)⁵⁸ populations. Great tit hatchlings need an abundance of caterpillars, so hatching should coincide with highest population of Winter moth caterpillars.⁵⁹ Too early or too late means there is not enough food and leads to low numbers of surviving offspring.⁶⁰ With a changing climate, spring is beginning earlier and oak bud burst is coming earlier as well.⁶¹ Evidence has shown that winter moths are also laying their eggs earlier, however, they are laying them too early and are hatching before bud burst.⁶² This leads to a decrease of winter moth caterpillars that also affects the great tit population.

To further complicate the issue of phenological mismatching, different populations of the same species do not react to climate changes in the same manner. The great tit population in Wytham Wood, United Kingdom, has advanced the time of reproduction, but when spring seasons warm rapidly and reproduction advances too early, hatchlings are born before caterpillar peak biomass.⁶³ Great Tit populations in Hoge Veluwe, Holland, have not adjusted their reproductive timing, although the winter moths that they feed on have advanced.⁶⁴ Other communities show phenological mismatches with negative impacts on trophic interactions and population size.⁶⁵ These phenological mismatches have large impacts on the populations feeling their effects and have the potential to completely change migration dynamics. In addition, since migrations are recurrent events that are influenced by the seasonality of resource use and breeding,⁶⁶ they are at particular risk of phenological mismatches. Long distance migrants face special risk since

⁵⁸ The great tit is a small bird that is an altitudinal migrant in Northern Europe. GEORGE W. COX, BIRD MIGRATION AND GLOBAL CHANGE 224 (2010).

⁵⁹ Visser & Both, *supra* note 51, at 2562.

⁶⁰ *Id.*

⁶¹ Mark D. Schwartz, Rein Ahas & Anto Aasa, *Onset of Spring Starting Earlier Across the Northern Hemisphere*, 12 GLOBAL CHANGE BIOLOGY 343, 344, (2006); Visser & Holleman, *supra* note 56, at 290.

⁶² Visser & Both, *supra* note 51, at 2564.

⁶³ Will Cresswell & Robin McCleery, *How Great Tits Maintain Synchronization of Their Hatch Date with Food Supply in Response to Long-Term Variability in Temperature*, 72 J. ANIMAL ECOLOGY 356, 357 (2003).

⁶⁴ Visser & Both, *supra* note 51, at 2562.

⁶⁵ Examples of phenological mismatches include: Pink salmon (*Oncorhynchus gorbuscha*) in Alaska experiencing a mismatch between migration and warming water temperatures, Sidney G. Taylor, *Climate Warming Causes Phenological Shift in Pink Salmon, Oncorhynchus Gorbuscha, Behavior at Auke Creek, Alaska*, 14 GLOBAL CHANGE BIOLOGY 229, 234 (2008); caribou (*Rangifer tarandus*) in Greenland experiencing a mismatch between migration, breeding, and plant growing season, Eric Post & Mads C. Forchhammer, *Climate Change Reduces Reproductive Success of an Arctic Herbivore Through Trophic Mismatch*, 363 PHIL. TRANSACTIONS ROYAL SOC'Y B 2369, 2372 (2008), and Eric Post et al., *Warming, Plant Phenology and the Spatial Dimension of Trophic Mismatch for Large Herbivores*, 275 PROC. ROYAL SOC'Y B 2005, 2005–2013 (2008); and many other migratory bird species in Europe, Nicola Saino et al., *Climate Warming, Ecological Mismatch at Arrival and Population Decline in Migratory Birds*, PROC. ROYAL SOC'Y B (forthcoming) (manuscript at 6), available at <http://www.ecco.cat/pdf/article4.pdf>.

⁶⁶ See Reed et al., *supra* note 40, at 6.

they interact with distant habitats.⁶⁷ There is a greater chance that distant habitats will undergo different types of climatic changes.⁶⁸

E. Migration Cessation

In recent years, some individuals within migratory populations of Canada Goose (*Branta canadensis*) in the Midwest United States and the white stork (*Ciconia ciconia*) in Spain have stopped migrating, taking up year-round residence in areas that were previously considered stop-over sites.⁶⁹ Anecdotal evidence and reports by local management agencies explain that some birds have begun staying through the entire year in mid-latitude regions and suggest that this may be due to warming temperatures and milder winters.⁷⁰ Certain populations of monarch butterflies in warm regions such as Florida, Hawaii, and South America have stopped migrating.⁷¹ One study shows that some short and mid-range migrants react to climate change by shortening their migration distance, rather than by ceasing migration entirely.⁷² If the trend in climate change continues, these migrations could be so shortened that any resemblance to past migrations would be lost.

It is not clear, however, why these individuals have taken up residence and stopped migrating. It is possible that climate change has improved the productivity of these areas. Some of the current situation with year-round resident Canada geese and white storks is likely due to human intervention by feeding. However, if the winters were more severe, it is likely that no amount of food could keep these species from migrating. These circumstances lend support to the earlier hypothesis that migration is driven by resource availability, and if resources become stable, migrants will stop migrating. Further study is needed to determine what factors are driving this loss of migration.

⁶⁷ Tim Jones & Will Cresswell, *The Phenology Mismatch Hypothesis: Are Declines of Migrant Birds Linked to Uneven Global Climate Change?*, 79 J. ANIMAL ECOLOGY 98, 98(2010).

⁶⁸ Inés Ibáñez et al., *supra* note 49, at 3257; Jones & Cresswell, *supra* note 67, 98.

⁶⁹ Alex Felsinger, *Geese Mysteriously Stop Migrating, Droppings Pollute Town*, PLANETSAVE, Jan. 26, 2009, <http://planetsave.com/2009/01/26/geese-mysteriously-stop-migrating> (last visited Apr. 13, 2011); Sinikka Tarvainen, *Spaniards' Beloved Storks Stop Migrating*, MONSTERS & CRITICS, May 2, 2007, http://www.monstersandcritics.com/science/nature/features/article_1299254.php/Spaniards_beloved_storks_stop_migrating (last visited (Apr. 13, 2011)); *see also* Jonathon W. Atwell, Dawn M. O'Neal & Ellen D. Ketterson, *Animal Migration as a Moving Target for Conservation: Intra-Species Variation and Responses to Environmental Change, as Illustrated in a Sometimes Migratory Songbirds*, 41 ENVTL. L. 289, 310 (2011) (discussing the establishment of a permanent population of Oregon Juncos at a traditional winter stop-over on the campus of the University of California-San Diego).

⁷⁰ Francisco Pulido & Peter Berthold, *Current Selection for Lower Migratory Activity Will Drive the Evolution of Residency in a Migratory Bird Population*, 107 PROC. NAT'L ACAD. SCI. 7341, 7343 (2010).

⁷¹ *See* Altizer et al., *supra* note 42, at 299.

⁷² Pulido & Berthold, *supra* note 70, at 7431.

F. Spatial Variability in Climate Change Effects

Since migratory species can cross thousands of kilometers to complete migrations, a potential threat is that climate change may alter habitat along the migration path in many different ways. For example, the American Redstart (*Setophaga ruticilla*) is a warbler that summers in the North American boreal forest and winters in Venezuela.⁷³ It is possible that the boreal forest in North America may become wetter, while the wintering area in Venezuela could become drier.⁷⁴ This would make it very difficult for populations to adapt to both conditions. The strength of this effect will vary depending on the scale of migration, so this will especially be a threat for long-distance migrants, as the chance of exposure to differing climate pressures increases as travel distance increases.

III. CONCLUSION

Climate change will have many effects on migration by altering habitat, shifting seasonality, changing resource availability, and increasing disturbance. Migratory species will react to these impacts by changing phenology, ceasing migration, and attempting to adapt to multiple (and sometimes divergent) changes. In habitats where biotic and abiotic cues are being altered by climate change, migrations are being disrupted (e.g., great tit in northern Europe, migratory shorebirds in Israel, and salmon in Alaska). Species that migrate to or from regions that are becoming warmer are developing shortened migrations or are ceasing to migrate (e.g., white storks in Spain, Canada geese in the United States, and monarch butterflies in North and South America).

To better react to the problems climate change poses for animal migrations, we need more information. We need to better understand if migratory species can survive with altered—or a complete absence of—migration. Migrations are already being disrupted and some migrations are showing signs of stopping completely. We need to better understand what that will do to the species as well as the community with which the migratory species interacts.

We also need to better understand how flexible migration routes are for migratory species. If one corridor becomes inhospitable, what is the likelihood of a species finding an alternate corridor to maintain migration? This question is especially complicated for long-distance migrations, as it can be very

⁷³ See Raymond McNeil, *Winter Resident Repeats and Returns of Austral and Boreal Migrant Birds Banded in Venezuela*, 53 J. FIELD ORNITHOLOGY 125, 125, 127 (1982).

⁷⁴ See *id.* at 125 (describing an area of wintering territory for North American migratory bird species in northeastern Venezuela); GRID-Arendal, U.N. Env't Programme, Projected Changes in Maize Crops, Venezuela, http://maps.grida.no/go/graphic/projected_changes_in_maize_crops_venezuela (last visited Apr. 9, 2011) (explaining how changes in precipitation and wind patterns could bring much a drier climate to northern Venezuela); INTERGOVERNMENTAL PANEL ON CLIMATE CHANGE, THE REGIONAL IMPACTS OF CLIMATE CHANGE: AN ASSESSMENT OF VULNERABILITY 364 (1998) (projecting wetter tundra soils in boreal forests as a result of climate change).

difficult to follow individuals through a complete migration.⁷⁵ However, with recent advancements in GPS technology, this is becoming easier.⁷⁶

We need to collect more data on a wider range of migratory species. Much long-term data on species migrations describes bird migrations. We need better information over long periods for other migratory taxa, both vertebrate and invertebrate.

As with any conservation issue, we often do not have the luxury of waiting to act until we have complete information. For a wildlife agency attempting to protect migratory species, climate change provides many new challenges that must be confronted as quickly as possible using the best available information. Protecting migratory species will be difficult because of the large distances and multiple jurisdictions traveled and the difficulty of protecting all the necessary areas—including stopover sites, breeding grounds, and wintering grounds. Even if the necessary areas can be protected, climate change may create novel ecosystems in these areas, with all the habitat change and community disruption that entails. This will potentially cause migration corridors and destinations to shift out of protected areas. The more corridors that are protected, the more options will be available for migratory species to adapt to changing climate.

Climate change will cause wildlife agencies to be confronted with new diseases and invasive species. The agencies must be watchful for new, previously unheard of threats to migratory species and habitats important to migrations as climate change opens up new areas to the spread of damaging species. In addition, agencies will need to be aware that migratory species themselves may be vectors of disease and carriers of other potentially dangerous species.⁷⁷ There is the chance, however, that migration may reduce the spread of disease.⁷⁸

Finally, it may be very difficult to save a species that is declining due to phenological mismatches. While it may be possible to provide resources such as food or water to assist migratory species during critical time periods, if the species cannot adapt to climate change, this approach will ultimately be futile. The best option is to avoid phenological mismatches by minimizing the driver, i.e., by mitigating climate change in the first place. The issue of climate change and animal migrations presents many problems that do not have easy solutions. New options must be brought to the table if we are to deal with the threat of climate change to animal migrations.

⁷⁵ See Peter P. Marra, David Hunter & Anne M. Perrault, *Migratory Connectivity and the Conservation of Migratory Animals*, 41 ENVTL. L. 317, 319 (2011).

⁷⁶ *Id.* at 325.

⁷⁷ Reynolds & Clay, *supra* note 2, at 379–80.

⁷⁸ See Altizer et al., *supra* note 42, at 296.