

SYMPOSIUM ARTICLES

ANIMAL MIGRATION AS A MOVING TARGET FOR CONSERVATION: INTRA-SPECIES VARIATION AND RESPONSES TO ENVIRONMENTAL CHANGE, AS ILLUSTRATED IN A SOMETIMES MIGRATORY SONGBIRD

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Identifying important “migratory species” and the characteristics of their migrations might sound like a simple starting point for efforts to conserve and protect animal migrations. However, migrations are dynamic phenomena that vary over space and time, and migratory behaviors can vary substantially among closely related species, subspecies, races, or populations, and even among individual animals within a single population. The migratory behaviors of populations or individuals can also change rapidly—or be lost entirely—in response to habitat alteration or climate change. These complexities present both challenges and opportunities for initiatives to conserve animal migrations. In this Article, we discuss the concepts of intra-species variation in migration and the sensitivity of migrations to

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environmental change, and we consider the implications of these topics for legal, policy, management, and research agendas.

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I. INTRODUCTION

Animal migrations are dynamic phenomena that vary over space and time, even among closely related species, populations, and individuals. For example, in many animals there is substantial geographic variation in the migratory tendencies of different subspecies, races, or populations—birds that breed in the north may migrate long distances south to spend the winter, whereas members of the same species that breed at lower latitudes may be entirely sedentary (i.e., non-migratory).¹ Further, even within a discrete population, there can be systematic differences in the distance, routes, endpoints, or seasonal timing of migrations among male versus female or younger versus older individuals.² Such variation in migratory behaviors can emerge rapidly over “evolutionary time scales” (e.g.,

¹ See *infra* Part III.A.

² See *infra* Part IV.A–B.

thousands of years)—including over contemporary times (e.g., years or decades) in response to human activities such as habitat alteration and climate change.³ Therefore, effective conservation agendas for animal migrations must consider the implications of both spatial and temporal variation in migratory behavior, even within a single “migratory species” or a single local population.

Our primary goal in this paper is to introduce the following three biological topics to nonspecialists, and to discuss their potential implications for legal, policy, management, and research agendas related to the conservation of migrations: 1) geographic variation in migratory behavior within-species (i.e., inter-population variation in migration), 2) variation in migration of different individuals within a single population (i.e., intra-population variation in migratory behavior among individuals), and 3) the sensitivity of migratory behavior to environmental change—with dramatic changes observed even over relatively short time scales.

To illustrate these topics, we use a common “backyard” North American songbird species, the Dark-eyed Junco (*Junco hyemalis*).⁴ We chose the “sometimes migratory” junco, not because this species’s migration is of immediate conservation concern (it is not),⁵ but because past scientific research has revealed the complexity of its migration,⁶ allowing it to serve as a model to convey why intra-species variation in migration—and the sensitivity of migratory behaviors to environmental change—provide important challenges and opportunities for policy efforts to protect migrations. Principles derived from the junco almost certainly apply to many other migratory species, including those of immediate conservation concern, and we provide selected examples.⁷ However, for most species, intra-specific variation in migration or the potential impacts of changing environments on migration have not been well characterized. Even for the junco, which has received much research attention from biologists studying migration, there remain many unanswered questions about migratory variation within and among junco subspecies and populations. These types of information gaps have the potential to confound or frustrate conservation initiatives and should be dealt with by future research efforts.

The rate at which migratory processes can be altered by environmental changes—habitat destruction or alteration, climate change, construction of barriers to migration, pollution, or anthropogenic food or water supplementation—underscores the need for immediate conservation action

³ See *infra* Part V.A.

⁴ See *infra* Part II.A.

⁵ See *infra* Part II.C.

⁶ See *infra* Parts II.D, III.A.

⁷ See *infra* Part III.B. For instance, one species with similar migratory patterns to the junco, the Chinook salmon, *infra* note 72, is listed as an endangered species and various conservation efforts are in effect to protect the species from further population decline. See Office of Protected Resources, Nat’l Oceanic Atmospheric Admin. Fisheries, Chinook Salmon (*Oncorhynchus tshawytscha*), <http://www.nmfs.noaa.gov/pr/species/fish/chinooksalmon.htm> (last visited Feb. 3, 2011).

and the articulation of ongoing research agendas—both of which must be drafted to accommodate intra-species variation and rapidly changing biological systems. Although both intra-species variation in migratory biology and the sensitivity of migrations to environmental change challenge the desire to generalize in the context of conservation law, policy, management, and research, these topics must be considered if the most effective migration conservation strategies are to be developed.

In Part II, we introduce the Dark-eyed Junco, providing relevant background information for this species, which we subsequently use as an example to illustrate our key points throughout the following three Parts. In Part III, we explain the extent of geographic (inter-population) variation in migration as a general phenomenon, and we consider the implications of this type of variation for conservation agendas. Part IV introduces the topics of “differential migration” and “partial migration” (both types of intra-population variation in migratory behavior among individuals), and we discuss the implications of such intra-population variation for conservation. In Part V, we highlight two recent landmark studies which demonstrate how contemporary environmental changes have rapidly altered migratory biology in the junco, and we consider how these types of studies can inform approaches to conservation. In Part VI, we conclude by summarizing our key points, emphasizing that future research, along with improved communication and collaboration among scientists, policymakers, and managers, could proceed to more effectively consider intra-species variation and response to environmental change in the context of conservation of animal migrations.

II. “SOMETIMES MIGRATORY SONGBIRD”: THE DARK-EYED JUNCO

The Dark-eyed Junco (*Junco hyemalis*) is a medium-sized (18–22 gram average) sparrow that breeds primarily in montane or higher latitude coniferous and mixed forest habitat throughout the northern part of North America and south through the Western United States.⁸ The winter range of the junco includes lower latitudes and lower altitudes throughout North America.⁹ The breeding and wintering ranges of Dark-eyed Juncos are illustrated in Figures 2a through 2d, and discussed in more detail below. Juncos forage and nest primarily on the ground, they form conspicuous

⁸ Basic descriptive information about the biology and natural history of the junco is summarized throughout the following species account: V. NOLAN JR. ET AL., BIRDS OF N. AM., NO. 716, DARK-EYED JUNCO (*JUNCO HYEMALIS*), at 1 fig.1 (A. Poole & F. Gill eds., 2002), available at <http://bna.birds.cornell.edu/bna/species/716/articles/introduction> (displaying its breeding range); *id.* at 2 (noting that the Dark-eyed Junco is a medium sized sparrow, averaging 18–22 grams); *id.* at 11 (noting that some Dark-eyed Juncos breed in high-altitude, coniferous forest regions).

⁹ See *id.*, at 1 fig.1 (displaying the lower altitude and lower elevation winter breeding range of the Dark-eyed Juncos).

wintering flocks of ten to fifteen individuals, and they flash their white outer tail feathers when they fly.¹⁰

Wintering flocks of juncos are common at birdfeeders and juncos actively feed during winter conditions, earning them the colloquial nickname “snowbirds.”¹¹ Where it occurs, the Dark-eyed Junco is typically one of the most common and abundant songbirds in both its breeding and wintering range, which visualized together, cover most of the United States and much of Canada (Figure 2a).¹² Thus, for millions of North Americans, the junco is arguably the easiest songbird to observe in their backyards and local habitats, including its seasonal arrival and departure on breeding and wintering grounds. The Dark-eyed Junco is technically considered a single species by current taxonomic criteria,¹³ but as we discuss below, there are many subspecies and races that differ in feather plumage coloration, body size, life-history and social behavior, and importantly, in their migratory tendencies.¹⁴

We refer to the Dark-eyed Junco as “sometimes migratory” because some junco populations are long-distance migrants while others are non-migratory (i.e., sedentary), and yet others are regional “short-range” or “altitudinal” migrants.¹⁵ This geographic variation among junco groups is introduced at the end of this Part and expanded upon in Part III. Further, even within particular junco populations, some individuals (e.g., females) migrate farther than others (e.g., males),¹⁶ and we discuss this intra-population variation below in Part IV. Recent studies, highlighted below in Part V, reveal how climate change and habitat alteration are associated with rapid changes in migratory behavior in some junco populations. As described above, we chose the junco to illustrate our main points regarding the ubiquity and relevance of intra-species variation and sensitivity of migrations to environmental change not because junco migrations are of immediate conservation concern, but because prior research in this species allows it to serve as a helpful model to convey the importance of understanding the variable and dynamic nature of migratory behaviors over space and time.

¹⁰ *Id.* at 1, 20.

¹¹ *See id.* at 1.

¹² *Id.* at 1 (noting the ubiquity of the Dark-eyed Juncos and their extensive annual range).

¹³ *Id.* at 2 (noting that until the 1970s, the Dark-eyed Junco was split into five distinct species, but that currently, all five groups of juncos are considered one species). *See generally* Int'l Ornithological Cong. (IOC), World Bird Names, <http://www.worldbirdnames.org/> (last visited Jan. 14, 2011) (listing bird names with links to the most recent taxonomic categorizations and proposed revisions).

¹⁴ NOLAN ET AL., *supra* note 8, at 2 (plumage color and size variations); *id.* at 8 (different migratory tendencies); *id.* at 18–23 (behavioral differences); *see id.* at 31–32 (differences in life history).

¹⁵ *Id.* at 8 (noting that all juncos that breed in the northern parts of the species' range do migrate, but that some species are mostly sedentary or are partial, altitudinal, short-distance migrants).

¹⁶ Daniel A. Cristol et al., *Differential Migration Revisited: Latitudinal Segregation by Age and Sex Class*, in 15 CURRENT ORNITHOLOGY 33, 36–37 (Val Nolan Jr. & Ellen D. Ketterson eds., 1999).

A. Diversity Within the Genus Junco

The genus *Junco* has historically been considered to include three species: Volcano Junco (*Junco vulcani*), found in Costa Rica; Yellow-eyed Junco (*Junco phaeonotus*), found in Mexico and Guatemala; and Dark-eyed Junco (*Junco hyemalis*), found in North America north of Mexico.¹⁷ The Dark-eyed Junco, which is the primary focus of this Article, is divided into at least fifteen subspecies,¹⁸ including a group of eight western subspecies collectively known as the “Oregon” Junco.¹⁹ The range of the Oregon Junco complex extends along the west coast of North America from Alaska into Martir Mountains in Baja California.²⁰ Each junco subspecies has distinctive markings and can be distinguished from the others based on size and coloration.²¹ Juncos are conspicuously patterned, and their plumage varies significantly with geography.²² Some of this variation is illustrated in Figure 1. For example, in the Oregon complex of the west, juncos have a dark hood, white breast, and rusty flanks.²³ In the East, the heads, backs, and flanks are more often gray, as found in the Slate-colored Junco and White-winged Junco groups of the Dark-eyed Junco species. *Junco phaeonotus* (the Yellow-eyed Junco) is also divided into at least three subspecies,²⁴ which means that, depending on how one counts, there are at least nineteen distinguishable groups of juncos. Because of the large geographic variation, as well as the species’ abundance and ease of study, the junco has been used as a classic model for speciation in progress.²⁵ Recent molecular evidence indicates that the diversity exhibited among the Dark-eyed Juncos has emerged very rapidly in evolutionary time, as birds re-colonized North America following glacial maxima in the last 10,000 to 100,000 years.²⁶

¹⁷ NOLAN ET AL., *supra* note 8, at 8 (noting the three species of junco as currently classified); see INT’L ORNITHOLOGICAL CONG. (IOC), WORLD BIRD NAMES, MASTER LIST OF WORLD BIRD RANGES, II, 12,231–35 (2006), available at http://www.worldbirdnames.org/Master_IOC_list_v2.7.xls.

¹⁸ NOLAN ET AL., *supra* note 8, at 5. See generally Alden H. Miller, *Speciation in the Avian Genus Junco*, 44 UNIV. CAL. PUBLICATIONS ZOOLOGY 173 (1941) (discussing and summarizing the general taxonomy and biogeographic diversity of the junco).

¹⁹ NOLAN ET AL., *supra* note 8, at 6.

²⁰ Miller, *supra* note 18, at 238.

²¹ NOLAN ET AL., *supra* note 8, at 2–3; Miller, *supra* note 18, at 375.

²² KIM A. SULLIVAN, THE BIRDS OF N. AM., NO. 464, YELLOW-EYED JUNCO (*JUNCO PHAEONOTUS*) 1, 2 (A. Poole & F. Gill eds., 1999).

²³ NOLAN ET AL., *supra* note 8, at 3.

²⁴ *Id.* at 4; SULLIVAN, *supra* note 22, at 2–4.

²⁵ NOLAN ET AL., *supra* note 8, at 2; E. Mayr, *Speciation in the Junco*, 23 ECOLOGY 378, 378 (1942) (book review); Miller, *supra* note 18, at 174–75.

²⁶ Borja Milá et al., *Recent Postglacial Range Expansion Drives the Rapid Diversification of a Songbird Lineage in the Genus Junco*, 274 PROC. ROYAL SOC’Y B 2653, 2658 (2007).

B. The Junco as a Model in Science

The junco was the first vertebrate animal in which photoperiodic time was measured.²⁷ William Rowan held juncos outdoors in Edmonton, Alberta during the winter and exposed them to artificial light at the end of the day.²⁸ Despite the cold and snow of Alberta, the light caused the birds to enter the “reproductive state,” while birds held under much milder conditions, but on shorter days, remained in the “winter state.”²⁹ The role of day length in regulating seasonal changes associated with both reproduction and migration has since been demonstrated in many species.³⁰ An area of intense research addresses the relative importance of day length as a cue that regulates events of the annual cycle, in concert with temperature and food as supplementary cues that contribute to the timing of migration and reproduction.³¹ The junco has also been a model for scientists studying hormones and behavior,³² neurobiology,³³ social dominance,³⁴ sexual selection,³⁵ trait evolution,³⁶ eco-immunology,³⁷ chemical ecology,³⁸ sex differences,³⁹ speciation,⁴⁰ and, of course, migration, as we will highlight in the following Parts. Therefore, although most junco populations are not

²⁷ William Rowan, *Relation of Light to Bird Migration and Developmental Changes*, 115 NATURE 494, 494–95 (1925).

²⁸ *Id.* at 495.

²⁹ *Id.* (suggesting that “daily increases in illumination . . . are conducive to developmental changes in sexual organs” and noting that comparison of data from California to data from Alberta “further suggests that favorable light conditions are more potent in this respect than favorable temperatures”).

³⁰ Bruce D. Goldman, *Mammalian Photoperiodic System: Formal Properties and Neuroendocrine Mechanisms of Photoperiodic Time Measurement*, 16 J. BIOLOGICAL RHYTHMS 283, 284 (2001).

³¹ See, e.g., J.C. Wingfield, H. Schwabl & P.W. Mattocks, Jr., *Endocrine Mechanisms of Migration*, in BIRD MIGRATION: PHYSIOLOGY AND ECOPHYSIOLOGY 232 (E. Gwinner ed., 1990).

³² See, e.g., Joel W. McGlothlin et al., *Natural Variation in a Testosterone-Mediated Trade-Off Between Mating Effort and Parental Effort*, 170 AM. NATURALIST 864 (2007).

³³ See, e.g., Daniel A. Cristol et al., *Migratory Dark-Eyed Juncos, Junco hyemalis, Have Better Spatial Memory and Denser Hippocampal Neurons Than Nonmigratory Conspecifics*, 66 ANIMAL BEHAV. 317 (2003).

³⁴ See, e.g., Daniel A. Cristol, *Food-Deprivation Influences Dominance Status in Dark-Eyed Juncos, Junco hyemalis*, 43 ANIMAL BEHAV. 117 (1992).

³⁵ See, e.g., Joel W. McGlothlin et al., *Correlational Selection Leads to Genetic Integration of Body Size and an Attractive Plumage Trait in Dark-Eyed Juncos*, 59 EVOLUTION 658 (2005).

³⁶ See, e.g., Pamela J. Yeh, *Rapid Evolution of a Sexually Selected Trait Following Population Establishment in a Novel Habitat*, 58 EVOLUTION 166 (2004).

³⁷ See, e.g., T. J. Greives et al., *Testosterone and Innate Immune Function Inversely Covary in a Wild Population of Breeding Dark-Eyed Juncos (Junco hyemalis)*, 20 FUNCTIONAL ECOLOGY 812 (2006).

³⁸ See, e.g., Danielle J. Whittaker et al., *Songbird Chemosignals: Volatile Compounds in Preen Gland Secretions Vary Among Individuals, Sexes, and Populations*, 21 BEHAV. ECOLOGY 608, 608–14 (2010).

³⁹ See, e.g., Devin A. Zysling et al., *Behavioral and Physiological Responses to Experimentally Elevated Testosterone in Female Dark-Eyed Juncos (Junco hyemalis carolinensis)*, 50 HORMONES & BEHAV. 200, 200–07 (2006).

⁴⁰ See, e.g., Milá et al., *supra* note 26.

facing extinction risks that would make them populations of conservation concern under traditional paradigms,⁴¹ protecting the geographic ubiquity and diversity of juncos while they are still abundant and common is of fundamental importance to science.

C. Conservation Issues and Status

With respect to conservation, the Dark-eyed Junco as a whole is a species of least concern,⁴² but at least one subspecies, the non-migratory Guadalupe Junco (*Junco hyemalis insularis*) was classified as critically endangered on the International Union for Conservation of Nature and Natural Resources (IUCN) Red List as recently as 2008, when the list stopped including subspecies.⁴³ The question of subspecies is beyond the limits of consideration here, but the junco's phylogeny is fluid, and the true status of the Guadalupe Junco remains to be determined, although recent molecular work indicates it should be listed as a separate species.⁴⁴ Although the Dark-eyed Junco is still abundant in most parts of its range, the species declined at a rate of almost two percent annually between 1980 and 2002 according to the National Breeding Bird Survey project.⁴⁵ Declines were particularly notable among breeding juncos in western Canada, where both Oregon and Slate-colored Junco subspecies migrate long distances to and from wintering grounds at more southerly latitudes.⁴⁶ Similarly, from 1959 to 1988, Dark-eyed Junco abundance declined nearly everywhere based on data from Christmas bird counts, and significant increases were observed only in Quebec and a few northern locations, perhaps indicating a shift in winter distribution in response to climatic warming.⁴⁷ Because juncos prefer areas of partial tree cover, including recent clear-cuts, logging is probably not a direct cause of junco population declines.⁴⁸ Hypothesized causes of junco declines include aerial application of insecticides and forest regeneration and succession on the breeding grounds as well as unknown factors during migration and winter.⁴⁹

⁴¹ See *infra* Part II.C.

⁴² J. Bird & S. Butchart, Int'l Union for the Conservation of Nature & Natural Res., Junco hyemalis, <http://www.iucnredlist.org/apps/redlist/details/151120/0> (last visited Jan. 27, 2011).

⁴³ BIRDLIFE INT'L, THE BIRDLIFE PREVENTING EXTINCTIONS PROGRAMME: ANNUAL REPORT (2009), available at http://www.birdlife.org/extinction/pdfs/PEP_report_final.pdf.

⁴⁴ Interview with Borja Milá, Ph.D., Researcher of Biodiversity and Biological Evolution, National Museum of Natural Sciences, Madrid, Spain (June 15th, 2010).

⁴⁵ Boreal Songbird Initiative, Selected Birds of the Boreal Forest of North America: Dark-Eyed Junco, http://www.borealbirds.org/birdguide/bd0307_species.shtml (last visited Mar. 13, 2011) (summarizing J.R. Sauer et al., USGS Patuxent Wildlife Research Center, Breeding Bird Survey, Summary and Analysis, Version 2003.1, (2003), <http://www.mbr-pwrc.usgs.gov/bbs/bbs2002.html> (last visited Mar. 13, 2011)).

⁴⁶ *Id.*

⁴⁷ See *id.*

⁴⁸ *Id.*

⁴⁹ *Id.*

D. Migration in the Junco

With respect to migration, the biological diversity represented in the junco species complex is striking, as described in Figure 1 and illustrated in Figures 2a through 2e. As we will describe below in Part III, there is great variation among junco subspecies and populations in their migratory dispositions. Further, within discrete subspecies and local populations, juncos exhibit differences in migratory behavior among both age and sex cohorts.⁵⁰ Finally, two recent studies presented in Part V highlight how junco migrations are sensitive to environmental change, including in response to recent climatic shifts and urbanization. Despite decades of research on this particular species, some of it focused directly on migration, there is still much that remains to be learned, and greater knowledge gaps exist for most migratory species.

III. GEOGRAPHIC AND SUBSPECIFIC VARIATION IN MIGRATION

“Migration is rarely a unitary phenomenon even in those species usually regarded as classic migrants.”⁵¹

Distinguishing between migratory and non-migratory species might sound like an ordinary exercise for field biologists, but if one looks closely, many species elude such simple categorizations. In a few cases—such as the long-distance,⁵² complete,⁵³ and obligate migrations⁵⁴ exhibited by Arctic Terns (*Sterna paradisaea*)—all members of the species must migrate or die.⁵⁵ For the Arctic Terns, the limited geographic distributions of their specific breeding and wintering habitat, as well as the dramatic environmental fluctuations at the poles, ensure that staying behind or making only part of the journey is not an option.⁵⁶ Even among Arctic Terns, however, variation exists in the form of the migratory routes taken between the contiguous

⁵⁰ See *infra* Part IV.C.

⁵¹ HUGH DINGLE, *MIGRATION: THE BIOLOGY OF LIFE ON THE MOVE* 293 (1996).

⁵² See Vicky J. Meretsky, Jonathan W. Atwell & Jeffrey B. Hyman, *Migration and Conservation: Frameworks, Gaps, and Synergies in Science, Law, and Management*, 41 ENVTL. L. 447, 460 (2011), for a brief discussion and examples of long-distance migration.

⁵³ See *id.* at 461–62, for a definition and examples of complete migration (in contrast to partial migration).

⁵⁴ See *id.* at 464, for a definition and examples of obligate migration (in contrast to facultative migration).

⁵⁵ John T. Curtis, *Bird Migration*, 3 BIOS 82, 87 (1932); see also Carsten Egevang et al., *Tracking of Arctic Terns *Sterna Paradisea* Reveals Longest Animal Migration*, 107 PROC. NAT'L ACAD. SCI. U.S. 2078 (2010), available at <http://www.pnas.org/content/early/2009/12/29/0909493107.full.pdf> (discussing migratory patterns of Arctic Terns).

⁵⁶ See Jeremy J. Hatch, *Arctic Tern* (*Sterna paradisaea*), THE BIRDS OF N. AM. ONLINE, <http://bna.birds.cornell.edu/bna/species/707> (last visited Jan. 27, 2011); see also Dep't of Env't & Natural Res., N.W.T., Can., Statement of the Environment Report, Natural Climate Fluctuations, http://www.enr.gov.nt.ca/_live/pages/wpPages/soe_natural_fluctuations.aspx (last visited Jan. 27, 2011).

polar ranges—the species splits into tracks, traveling down different coasts of the Americas, Eurasia, and Africa.⁵⁷

A. Migratory Diversity Among Junco Groups

In many species, however, distances of migrations vary, as exemplified by the junco species complex, in which some subspecies and populations can be entirely sedentary, while others migrate long distances. This geographic variation is described in Figure 1 and illustrated in Figures 2a through 2e. The Slate-colored group of Dark-eyed Juncos (*Junco hyemalis hyemalis*) (SCJU), which breeds throughout boreal forests ranging through Alaska, Canada, and New England, is generally considered a relatively long-distance migrant, with most SCJUs migrating hundreds of kilometers to spend the winter across the southern United States (see Figure 2b).⁵⁸ In stark contrast, another Dark-eyed Junco, the Guadalupe Island Junco (*Junco hyemalis insularis*) (GUJU), is entirely sedentary, with its range restricted to “an island within an island”: small groves of cypress trees (<5 square kilometers) on a small island (<400 square kilometers) more than 300 kilometers off the coast of Baja California, Mexico (see Figure 2c).⁵⁹

Between these extremes, natural populations of the junco exhibit a full range of variation in the distances and directions they migrate. Another distinct group, the White-winged Junco (*Junco hyemalis aikeni*) (WWJU), which breeds in a small region of the Black Hills, migrates regionally towards the Southwest, probably some few hundreds of kilometers (see Figure 2c).⁶⁰ Both Pink-sided Juncos (*Junco hyemalis mearnsi*) (PSJU) and the Gray-headed Juncos (*Junco hyemalis caniceps*) (GHJU) that breed in the Rocky Mountains and the Southwest, respectively, migrate variable distances westward and southward towards coastal mountains or lower elevations (Figure 2c).⁶¹ The Red-backed Juncos (*Junco hyemalis dorsalis*) (RBJU) as well as most Yellow-eyed Junco subspecies (*Junco phaeonotus palliatus*) (YEJU) seem to be primarily facultative altitudinal migrants, leaving their higher elevation breeding sites only during harsh winter conditions (see Figures 2d and 2e, respectively).⁶²

Among the different varieties of Oregon Dark-eyed Junco (*Junco hyemalis*) (ORJU), different subspecies span the full range of migratory dispositions—from long-distance migrants that breed in the northern part of the breeding range (e.g., British Columbia) and winter in southern and coastal California, to altitudinal migrants that breed in southern California

⁵⁷ See Hatch, *supra* note 56.

⁵⁸ NOLAN ET AL., *supra* note 8, at 2–3.

⁵⁹ See Miller, *supra* note 18, at 306, 309–11 (explaining insular Guadalupe Island Juncos occur only on the Guadalupe Island and are predominantly found in pines and cypresses).

⁶⁰ See *id.* at 350–51.

⁶¹ See *id.* at 185–86, 242, 244.

⁶² See *id.* at 209–10; Eric G. Horvath & Kimberly A. Sullivan, *Facultative Migration in Yellow-Eyed Juncos*, 90 CONDOR 482, 482–83 (1988).

and migrate less than fifty kilometers during periods of harsh winter weather (see Figure 2d).⁶³ As detailed below, another distinct population of Oregon Juncos has become entirely sedentary following its recent colonization of a novel urban and climatically mild breeding habitat in San Diego, California.⁶⁴ Similarly, within the Slate-colored Juncos, which are typically referred to as long-distance latitudinal migrants, there exists the Carolina subspecies (*Junco hyemalis carolinensis*), which breeds in the Appalachian Mountains and migrates only short distances attitudinally (see Figure 2b).⁶⁵

B. The Generality of Intra-Species Variation in Migrations

Importantly, although the geographic diversity of migratory groups exhibited within the junco complex is extraordinary, it is apparently not unique. Within species variation in migration appears to be quite common.⁶⁶ However, in most species, extensive efforts have not been made to characterize this variation, or logistical challenges (e.g., tracking small birds) has made it very difficult. In Mr. Hugh Dingle's discussion of population and species differences from his text *Migration: the Biology of Life on the Move*, he presents examples from a diverse array of taxa in which intra-specific and geographic variation have been observed when scientists have looked closely.⁶⁷ These include milkweed bugs,⁶⁸ grasshoppers,⁶⁹ Old World warblers of the genus *Sylvia*,⁷⁰ killer whales,⁷¹ Chinook salmon,⁷² Brown trout,⁷³ and American shad.⁷⁴

In the case of the junco, as opposed to other songbirds, investigators were able to observe and characterize this variation more readily because it is associated, at least roughly, with distinct differences in plumage coloration.⁷⁵ We are confident that far less would be known about the variable migratory propensities of junco subspecies with overlapping wintering ranges if they all looked the same through binoculars or in the hand. How could it be known which ones migrate, how far, and to where? Thus we suspect, and studies have shown for a few,⁷⁶ that there are many species that share similar

⁶³ See generally Miller, *supra* note 18, at 250–307.

⁶⁴ See *infra* text accompanying notes 142–46.

⁶⁵ See *infra* Part IV.C (long-distance latitudinal migrants); see also Cristol et al., *supra* note 33, at 317–18.

⁶⁶ DINGLE, *supra* note 51, at 293.

⁶⁷ *Id.*

⁶⁸ *Id.* at 294.

⁶⁹ *Id.* at 295.

⁷⁰ *Id.* at 297.

⁷¹ *Id.* at 299.

⁷² *Id.* at 300.

⁷³ *Id.* at 301–02.

⁷⁴ *Id.* at 303.

⁷⁵ See *supra* Part II.A.

⁷⁶ See, e.g., Borja Milá et al., *Speciation and Rapid Phenotypic Differentiation in the Yellow-Rumped Warbler Dendroica coronata Complex*, 16 MOLECULAR ECOLOGY 159, 169–70 (2007), available at <http://www.environment.ucla.edu/ctr/research/NeoMig/Mila-Mol-Eco-Speciation->

biogeographic history and breadth of diversity among migratory subspecies and types, but without the same dramatic diversification in plumage,⁷⁷ their migratory diversity has been harder to detect.

Another axis of variation in the junco, wing shape and wing length, is associated with differences between migratory and sedentary groups, with migrants exhibiting larger wings better suited to long sustained flights.⁷⁸ This biogeographic variation in wing morphology has been documented in many other avian species,⁷⁹ but is far more subtle than plumage variation and can typically only be detected with a captured bird.

Other methods for establishing geographic variation have also presented difficulties in the past. The small body size of most songbirds has made large-scale radio-tracking impossible.⁸⁰ Banding individual birds of local populations over small geographic scales allows the tracking of altitudinal or shorter distance migrants, but banding programs are not effective over long distances.⁸¹ There are simply too many birds and too few banders. For larger birds and other larger animals, radio- and satellite-telemetry have been available for some time, but in many cases their widespread implementation has been prohibited by high costs, and they are deployed on few individuals from a limited number of populations.⁸² Only recently have technological advances in radio-, satellite-, and photosensitive-tracking devices and stable isotope analyses provided the tools to elucidate biogeographic diversity of migrations.⁸³ Thus, obtaining a detailed understanding of geographic variation among populations, races, or subspecies has been quite challenging for most animal groups, but we have reason to expect significant breakthroughs in the coming decades for many species, which should prove empowering for those committed to the successful conservation of migrations.

warbler-2007.pdf (describing the role of Pleistocene glacial cycles in driving speciation and the evolution of migration in songbirds, ultimately inferring evolutionary processes from mitochondrial DNA and morphological data).

⁷⁷ *Id.* at 170.

⁷⁸ Robert S. Mulvihill & C. Ray Chandler, *The Relationship Between Wing Shape and Differential Migration in the Dark-Eyed Junco*, 107 AUK 490, 493–95 (1990).

⁷⁹ See Rowan Lockwood, John P. Swaddle & Jeremy M. V. Rayner, *Avian Wingtip Shape Reconsidered: Wingtip Shape Indices and Morphological Adaptations to Migration*, 29 J. AVIAN BIOLOGY 273 (1998) (discussing and analyzing avian wing morphologies associated with migratory variation).

⁸⁰ W. Douglas Robinson et al., *Integrating Concepts and Technologies to Advance the Study of Bird Migration*, 8 FRONTIERS ECOLOGY & ENV'T 354, 359 (2010). Although as a generality, tracking small songbirds has been logistically challenging and rarely achieved, there have been some notable and successful efforts, for example, see Martin Wikelski et al., *Costs of Migration in Free-Flying Songbirds*, 423 NATURE 704 (2003).

⁸¹ Robinson et al., *supra* note 80, at 355.

⁸² *Id.*

⁸³ For a discussion of emerging technologies applicable to studying bird migrations, see Peter P. Marra, David Hunter & Anne M. Perrault, *Migratory Connectivity and the Conservation of Migratory Animals*, 41 ENVTL. L. 317, 325–28 (2011), and Robinson et al., *supra* note 80, at 355–56, 358.

C. Geographic Variation in Migrations: Implications for Conservation

The existence of geographic and intra-specific variation in migrations described above—that is, the degree to which the distances or routes traveled by migrants vary among different subgroups (i.e., subspecies, races, and geographically-separated populations)—poses both challenges and opportunities for conservation of migrations that must be considered.

With respect to challenges, for example, the research efforts required to obtain knowledge of patterns of migratory connectivity⁸⁴ between breeding and wintering grounds and to characterize the migratory routes and stopover requirements for particular animal groups becomes greater, more expensive, and more logistically demanding when intra-species variation must be considered. However, once this knowledge is obtained, only certain subspecies or races may prove to exhibit migratory behavior or traverse imperiled landscapes on their journey. Here lies the opportunity: armed with the knowledge of which populations migrate, conservation specialists will be better able to design policies and management strategies that are targeted, smaller-scale, more efficient, and ideally more effective at protecting the most important migrations per se rather than the “migratory species” as a whole. If limited funds and resources are mandated to protect a particular migration, prioritization efforts would be aided by a clear understanding of which geographic variants exhibit the most ecologically or culturally valuable, or the most imperiled migrations.

Many conservation laws, policies, and management strategies include species-level mandates and goals, which has forced scientists and conservationists to merge theory and practice in confronting the challenges associated with defining “species” and species’ boundaries.⁸⁵ These scientific and policy debates are beyond the scope of this article,⁸⁶ but to generalize, some consensus has been reached recognizing subspecies and local populations as independent targets of conservation if they represent “evolutionarily significant units” that contain unique genetic or biological characteristics that distinguish them from other such groups.⁸⁷ However, defining criteria that effectively discriminate between groups on separate evolutionary trajectories is challenging and contentious, because in most species, the extent of phenotypic and genetic variation is not well-sampled,

⁸⁴ For definitions and detailed discussions of “migratory connectivity,” see Marra et al., *supra* note 83, at 316–17, 327–32.

⁸⁵ For a detailed discussion of these topics see Georgina M. Mace, *The Role of Taxonomy in Species Conservation*, 359 PHIL. TRANSACTIONS ROYAL SOC’Y B 711, 711–19 (2004), and Jody Hey et al., *Understanding and Confronting Species Uncertainty in Biology and Conservation*, 18 TRENDS ECOLOGY & EVOLUTION 597, 597–603 (2003).

⁸⁶ For a detailed analysis of the “species problem” in biology and conservation, see Jody Hey, *The Mind of the Species Problem*, 16 TRENDS ECOLOGY & EVOLUTION 326, 326–29 (2001), and Hey et al., *supra* note 85.

⁸⁷ Dylan J. Fraser & Louis Bernatchez, *Adaptive Evolutionary Conservation: Towards a Unified Concept for Defining Conservation Units*, 10 MOLECULAR ECOLOGY 2741, 2741–42 (2001).

and consensus on quantitative genetic divergence thresholds is lacking.⁸⁸ Elucidating intra-specific variation in migratory disposition and geographic connectivity could provide highly relevant criteria for the distinct evolutionary history and evolutionary future of particular migratory (or sedentary) populations,⁸⁹ perhaps allowing for their inclusion in targeted species-level legal, policy, and management mandates such as those invoked by the Endangered Species Act.⁹⁰ For example, in his recent monograph, Kevin Winker argues that geographic variation in migratory behavior has been a key ecological driver of differentiation leading to speciation throughout the evolutionary history of avian lineages, suggesting that populations that differ in their migratory behavior are likely to be on divergent evolutionary trajectories.⁹¹

IV. INTRA-POPULATION VARIATION: PARTIAL AND DIFFERENTIAL MIGRATION

Even *within* a local population or subspecies, migratory animals can vary in two important ways. “Partial migration” refers to those populations in which some individuals migrate and some remain sedentary.⁹² “Differential migration” refers to those migrations where different groups of migrating individuals, such as age and sex cohorts, move varying distances.⁹³ These two categories of migratory variation are not mutually exclusive.⁹⁴ We bias our subsequent attention here to focus more on differential migration, though most of the implications for conservation are the same—both invoke the need to consider types of individuals within a population differently, with respect to both the biogeographic and demographic consequences that ensue for conservation policy and planning.

A. Partial Migration

Partial migration has been documented in a wide variety of taxa from birds to fish, and is likely to be much more widespread than has historically been appreciated.⁹⁵ Partial migration appears to have a genetic basis in some taxa (i.e., the propensity for individuals to be migratory or sedentary is heritable),⁹⁶ but in other systems migration is known to be a conditional

⁸⁸ *Id.* at 2746.

⁸⁹ KEVIN WINKER, AM. ORNITHOLOGISTS' UNION, ORNITHOLOGICAL MONOGRAPHS NO. 69, ON THE ORIGIN OF SPECIES THROUGH HETEROPATRIC DIFFERENTIATION: A REVIEW AND A MODEL OF SPECIATION IN MIGRATORY ANIMALS 19–22 (2010).

⁹⁰ Endangered Species Act of 1973, 16 U.S.C. § 1531–1544 (2006). For example, see *id.* § 1533.

⁹¹ WINKER, *supra* note 89, at 22.

⁹² For further definition and discussion of “partial migration,” see DINGLE, *supra* note 51, at 304, and Meretsky et al., *supra* note 52, at 462.

⁹³ For further definition and discussion of “differential migration,” see DINGLE, *supra* note 51, at 304, and Meretsky et al., *supra* note 52, at 462.

⁹⁴ DINGLE, *supra* note 51, at 304.

⁹⁵ *Id.*

⁹⁶ *Id.*

strategy that varies in frequency with respect to habitat characteristics.⁹⁷ Demographic models and field data from certain species suggest that residents should gain major fitness advantages (e.g., earlier onset of reproduction in spring and perhaps reduced mortality associated with migratory journeys), for which the benefits of migration outweigh the benefits of staying put, despite any costs of making the journey.⁹⁸ In other species, residents (i.e., non-migrants) may pay high mortality costs by overwintering in harsh climates, so similarly, the net expected benefits of remaining (i.e., not migrating) in terms of overall fitness must be even greater.⁹⁹ Dominance interactions have been implicated as a major driver of both partial migration and differential migrations; both of these types of migration can segregate non-breeding populations with respect to age cohorts or sex cohorts, as older animals and males versus females, are typically more dominant.¹⁰⁰

In the junco, several populations that are altitudinal migrants (e.g., Yellow-eyed Juncos, Carolina Juncos, Red-backed Juncos, and southern races of the Oregon Junco group) also appear to be partial migrants to a large degree. Some individuals, especially males, stay on or very close to the montane breeding grounds, even during winter storms, while females and younger individuals are more likely to depart.¹⁰¹

B. Differential Migration

Among migratory members of a population, differential migration refers to variation in distance traveled, some long, some short; and it can give rise to habitat-related segregation of classes of individuals (e.g., by sex or age).¹⁰² If, for example, males are more likely to survive in one habitat type and females in another, then evolution will favor divergence in habitat preferences and dispersal behavior, causing the sexes to settle in different locations.¹⁰³ Diverse ecological mechanisms have been proposed to underlie

⁹⁷ *Id.* at 305.

⁹⁸ *Id.* (comparing survival rates and mating success rates for resident and migrant males). Survival rate was 50% for resident males and 17% for migrants.; mating success rate was 74% for resident males and 44% for migrants. *Id.*

⁹⁹ Ellen D. Ketterson & Val Nolan Jr., *The Role of Migration and Winter Mortality in the Life History of a Temperate-Zone Migrant, the Dark-Eyed Junco, as Determined from Demographic Analyses of Winter Populations*, 99 AUK 243, 243, 251 (1982).

¹⁰⁰ *Id.* at 243–44.

¹⁰¹ Horvath & Sullivan, *supra* note 62, at 482–83. See generally PHILIP UNITT, SAN DIEGO COUNTY BIRD ATLAS 542–45 (2004) (describing the breeding distribution, nesting, migration, winter habitat, conservation, and taxonomy characteristics of the Dark-eyed Junco); Miller, *supra* note 18, at 175.

¹⁰² Ellen D. Ketterson & Val Nolan Jr., *The Evolution of Differential Bird Migration*, in 1 CURRENT ORNITHOLOGY 357, 357–58 (Richard F. Johnston ed., 1983), available at <http://www.indiana.edu/~kettlab/pubs/Ketterson1983b.PDF>.

¹⁰³ Larissa Conradt, *Definitions, Hypotheses, Models and Measures in the Study of Animal Segregation*, in SEXUAL SEGREGATION IN VERTEBRATES: ECOLOGY OF THE TWO SEXES 11, 15–16 (K.E. Ruckstuhl & P. Neuhaus eds., 2005).

the evolution of differential migration among sex and age classes, including: differences in nutritive requirements (e.g., in Northern Elephant Seals, *Mirounga angustirostris*);¹⁰⁴ variable abilities to cope with thermally exposed habitats (e.g., in the Great Bustard, *Otis tarda*);¹⁰⁵ differential predation risk (e.g., in Western Sandpipers, *Calidris mauri*);¹⁰⁶ or intrasexual competition for breeding resources that may lead one sex (usually males) to travel shorter distances than the other sex so as to remain closer to the breeding range in autumn and to arrive earlier in spring to breeding grounds (e.g., in the White-Throated Sparrow, *Zonotrichia albicollis*),¹⁰⁷ a pattern that is probably common in many avian migrants. Additionally, other selective factors, such as climate and disease prevalence, may play a role in mediating differential migration.¹⁰⁸ It is also important to note that differential migration can lead to differences among age or sex or dominance cohorts not just in distances traveled, but also in the seasonal timing of migration—e.g., those that migrate farther from the breeding grounds may begin the return journey sooner.¹⁰⁹

C. The Junco, a Differential Migrant

In the winter, the range of the of the Slate-colored Junco (*Junco hyemalis hyemalis*) in eastern North America extends from the northern United States and the extreme southeast of Canada to the southern United States (as illustrated in Figure 2b).¹¹⁰ Settlement of the winter grounds occurs between mid-October and early December more or less simultaneously as the sex and age classes that migrate farther also migrate

¹⁰⁴ Brent S. Stewart, *Ontogeny of Differential Migration and Sexual Segregation in Northern Elephant Seals*, 78 J. MAMMOLOGY 1101, 1101 (1997).

¹⁰⁵ Carlos Palacín et al., *Differential Migration by Sex in the Great Bustard: Possible Consequences of an Extreme Sexual Size Dimorphism*, 115 ETHOLOGY 617, 617 (2009).

¹⁰⁶ Silke Nebel & Ronald C. Ydenberg, *Differential Predator Escape Performance Contributes to a Latitudinal Sex Ratio Cline in a Migratory Shorebird*, 59 BEHAV. ECOLOGY & SOCIOBIOLOGY 44, 44 (2005).

¹⁰⁷ See Daniel F. Mazerolle & Keith A. Hobson, *Patterns of Differential Migration in White-Throated Sparrows Evaluated with Isotopic Measurements of Feathers*, 85 CANADIAN J. ZOOLOGY 413, 417 (2007).

¹⁰⁸ See John T. Altringham & Paula Senior, *Social Systems and Ecology of Bats*, in SEXUAL SEGREGATION IN VERTEBRATES: ECOLOGY OF THE TWO SEXES, *supra* note 103, at 280, 301; Paulo Catry et al., *Sexual Segregation in Birds: Patterns, Processes, and Implications for Conservation*, in SEXUAL SEGREGATION IN VERTEBRATES: ECOLOGY OF THE TWO SEXES, *supra* note 103, at 352, 353; see also Sonia M. Altizer et al., *Associations Between Host Migration and the Prevalence of a Protozoan Parasite in Natural Populations of Adult Monarch Butterflies*, 25 ECOLOGICAL ENTOMOLOGY 125, 136 (2000) (discussing relationships between migration and disease prevalence).

¹⁰⁹ Catry et al., *supra* note 108, at 354.

¹¹⁰ NOLAN ET AL., *supra* note 8, at 5.

earlier.¹¹¹ Junco males are generally larger and dominate females, limiting their access to food resources.¹¹²

Data collected between 1950 and 1976 on migration schedules and population structure for *Junco hyemalis hyemalis* overwintering near Bloomington, Indiana, as well as data obtained from museum collections and from populations sampled at other locations throughout the winter range, revealed the historic pattern of geographic variation in winter population structure and dynamics of the junco.¹¹³ These data showed that females and older birds move farther south (i.e., farther from the breeding range) in winter than did males or younger birds.¹¹⁴ They also showed that overwinter survival was greater at lower than at higher latitudes but that annual survival did not differ by latitude.¹¹⁵

Assuming equilibrium population dynamics (i.e., a stable and equal population-wide sex annual rate of survival over time),¹¹⁶ the implication of these findings is that juncos making longer migrations to winter in the south (primarily females), where winter survivorship is higher, must face higher risk of mortality during migration; while juncos making shorter migrations (primarily males), given their observed lower winter survivorship due to extreme and unpredictable northern climates, must face lower risk of mortality during migration.¹¹⁷ Subsequent research ongoing to the present has examined both the proximate and ultimate factors underlying differential migration in the junco. It appears that the propensity for males and females to migrate different distances has at least a partial genetic basis, but it also depends on the environmental conditions (both the social environment and climatic environment) that they encounter along the way.¹¹⁸ And although behavioral data on dominance interactions indicate that male-dominance at feeding sites drives females southward,¹¹⁹ it is less clear why older birds migrate farther south. One idea is that because juveniles start migrating earlier in the autumn while adults finish their molt, they are able to establish themselves sooner as “owners” of wintering sites farther north.¹²⁰

¹¹¹ Val Nolan Jr. & Ellen D. Ketterson, *Timing of Autumn Migration and Its Relation to Winter Distribution in Dark-Eyed Juncos*, 71 *ECOLOGY* 1267, 1267, 1269 (1990).

¹¹² See Ellen D. Ketterson, *Aggressive Behavior in Wintering Dark-Eyed Juncos: Determinants of Dominance and Their Possible Relation to Geographic Variation in Sex Ratio*, 91 *WILSON BULL.* 371, 375–76 (1979).

¹¹³ Ellen D. Ketterson & Val Nolan Jr., *Geographic Variation and Its Climatic Correlates in the Sex Ratio of Eastern-Wintering Dark-Eyed Juncos (Junco hyemalis hyemalis)*, 57 *ECOLOGY* 679, 679–80 (1976).

¹¹⁴ See Ketterson & Nolan, *supra* note 102, at 358, 360.

¹¹⁵ Ketterson & Nolan, *supra* note 99, at 243.

¹¹⁶ Henk Wolda, *The Equilibrium Concept and Density Dependence Tests: What Does it All Mean?*, 81 *OECOLOGIA* 430, 430–31 (1989).

¹¹⁷ Ketterson & Nolan, *supra* note 99, at 251–52.

¹¹⁸ Ellen D. Ketterson & Val Nolan Jr., *Intraspecific Variation in Avian Migration: Evolutionary and Regulatory Aspects*, in *MIGRATION: MECHANISMS AND ADAPTIVE SIGNIFICANCE* 553, 567 (Mary Ann Rankin ed., 1985).

¹¹⁹ Cristol et al., *supra* note 16, at 36–37.

¹²⁰ Nolan & Ketterson, *supra* note 111, at 1268.

These studies of differential migration in the junco were some of the first to carefully document the phenomenon and examine its underlying causes and consequences in an ecological and evolutionary framework.

D. Differential Migrations: Implications for Conservation

Regardless of the specific ecological mechanisms, the key implication of both differential and partial migrations for conservation is that males versus females or young versus older birds may be found in different geographic regions during the non-breeding season and thus along different points in their migratory routes at different times of the year, and if one area were to be rendered uninhabitable or impassible, the consequences for the species or the migration could be far reaching and more damaging than the area involved might predict.

Thus, the task of conserving migrations in species that exhibit differential migration is made more complex and challenging. In extreme cases of segregation of sub-populations (e.g., males and females) for example, it has been proposed that to ease the implementation of conservation policy, management practices should consider the classes as completely different species.¹²¹ At the very least, management policies must include strategies that protect habitat at breeding and winter locations, migration corridors, and stop-over sites that may differ in usable food and shelter resources by sex or age. In most cases, migration corridors are unknown, particularly for neotropical migrants, and in many cases basic knowledge of migratory connectivity is nonexistent with respect to breeding and wintering grounds.¹²² Moreover, when conserving these habitats, policies must also take into account class differences in predator-prey dynamics, potential competitive interactions between classes, and effects of disease communities. Current data, however, are very limited with respect to the ecological mechanisms underlying differential migration.¹²³ Furthermore, while differential migration has been documented in a number of birds,¹²⁴ it is only recently that differential migration has been studied and fully characterized in Old World warbler families,¹²⁵ raising questions about even relatively well-studied species in which this phenomenon may be overlooked.

It is important to note that the benefits of conserving and the consequences of losing differential migrations are not clear. For example, is differential migration a mechanism to reduce competition between sex and

¹²¹ R. Terry Bowyer, *Sexual Segregation in Ruminants: Definitions, Hypotheses, and Implications for Conservation and Management*, 85 J. MAMMALOGY 1039, 1047, 1049 (2004).

¹²² Sievert Rohwer et al., *Ecology and Demography of East-West Differences in Molt Scheduling of Neotropical Migrant Passerines*, in BIRDS OF TWO WORLDS: THE ECOLOGY AND EVOLUTION OF MIGRATION 87, 96 (Russell Greenberg & Peter P. Marra eds., 2005).

¹²³ Bowyer, *supra* note 121, at 1047; Cristol et al., *supra* note 16, at 35.

¹²⁴ Cristol et al., *supra* note 16, at 33–35.

¹²⁵ Paulo Catry et al., *Differential Migration of Chiffchaffs* *Phylloscopus collybita* and *P. ibericus* in Europe and Africa, 36 J. AVIAN BIOLOGY 184, 185 (2005).

age classes, or does it place a heavier burden (e.g., migration distance traveled) on subordinate sex classes such that relaxation of segregation may be beneficial to the subordinate sex? In the junco, differential migration apparently results in sex differences in overwinter mortality versus that incurred during migration.¹²⁶ Recent changes in climate, however, are reducing the level of segregation between the sexes.¹²⁷ Relaxing segregation could reduce migrational mortality for females while increasing overwinter mortality due to extreme weather events, which could lead to skewed sex ratios and subsequent selective sweeps, fundamentally changing the genetic or phenotypic architecture of a population. It is worth noting again, however, that despite the depth of knowledge about the junco, it is extremely difficult to predict the consequences of any potential change in demography or distribution. This holds to an even greater degree for the vast majority of species whose migratory biology remains undocumented.

V. MIGRATIONS AS DYNAMIC PHENOMENA: RESPONSES TO ENVIRONMENTAL CHANGE

In addition to the *spatial* (i.e., geographic) variation in migratory biology observed both among and within populations, migrations also vary within species across another important axis: time. Over both contemporary and historical time scales, the characteristics of migrations are constantly changing in response to shifting environmental conditions. As anthropogenic climate change and habitat alteration progress at alarming rates, this reality must be an especially important aspect of research, policy, and management agendas for migration—both with respect to researching and mitigating the detrimental effects of altered environments on migrations, but also insofar as the habitat ranges and phenologies of migratory animals represent “moving targets.”

Below, we highlight two examples from the Dark-eyed Junco, both of which illustrate how human activities may have led to dramatic shifts in migratory processes over time, even over just a few decades. While these examples are striking because we can time their occurrence, the diversity of migratory phenomena across closely related species and populations (which indicates repeated and relatively recent evolutionary changes), as well as additional contemporary examples that also demonstrate recent and rapid shifts in migration in response to changing climates¹²⁸ and urbanization, indicate that migrations can be quickly gained, lost, or altered as environments change.

¹²⁶ Ketterson & Nolan, *supra* note 99, at 251–57.

¹²⁷ See *infra* Part V.A.

¹²⁸ For several examples, see Thomas Moore, *Climate Change & Animal Migration*, 41 ENVTL. L. 393, 402–03 (2011).

*A. Shifts in Junco Winter Distribution and Sex Ratio Associated
with Climatic Warming*

Over the past 100 years, the Earth's mean temperature has increased at least 0.6 degrees Celsius.¹²⁹ This increase has resulted in long-term, large-scale alterations in phenology, distribution, and population dynamics of eighty-five percent of the animal and plant species that have been studied.¹³⁰ Warmer temperatures have also been associated with a ten percent reduction in winter snow cover, permitting increases in available winter seed biomass and the migration of several plant species into previously unavailable northern habitats.¹³¹ For ground-feeding birds, these changes may have lessened the cost of overwintering at higher latitudes by reducing the number of extreme temperature drops that induce fasting events or by decreasing competition for winter resources,¹³² thereby decreasing the *relative* benefits of prolonged migration farther south.

To date, the main focus of study with respect to distribution changes following climate warming has not included differential migrants.¹³³ As we mentioned above, for differential migrants, the consequences of changes in climate and distribution may be especially problematic to predict, as relaxation in segregation may impact one sex more than the other, resulting in significant changes in demography, population dynamics, and possibly changes in abundance.¹³⁴ Furthermore, climate change can have significant effects on wintering physiology impacting survival as well as reproductive success. In the junco, where the correlation between historical sex ratio during winter (the result of sex differences in distance migrated) and climate measures is high,¹³⁵ one would predict that with milder climates females may no longer migrate as far south as they did previously.

When recent demography of wintering populations across the junco's winter range was compared to data collected thirty years ago to assess whether recent warming has led to detectable changes in the population structure of the Dark-eyed Junco (*Junco hyemalis hyemalis*), the

¹²⁹ James Hansen et al., *Global Temperature Change*, 103 PROC. NAT'L ACAD. SCI. 14,288, 14,288-89 (2006); Terry L. Root et al., *Fingerprints of Global Warming on Wild Animals and Plants*, 421 NATURE 57, 57 (2003).

¹³⁰ Peter A. Cotton, *Avian Migration Phenology and Global Climate Change*, 100 PROC. NAT'L ACAD. SCI. 12,219, 12,221-22 (2003); Root et al., *supra* note 129, at 87.

¹³¹ Catriona E. Rogers & John P. McCarty, *Climate Change and Ecosystems of the Mid-Atlantic Region*, 14 CLIMATE RES. 235, 237-40 (2000); Hans-Christian Schaefer et al., *Impact of Climate Change on Migratory Birds: Community Reassembly Versus Adaptation*, 17 GLOBAL ECOLOGY & BIOGEOGRAPHY 38, 38-47 (2008).

¹³² Gian-Reto Walther et al., *Ecological Responses to Recent Climate Change*, 416 NATURE 389, 389-91 (2002).

¹³³ See generally Katrin Böhning-Gaese & Nicole Lemoine, *Importance of Climate Change for the Ranges, Communities and Conservation of Birds*, in 35 ADVANCES IN ECOLOGICAL RESEARCH: BIRDS AND CLIMATE CHANGE 211, 212-13 (2004) (reviewing current research and suggesting urgent questions for future research).

¹³⁴ See *supra* Part IV.D.

¹³⁵ Ketterson & Nolan, *supra* note 99, at 243.

comparison supports this prediction.¹³⁶ Recent data suggest significant changes in sex ratio across the junco's winter range with relatively more females at more northern latitudes and relatively fewer males at southern latitudes.¹³⁷ Additionally, these changes in sex ratio appear to be highly correlated with the milder present-day winter climate.¹³⁸ In association with increases in the proportion of females making shorter migrations, there has also been a distributional shift. The number of juncos wintering further north has increased and the number in more southerly regions has declined.¹³⁹ Current data also suggest that in years in which climate is milder, females truncate their migratory journey and remain in larger numbers at northern and intermediate latitudes.¹⁴⁰ "When climate is more like historic conditions (i.e., more days with extreme minimum temperatures and snow fall), females make longer migrations and winter sex ratios match historic data."¹⁴¹ Such instability in sex ratio between years suggests plasticity in junco migratory behavior and a possible adaptation to changing climate.

B. Rapid Loss of Junco Migration Following Establishment in a Novel Urban Environment

As discussed above with respect to geographic variation, a full range of migratory diversity is represented within the western Oregon Junco group, with northern breeding populations migrating thousands or hundreds of kilometers southwards to spend the winter, whereas southern groups are facultative altitudinal migrants, leaving their montane breeding grounds to winter on the coast. In San Diego County, California, the *thurberi* race of the Oregon Junco (*Junco hyemalis thurberi*) has historically been found breeding only in higher elevation (e.g., >1500 meters) forest habitats in the mountains seventy kilometers inland from the coast.¹⁴² These juncos migrate variable distances to lower elevations and coastal areas during harsh winter weather.¹⁴³ In the early 1980s, however, a small isolated breeding population (approximately eighty breeding pairs), colonized an atypical and previously unoccupied habitat: the urban and coastal campus of the University of California-San Diego—presumably as the result of some wintering individuals failing to return to the breeding grounds, but instead remaining on the coast to breed.¹⁴⁴ Since then, a stable breeding population has persisted as an effective biogeographic island. Many biological changes have

¹³⁶ D. M. O'Neal et al., *Immune Function Across Latitudinal and Urban Gradients in a Differential Migrant*, 50 INTEGRATIVE & COMP. BIOLOGY (forthcoming).

¹³⁷ *Id.*

¹³⁸ *Id.*

¹³⁹ *Id.*

¹⁴⁰ *Id.*

¹⁴¹ *Id.*

¹⁴² UNITT, *supra* note 101, at 542.

¹⁴³ *Id.* at 544; Miller *supra* note 17, at 289.

¹⁴⁴ Yeh, *supra* note 36; Pamela J. Yeh & Trevor D. Price, *Adaptive Phenotypic Plasticity and the Successful Colonization of a Novel Environment*, 164 AM. NATURALIST 531, 532 (2004).

since been documented,¹⁴⁵ including that the colonist population is entirely sedentary, remaining on or near its breeding territories year round.¹⁴⁶

Preliminary data suggest that the differences in migratory disposition (i.e., the lack of migration) in the colonist population have a genetic basis, as evidenced by differences in migratory restlessness behaviors in captive birds from the colonist (sedentary) population and a population from the nearby ancestral-range (altitudinal migrants) when raised under identical environmental conditions.¹⁴⁷ Though colonist birds still exhibited seasonal migratory restlessness behaviors in the common captive environment, the intensity of these behaviors were greatly reduced in the captive birds originating from the colonist population when compared to birds originating from the montane ancestral-range.¹⁴⁸

Although the exact sequence of events leading to population establishment and the cessation of migration in this system is not entirely clear, one thing is certain: the Mediterranean climate and natural coastal sage scrub habitats of San Diego County do not include suitable junco habitat (which is typically seasonal and forested). However, the presence of thousands of landscaped eucalyptus trees as well as ornamental vegetation and abundant anthropogenic water and food resources, has created an “artificial habitat,” allowing juncos to establish this population in a climatically mild and urban environment. Increased sedentary behavior (i.e., loss of migration) following colonization of urban habitats has also been documented in European blackbirds, apparently over the course of just a few hundred years since these birds recolonized cities.¹⁴⁹

*C. Migration as Dynamic in Response to Changing Environments:
Implications for Conservation*

The sensitivity of migrations to environmental change has several important implications for conservation agendas. As the above examples from the junco indicate, climate change and habitat alteration have the potential to lead to geographic range shifts, changes in intra- or inter-species

¹⁴⁵ For additional examples of ways in which the biology of the recently established urban colonist juncos population differs, see Gonçalo C. Cardoso & Jonathan W. Atwell, *Directional Cultural Change by Modification and Replacement of Memes*, 65 *EVOLUTION* 295, 296 (2011), Melissa M. Newman et al., *Reduced Territorial Responses in Dark-Eyed Juncos Following Population Establishment in a Climatically Mild Environment*, 71 *ANIMAL BEHAVIOUR*, 893, 893 (2006), C. A. Rasner et al., *Genetic and Morphological Evolution Following a Founder Event in the Dark-Eyed Junco, Junco hyemalis thurberi*, 13 *MOLECULAR ECOLOGY* 671, 672, 679 (2004), Whittaker et al., *supra* note 38, at 611, Yeh, *supra* note 36, at 166–67, and Yeh & Price, *supra* note 144, at 534, 540.

¹⁴⁶ Yeh & Price, *supra* note 144, at 533.

¹⁴⁷ Rebecca J. Rice et al., *Sleepless in San Diego: Migratory Restlessness Behavior Differs Between Two Recently Diverged Songbird Populations* (unpublished manuscript) (on file with author).

¹⁴⁸ *Id.*

¹⁴⁹ Jesko Partecke & Eberhard Gwinner, *Increased Sedentariness in European Blackbirds Following Urbanization: A Consequence of Local Adaptation?*, 88 *ECOLOGY* 882, 882 (2007).

competition, and even the cessation of migration altogether. Thus, it is easy to imagine scenarios in which a species could be “conserved” from a demographic standpoint, but the phenomenon of its migration could be lost or dramatically altered in response to changing environments.

Scientists generally consider such changes in the biology (e.g., physiology, behavior, appearance) of animals in response to environmental change to be the result of either genetic changes (evolution), developmental changes induced by the environment (phenotypic plasticity), or perhaps most typically, some combination of both.¹⁵⁰ This is true for migrations, as evidenced by prior research that indicates both a genetic and an environmental basis for the timing and distance of migrations.¹⁵¹ This means that observed shifts in breeding or wintering ranges of migratory animals, or changes in the onset or duration of migration, could result from either 1) rapid genetic evolution of the population in response to new (natural) selective forces, or 2) from individual organismal responses to new environmental regimes.

In most cases, these alternatives can be difficult to distinguish, but they have important implications for conservation. In short, species that lack the genetic variance in migratory disposition (e.g., complete, obligate migrants) to adapt via natural selection may be more imperiled, as might species that exhibit strong but maladaptive developmental responses to environmental change (e.g., “mis-timing” of migration due to shifting temperature cues). Although migratory species that exhibit sufficient genetic variation or adaptive plastic responses to environmental change may be less at risk of extinction, adaptation to novel climatic regimes or altered habitats could include range shifts, or attenuation, or cessation of migratory behavior. In some cases, it is plausible that the effects of changing environments on migrations could be reversed by management efforts, and this would probably be more likely and occur more quickly in the case of plastic responses.

Future efforts to conserve migrations should incorporate the temporally dynamic nature of migrations in two possible ways. First, following from current and future science-based understandings of how changing climates and altered habitats influence migratory biology, policy mandates and management activities could be pursued that minimize or reverse these impacts. For example, food supplementation, predator or competitor removal or mitigation, or management of local vegetation could aid breeding animals who have “mis-timed” their migrations to no longer coincide with the emergence of local food supplies or who have shifted their ranges maladaptively in response to changing climates. Similarly, planning of suburban development could include restrictions and policies that prevent the availability of *ad libitum* anthropogenic food and water sources to migratory wildlife on wintering grounds that could induce them to become sedentary. Second, an awareness of how migrations might respond to

¹⁵⁰ For additional discussion on this topic, see Meretsky, Atwell & Hyman, *supra* note 52, at 467.

¹⁵¹ *Id.* at 463–64, 468; DINGLE *supra* note 51, at 293–94.

changing environments can allow conservationists to use predictive tools to prioritize the best habitats or mitigation strategies based not on current environmental conditions and habitat ranges, but based on those conditions that may be predicted by climatic or land-use models.

VI. CONCLUSION

Characterizing and incorporating the spatially and temporally variable nature of animal migrations into conservation agendas is a formidable objective, and one that adds layers of complexity to an already complex set of legal, political, and management challenges. Even for a single migratory species, achieving the tasks of documenting geographic variation among populations, evaluating whether there is variation among sex or age cohorts within populations, and investigating how habitat alteration or climate change might likely impact migratory behaviors is daunting. Nevertheless, these pieces of information are essential considerations for the development of conservation strategies, and even limited knowledge—generated with the assistance of emerging technologies and collaborative approaches—can present opportunities to develop targeted, smaller-scale, more efficient, and ultimately more effective conservation laws, policies, and management plans for animal migrations.










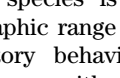
	Form	Subgroup	Migratory Behavior	Range
Dark-Eyed Juncos (<i>Junco hyemalis</i>)		Slate-colored Junco (SCJU)	Long-distance (northern race); Altitudinal (Appalachian mtns.)	Fig. 2b
		White-winged Junco (WWJU)	Long-distance or short-range	Fig. 2c
		Oregon Junco (ORJU)	Long distance (northern groups); Altitudinal (southern mtns.)	Fig. 2d
		Red-backed Junco (RBJU)	Altitudinal and/or short-range	Fig. 2d
		Pink-sided Junco (PSJU)	Long-distance or short-range	Fig. 2c
		Gray-headed Junco (GHJU)	Long-distance or short-range	Fig. 2c
		Guadalupe Junco (GUJU)	Sedentary	Fig. 2c
Yellow-eyed Juncos (<i>Junco phaeonotus</i>)		Mexico Yellow-eyed Junco (YEJU MX)	Altitudinal or sedentary	Fig. 2e
		Guatemala Yellow-eyed Junco (YEJU GU)	Sedentary	Fig. 2e
		Volcano Junco (VOJU)	Sedentary	Fig. 2e

Figure 1. Variation in the appearance and migratory behavior within junco species is shown, along with a reference to figures of the geographic range for each group. Juncos exhibit extensive variation in migratory behavior among groups, ranging from long-distance to sedentary, with geographic overlap in the wintering ranges. Such migratory variation exists within many species, but it is more easily observed in juncos due to the striking differences in feather plumage color of the various sub-species and races.

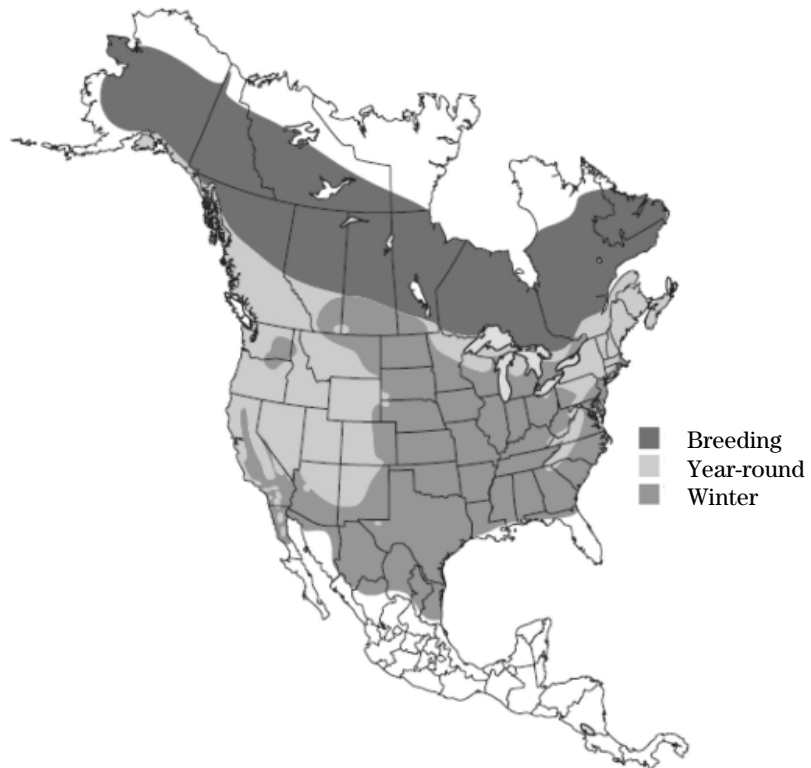


Figure 2a. The breeding, wintering, and year-round ranges of the Dark-eyed Junco species (*Junco hyemalis*) as a whole is shown. Throughout their range, Dark-eyed Juncos vary extensively in migratory behavior and plumage coloration, including long-distance, short-range, and altitudinal migrants, as well as sedentary populations (see Figures 1, 2b, 2c, & 2d).

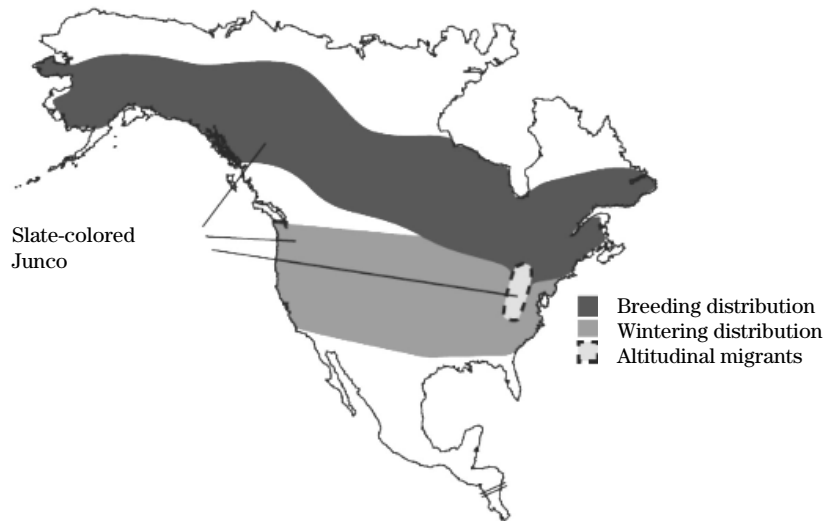


Figure 2b. The map shows stylized geographic ranges of the Slate-colored Junco group of the Dark-eyed Junco species. Slate-colored Juncos are either long-distance or short-range migrants (northern breeder) or altitudinal migrants (Appalachian Mountains).

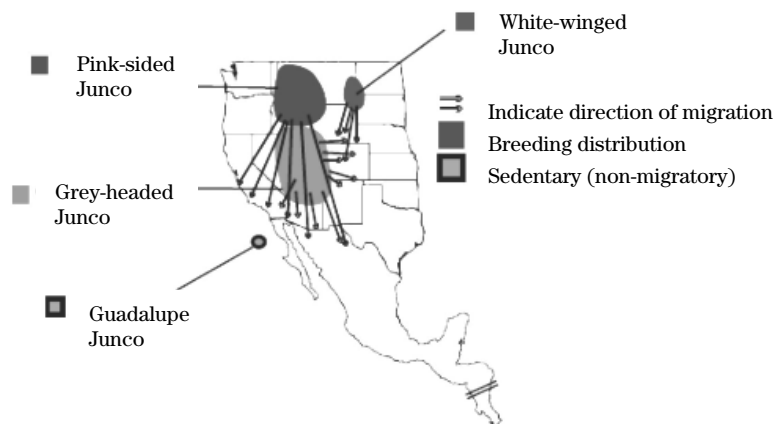


Figure 2c. Breeding ranges of the Pink-sided Junco, White-winged Junco, and Grey-headed Junco groups of the Dark-eyed Junco species are shown, with arrows indicating the direction of long-distance or short-range migration to overlapping wintering ranges. Also shown is the year-round range of the sedentary Guadalupe Junco, also part of the Dark-eyed Junco species complex.

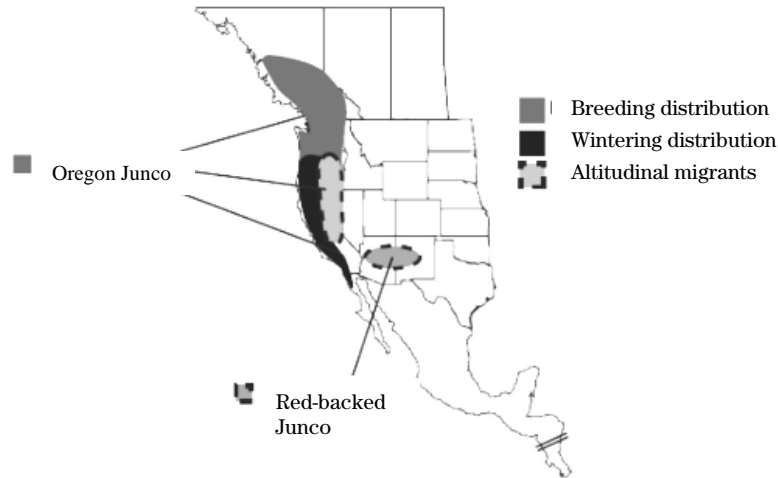


Figure 2d. The Oregon Junco group of Dark-eyed Juncos includes long-distance, short-range, and altitudinal migrants throughout its range, and even a recently established sedentary population in San Diego County (see Part V.B.). The Red-backed group of Dark-eyed Juncos is mostly altitudinal in its migration.

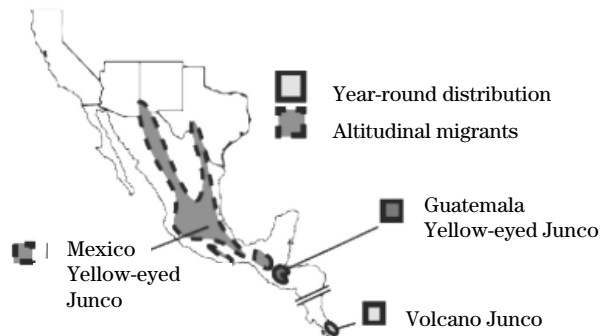


Figure 2e. The Yellow-eyed Junco Species includes both altitudinal migrants and sedentary groups throughout its range, which extends from the highlands of Guatemala northwards into the mountains of Mexico and the southwestern US. The southernmost junco species, the Volcano Junco, is found in the highlands of western Panama and Costa Rica and is entirely sedentary.