

THE ADIRONDACK ARCHIPELAGO

JEREMY J. KIRCHMAN¹ AND JOEL RALSTON^{2,3}

1. New York State Museum, 3140 Cultural Education Center, Albany, NY 12230. jeremy.kirchman@nysed.gov

2. Department of Environmental Conservation, University of Massachusetts, 160 Holdsworth Way, Amherst, MA 01003

3. Current address: Department of Biology, Saint Mary's College, Notre Dame, IN 46556

The Adirondacks comprise an uplifted, highly dissected dome of Canadian Shield rocks that formed between 880 million to 1.1 billion years ago (Wiener et al. 1984). This dome of ancient rock rose up and out of the surrounding strata of Paleozoic bedrock a mere 5.5 million years ago, forming a well-circumscribed mountain range that rises to a maximum elevation of 1629 m. Thus, to geologists, the Adirondacks are relatively new mountains made of very old rocks, an easily accessible window into the deep past of North America, and a trove of mineral riches. To biologists the Adirondacks are no less interesting, and for a similar reason. Just as the ancient basement rocks of North America protrude like an island above the surrounding sea of younger rocks, so too does a distinct ecosystem. The evergreen-dominated boreal forest that stretches from Alaska to the Canadian Maritimes protrudes on Adirondack mountains above the surrounding deciduous forests that dominate the landscape elsewhere in New York and New England. Sitting at 43° N - 45° N latitude, the Adirondacks are an isolated southern outpost of the boreal forest biome that, at lower elevations, reaches its southern boundary north of us at 48° N - 50° N (Figure 1).

Species that are adapted to the moist, cool climate of the boreal forest occupy two distinct habitat types in the Adirondacks, as defined by the comprehensive Northeast Terrestrial Habitat Classification System: Boreal Upland Forest, and Northern Peatland (NETHCS, available at www.conservationgateway.org). Boreal Upland Forest is the spruce (*Picea*) and fir (*Abies*) dominated forest one finds on mountain slopes from 850 m—1450 m (Whitehead

and Jackson 1990). It comprises 11% of the area of the Adirondack Park, whereas Northern Peatlands, the bogs and fens found at lower elevations, comprise only 1% of the Park (Glennon and Curran 2013). Both of these habitat types are naturally patchy, making the Adirondacks more like an archipelago than a single island of boreal habitat. Boreal forest specialists in the Adirondacks are therefore distributed in disjunct “island” populations, isolated from one another and from the contiguous boreal forest farther north. To a biologist, the Adirondacks are an archipelago of isolated habitat islands, a natural laboratory for studying ecology and evolution.

Biologists studying life on islands have contributed much to our understanding of how evolution works. Charles Darwin and Alfred Russel Wallace independently developed the theory of natural selection by studying the subtle differences between populations from different oceanic islands (Darwin 1859). They both noted that birds often differ in color or body size from island to island, indicating that isolated populations may be evolving independently of one another, adapting to the local conditions. The patterns they observed as they traveled and collected specimens in the Galapagos Islands and the Indo-Pacific revealed to them the primary mechanisms of evolution and the importance of isolation in generating biodiversity. In the 150 years that have followed Darwin and Wallace’s discovery, the study of geographic patterns of variation among isolated populations has become a foundation of our current understanding of how new species are formed, and how they are lost to extinction (Mayr and Diamond 2001, Steadman 2006, Price 2008).

Geographically isolated populations of the same species may evolve to become genetically or physically distinct depending on the relative connectivity among populations (Avice 2004). Interbreeding between populations, what population biologists call “gene flow,” will preserve the similarities among isolated populations. Population biologists are therefore interested in the amount of genetic diversity and the relative levels of divergence versus gene flow among geographically disjunct populations such as those on archipelagos. Populations with low levels of genetic diversity may suffer from increased inbreeding depression, decreased reproductive fitness, and increased extinction risk (Westemeier et al. 1998, Frankham 2005). Conservation efforts focused on disjunct populations therefore often aim to promote genetic diversity or conserve genetically unique conservation units (Moritz 2004).

The genetics of species living in “sky island” archipelagos like we find in the Adirondacks have been well studied in the Rocky Mountains, the European Alps, in tropical montane forests in the Andes, and in the American Southwest where pinion-juniper forest is found on mountain slopes above the surrounding desert (Bech et al. 2009, DeChaine and Martin 2005, McCormack et al. 2008, Knowles 2000, Särkinen et al. 2012). Despite their promise as a sky island study system, the Adirondacks are understudied by evolutionary biologists,

and little is known regarding patterns of genetic divergence among Adirondack bird populations. Within the last few years, our genetics research at the New York State Museum and by ornithologists at other institutions has begun to reveal the evolutionary history and relationships among bird species within the Adirondack archipelago. In the sections that follow, we describe some of the results of this ongoing research, focusing on these questions: (1) Are Adirondack populations of boreal forest birds genetically distinct from other populations? (2) Do different bird species share similar biogeographic histories? and (3) How is climate change likely to influence the genetic diversity of Adirondack birds?

The work of answering these questions begins in the field, where wild birds from different mountains or bogs in the Adirondacks and from neighboring mountain ranges are captured, and small tissue samples (blood or feathers) are preserved for analysis in the genetics lab. DNA is extracted from tissues, specific genes with known rates of mutation are isolated from each bird's genome, and the sequence of its DNA nucleotides is determined biochemically. Finally, the gene sequences from all the birds are compared for differences and birds are grouped by which version of the gene (allele) they are carrying. Birds whose sequences are identical at all nucleotides are said to share the same allele. Population level diversity is measured by calculating the number of alleles in the sample and the number of "private alleles," which are those that are found only in one geographic population.

ARE ADIRONDACK POPULATIONS OF BIRDS GENETICALLY UNIQUE?

Genetic research targeting a well-studied gene from the mitochondrial genome, the control region, has been conducted for three species that have been sampled from multiple sites in the Adirondacks: Spruce Grouse (*Falciennus canadensis*) (Kirchman, unpublished data), Boreal Chickadee (*Poecile hudsonicus*) (Lait and Burg 2013) and Blackpoll Warbler (*Setophaga striata*) (Ralston and Kirchman 2012). Patterns of variation in the mitochondrial control region for these species are summarized in Table 1. The contrasting levels of genetic diversity and distinctiveness of the Adirondack populations demonstrate the different ways that wild populations can be genetically structured. The Adirondack population of Spruce Grouse is unique, with very low genetic diversity. Of the 22 individuals sequenced, we found only 3 alleles, and all three of these were private to the Adirondacks, meaning they were not found in neighboring populations. Spruce Grouse from Vermont, Maine, and Ontario, however, were more diverse with almost every individual being genetically distinct. These results indicate to us that Adirondack Spruce Grouse are reproductively isolated from neighboring populations. The low level of heterozygosity (h) in this population suggests a genetic "bottleneck" that likely results from the well-documented decline of the Adirondack population over the last 100+ years (Ross and Johnson 2012). Conservation actions aimed at increasing genetic diversity in Adirondack Spruce Grouse, including the current program of translocation of birds from outside populations by the NYSDEC, might be beneficial and could stave off extirpation of this population.

Blackpoll Warblers, on the other hand, are equally diverse in the Adirondacks and in surrounding populations in the Northeast, and the Adirondacks hold very few unique alleles for this species (Table 1). Blackpoll Warblers from the Adirondacks have nearly three times the level of heterozygosity of Adirondack Spruce Grouse, whereas both species have high heterozygosity in neighboring populations. This suggests that geographically isolated Blackpoll Warbler populations, unlike Spruce Grouse, are genetically well connected with gene flow occurring regularly. The Adirondack population of the Boreal Chickadee is intermediate to extremes exemplified by Spruce Grouse and Blackpoll Warbler. Boreal Chickadees have lower genetic diversity in the Adirondacks than in neighboring populations, but the reduction is much less drastic than that seen in Spruce Grouse.

These different patterns across species may be related to the relative isolation of the habitat types preferred by each species, to their different migratory behaviors, or to the different effective population sizes of these species in the Adirondacks. The Spruce Grouse is a rare, non-migratory resident species that prefers Northern Peatlands, while Blackpoll Warblers are long-distance migrants found in high abundance in the Boreal Upland Forest. Not surprisingly, the Boreal Chickadee falls between these two ends of the spectrum: it is a locally common, non-migratory resident species that can be found in both Northern Peatlands and the Boreal Upland Forest. It is possible that the small area and greater isolation of Northern Peatlands has contributed to the genetic isolation of its bird populations, compared to Boreal Upland Forests which have a greater area and may be more spatially connected. Alternatively, the long distance migratory behavior of Blackpoll Warblers may give this species stronger dispersal abilities compared to the non-migratory Spruce Grouse and Boreal Chickadee. Ongoing work in our lab is aimed at testing these alternative hypotheses by analyzing a larger sample of genetic data from Boreal Chickadees and additional species such as the Yellow-bellied Flycatcher and Bicknell's Thrush. Both the Yellow-bellied Flycatcher and Bicknell's Thrush are migrant species of the Upland Boreal Forests, and the former also breeds in Northern Peatlands.

DO DIFFERENT BOREAL BIRD SPECIES SHARE SIMILAR BIOGEOGRAPHIC HISTORIES?

Much like Adirondack geology, Adirondack biota and genetic patterns held within them can offer a glimpse into the history of North America. Intermittently throughout the glacial cycles of the last two million years, vast portions of North America were covered in boreal forests similar to those that remain in the Adirondacks (Whitehead and Jackson 1990). As forests expanded and contracted across the landscape, boreal bird populations were reconfigured, combining at times into large contiguous populations, followed by periods during which populations were sundered into smaller isolates. Animal populations

still retain the signature of these historic distributional changes in their genomes, and we can use genetic patterns found in modern populations to understand the timing and the path by which different species came to occupy their current distributions (Avice 2004). This approach, known as comparative phylogeography, aims to understand how and why genetic patterns differ across species (Zink 1996). Whereas in the previous section we interpreted differences in the genetic patterns of Spruce Grouse, Boreal Chickadee, and Blackpoll Warbler in terms of modern gene flow and isolation, comparative phylogeography uses genetic variation sampled throughout species' ranges to infer the extent to which biogeographic histories are shared among different species. Here we are interested in comparing genetic patterns across boreal bird species to understand whether these species survived the Pleistocene in different places and how long these species have co-occurred in the Adirondacks.

Phylogeographic studies have been published for seven species of boreal forest birds that breed in the Adirondacks, and the patterns observed are as diverse as the species themselves. Our work on Blackpoll Warblers shows that all modern populations of this species, including those as far away as Alaska, are descendent from a single, Late-Pleistocene population that was likely located in eastern North America south of the ice sheet at the last glacial maximum (Ralston and Kirchman 2012). Studies of other boreal species have differed in the number and location of inferred ancestral populations that dwelled in Pleistocene refugia (Brelsford et al. 2011, Burg et al. 2014, Milá et al. 2007, Ruegg et al. 2006, van Els et al. 2012). A split into eastern and western refugia has been suggested for Boreal Chickadee (*Poecile hudsonicus*), Golden-crowned Kinglet (*Regulus satrapa*), and Swainson's Thrush (*Catharus ustulatus*), and multiple refugia are also likely for the Yellow-rumped Warbler species complex (*Setophaga coronata*). Despite the different number of inferred refugia in these species, they may have colonized the Adirondacks at similar times given that they all persisted in eastern North American refugia. Gray Jay (*Perisoreus canadensis*) and Dark-eyed Junco (*Junco hyemalis*), on the other hand, are suggested to have survived the Pleistocene in a single or multiple southwestern refugia and expanded into their current distribution by first colonizing northern regions of western North America and later expanding eastward from the western boreal forest (Milá et al. 2007, van Els et al. 2012). Together, these results suggest that the Adirondack avifauna may have been pieced together at different times and via different routes. The community of boreal bird species that inhabit the Adirondack Archipelago today has changed in response to past climate changes and is expected to change further in response to anthropogenic climate warming in the coming century. Let us now turn to our final research question and combine predictive models of climate change with what we know about genetic diversity.

HOW WILL CLIMATE CHANGE INFLUENCE THE GENETIC DIVERSITY OF ADIRONDACK BIRDS?

As global climates warm, North American birds are shifting their distributions to higher latitude and higher elevation to track suitable conditions (Tingley et al. 2009, Zuckerburg et al. 2009, Auer and King 2014). Adirondack populations of boreal forest birds already located at high elevations and at the southern edge of species' ranges may be especially vulnerable to climate change as warming threatens to push these species out of the Adirondack archipelago. Analysis of long-term bird population trends shows that several boreal forest specialists are already declining at the southern periphery of the boreal forest (Ralston et al. 2015). To the extent that isolated, peripheral bird populations are genetically distinct, climate change may threaten genetic diversity and increase extinction risk. To examine this potential we have used computer models of boreal bird species distributions to predict whether mountain populations found in New York and neighboring states will be extirpated in the current century. These models overlay maps of current species occurrences with maps of climatic conditions (various measures of temperature and precipitation) and then use predicted climate conditions to project where a species will likely be distributed in the future. Finally, we combine these modeled distributions with our genetic data to predict whether climate change will have significant effects on the genetic diversity of boreal birds.

We have modeled the distribution of 15 boreal forest bird species to the year 2080 to predict the extent to which ranges will shift, leading to the extirpation of isolated populations at the southern periphery of the boreal forest (Ralston and Kirchman 2013). Our climate-based distribution models predict substantial range shifts to the north and northwest up to 1400 km, and that nearly all 15 species we modeled will be extirpated from high elevations in New York, Vermont, and New Hampshire by 2080 (Table 2, Figure 2). It is important to note that these models are based only on predicted climate change and that habitats may change more slowly than climate, allowing birds to persist in mountain populations longer than predicted by climate alone. Climate-only distribution models probably are worst-case scenarios, and some species will surely tolerate the changes better than others. These predictions are nevertheless alarming, as they suggest the possibility of whole-scale faunal turnover at the southern edge of the boreal forest in the present century.

For the species with the most comprehensive genetic sampling, the Blackpoll Warbler, we compared genetic data from mountain populations predicted to be extirpated to more northern populations predicted to persist. As noted above, the DNA data indicate that Blackpoll Warblers are highly dispersive and likely have high levels of gene flow among populations. Due to this, very few alleles in Blackpoll Warblers are unique to mountain

populations, and population extirpations due to predicted climate change are not likely to affect heterozygosity or allelic richness significantly (Ralston and Kirchman 2013). The same cannot be said to be true for Spruce Grouse, which has a distinctive gene pool in the Adirondacks. Thus, the genetic consequences of climate change will vary across species according to their dispersal ability, history of isolation, and extent of their distribution north of the Adirondacks. Ongoing work in our labs is aimed at determining whether the predicted effects of climate change are consistent across species. One species we find particularly interesting in this regard is Bicknell’s Thrush; like Blackpoll Warbler, it is migratory and is expected to have high levels of gene flow among isolated populations. But Bicknell’s Thrush is found only in high elevation forests of the northeast United States and eastern Canada. Loss of the southernmost populations in this species may therefore represent a more significant proportion of the gene pool than for species distributed across the Canadian boreal forests such as Blackpoll Warbler.

The great island biogeographer Alfred Russel Wallace wrote that the distributions of species are “in their very nature the visible outcome and residual product of the whole past history of the earth” (Wallace 1881). The bird species of the Adirondacks have much to teach us about their own evolutionary histories and about the history of the great boreal forest ecosystem. Ongoing efforts to document geographic patterns of genetic variation in Adirondack birds will, we hope, push farther open the window on the past and enable clearer views of the future of the Adirondack archipelago.

Table 1. Genetic diversity of boreal forest bird species that breed in the Adirondacks. Data are DNA sequences (mitochondrial control region) obtained from multiple birds from the Adirondacks and from neighboring populations. Summary includes the length of the sequences (in base-pairs, “bp”), sample size (number of birds, “n”), number of distinct sequences identified in the sample (“alleles”), number of “private” alleles found only in the Adirondack population, and haplotype diversity (“h”), which is a measure of population level genetic diversity. Spruce Grouse and Boreal Chickadee are non-migratory, and Blackpoll Warbler migrates to the tropics for the non-breeding season.

SPECIES	LENGTH	ADIRONDACKS				NEIGHBORING POPULATIONS		
		n	ALLELES	PRIVATE	h	n	ALLELES	h
Spruce Grouse	1129 bp	22	3	3	0.255	17 ¹	14	0.971
Boreal Chickadee	776 bp	6	3	2	0.600	83 ²	45	0.879
Blackpoll Warbler	355 bp	23	7	2	0.731	158 ³	41	0.813

1. Samples from Vermont, Maine, Ontario.
2. Samples from Catskills, Vermont, Maine, Quebec, New Brunswick, Nova Scotia.
3. Samples from Ontario, Quebec, New Brunswick, Nova Scotia, Newfoundland.

Table 2. Predicted geographic shifts of entire breeding ranges (measured from the centroid of the range) and percent change in occupied area in New York, Vermont, and New Hampshire by the year 2080, for 15 boreal forest bird species. The predicted climate conditions for 2080 are from the Hadley Centre Coupled Model version 3 under carbon emissions scenario B2 of the Intergovernmental Panel on Climate Change (Intergovernmental Panel on Climate Change 2000). Data from Ralston and Kirchman (2013).

SPECIES	RANGE SHIFT (km), DIRECTION	CHANGE IN AREA (%) IN NY, VT, NH
Spruce Grouse	903, NW	-99.9
American Three-toed Woodpecker	532, NW	-100.0
Black-backed Woodpecker	1160, NW	-100.0
Yellow-bellied Flycatcher	493, NW	-67.9
Gray Jay	811, NW	-100.0
Boreal Chickadee	1014, NW	-99.9
Ruby-crowned Kinglet	600, NW	-100.0
Bicknell's Thrush	180, NW	-81.8
Swainson's Thrush	660, NW	-98.5
Tennessee Warbler	841, NW	-80.5
Blackpoll Warbler	1408, NW	-97.4
Bay-breasted Warbler	811, NW	-50.2
Cape May Warbler	721, NW	-94.3
Yellow-rumped Warbler	833, NW	-98.7
White-throated Sparrow	615, NW	-99.3

Figure 1. Range Maps of Spruce Grouse (resident) and Blackpoll Warbler (migratory), two of the many bird species that breed throughout the huge North American boreal forest and meet the southern periphery of their ranges in the mountains of New York. Inset maps show “possible,” “probable,” and “confirmed” breeding records for each species from *The Second Atlas of Breeding Birds in New York State* (summarizing data collected from 2000-2005).

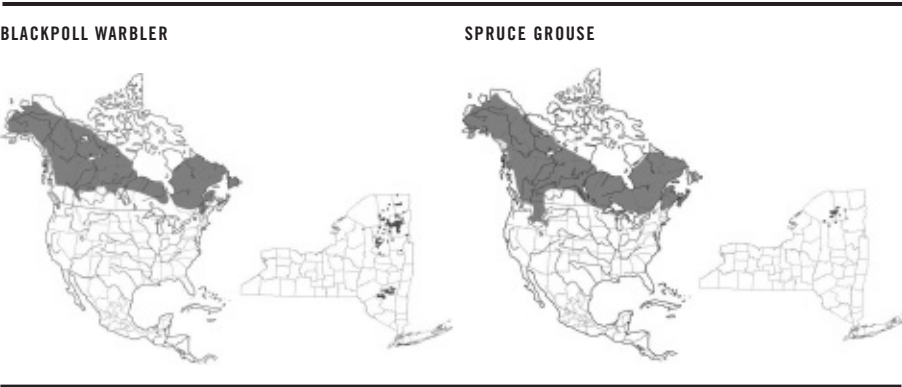
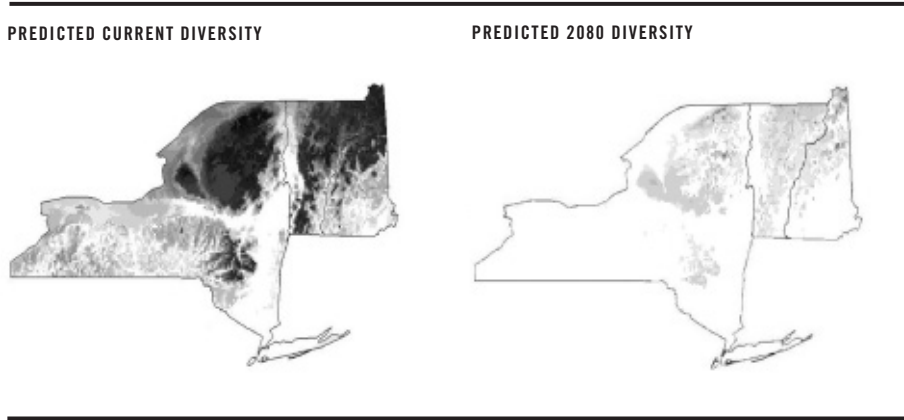


Figure 2. Modeled current diversity and predicted 2080 diversity of boreal forest bird species in New York, Vermont, and New Hampshire according to species distribution models based on climate change projections (Ralston and Kirschman 2013). Darker shading represents higher diversity.



LITERATURE CITED

- Auer, S.K., and D.I. King. 2014. "Ecological and life-history traits explain recent boundary shifts in elevation and latitude of western North American songbirds," *Global Ecology and Biogeography*, 23: 867-875.
- Avise, J.C. 2004. *Molecular markers, natural history, and evolution*. Sunderland, MA, USA: Sinauer.
- Bech, N., J. Boissier, S. Drovetski, and C. Novoa. 2009. "Population genetic structure of rock ptarmigan in the 'sky islands' of French Pyrenees: implications for conservation," *Animal Conservation*, 12:138-146.
- Brelsford, A., B. Milá, and D.E. Irwin. 2011. "Hybrid origin of Audubon's warbler," *Molecular Ecology*, 20: 2380-2389.
- Burg, T.M., S.A. Taylor, K.D. Lemmen, A.J. Gaston, and V.I. Friesen. 2014. "Postglacial population genetic differentiation potentially facilitated by a flexible migratory strategy in Golden-crowned Kinglets (*Regulus satrapa*)," *Canadian Journal of Zoology*, 92: 163-172.
- Darwin, C. 1859. *On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life*. London: John Murray.
- DeChaine, E.G. and A.P. Martin. 2005. "Marked genetic divergence among sky island populations of *Sedum lanceolatum* (Crassulaceae) in the Rocky Mountains," *American Journal of Botany*, 92:477-486.

- Frankham, R. 2005. "Genetics and extinction," *Biological Conservation*, 126:131–140.
- Glennon, M., and R.P. Curran. 2013. "How Much is Enough? Distribution and protection status of habitats in the Adirondacks," *Adirondack Journal of Environmental Studies*, 19: 36-46.
- Hewitt, G. 2000. "The genetic legacy of the Quaternary ice ages," *Nature*, 405: 907-913.
- Intergovernmental Panel on Climate Change. 2000. *IPCC Special Report: Emissions Scenarios*, IPCC. Cambridge University Press, Cambridge.
- Knowles, L.L. 2000. "Tests of Pleistocene speciation in montane grasshoppers (genus *Melanoplus*) from the sky islands of western North America," *Evolution*, 54:1337-1348.
- Lait, L.A., and T.M. Burg. 2013. "When east meets west: population structure of a high-latitude resident species, the boreal chickadee (*Poecile hudsonicus*)," *Heredity*, 111: 321-329.
- Mayr, E. and J. Diamond. 2001. *The birds of Northern Melanesia*. New York: Oxford University Press.
- McCormack, J.E., B.S. Bowen, and T.B. Smith. 2008. "Integrating paleoecology and genetics of bird populations in two sky island archipelagos," *BMC Biology*, 6:28 doi:10.1186/1741-7007-6-28.
- Milá, B., J.E. McCormack, G. Castañeda, R.K. Wayne, and T.B. Smith. 2007. "Recent postglacial range expansion drives the rapid diversification of a songbird lineage in the genus *Junco*," *Proceedings of the Royal Society of London Series B* 274: 2653-2660.
- Mortiz, C. 2004. "Defining 'Evolutionary Significant Units' for conservation," *Trends in Ecology and Evolution*, 9:373–375.
- Price, T. 2008. *Speciation in birds*. Greenwood Village, Colorado: Roberts and Company.
- Ralston, J., and J.J. Kirchman. 2012. "Continent-scale genetic structure in a boreal forest migrant, the Blackpoll Warbler (*Setophaga striata*)," *The Auk*, 129: 467-478.
- Ralston, J., and J.J. Kirchman. 2013. "Predicted range shifts in North American boreal forest birds and the effect of climate change on genetic diversity in blackpoll warblers (*Setophaga striata*)," *Conservation Genetics*, 14: 543-555.
- Ralston, J., D.I. King, W.V. DeLuca, G.J. Niemi, M.J. Glennon, J.C. Scarl, J.D. Lambert. 2015. "Analysis of combined data sets yields trend estimates for vulnerable spruce-fir birds in northern United States," *Biological Conservation*, 187: 270-278.

Ross, Angelina M., and Glenn Johnson. 2012. "Recovery Plan for New York State Populations of Spruce Grouse" NYSDEC Report. Available at http://www.dec.ny.gov/docs/wildlife_pdf/sprucegrouserecplan2013.pdf.

Ruegg, K.C., R.J. Hijmans, and C. Moritz. 2006. "Climate change and the origin of the migratory pathways in the Swainson's thrush, *Catharus ustulatus*," *Journal of Biogeography*, 33: 1172-1182.

Särkinen, T., R.T. Pennington, M. Lavin, M.F. Simon, and C.E. Hughes. 2012. "Evolutionary islands in the Andes: persistence and isolation explain high endemism in Andean dry tropical forests," *Journal of Biogeography*, 39: 884-900.

Steadman, D.W. 2006. *Extinction and biogeography of tropical Pacific birds*. Chicago: The University of Chicago Press.

Tingley, M.W., W.B. Monahan, S.R. Beissinger, C. Moritz. 2009. "Birds track their Grinnellian niche through a century of climate change," *Proceedings of the National Academy of Science*, 106: 19637-19643.

van Els, P., C. Cicero, and J. Klicka. 2012. "High latitudes and high genetic diversity: Phylogeography of a widespread boreal bird, the gray jay (*Perisoreus canadensis*)," *Molecular Phylogenetics and Evolution*, 63: 456-465.

Wallace, A.R. 1881. *Island Life*. New York: Harper and Bros.

Westemeier, R.L., J.D. Brawn, S.A. Simpson, T.L. Esker, R.W. Jansen, J.W. Walk, E.L. Kershner, J.L. Bouzat, and K.N. Paige. 1998. "Tracking the long-term decline and recovery of an island population," *Science*, 282:1695-1698.

Whitehead, D.R., and S.T. Jackson. 1990. "The regional vegetational history of the high peaks (Adirondack Mountains) New York," *New York State Museum Bulletin No. 478*.

Wiener, R.W., J.M. McLelland, Y.W. Isachsen, and L.M. Hall. 1984. "Stratigraphy and structural geology of the Adirondack Mountains, New York: Review and synthesis," *GSA Special Papers*, 194:1-56.

Zink, R.M. 1996. "Comparative phylogeography in North American birds," *Evolution*, 50: 308-317.

Zuckerburg, B., A.M. Woods, and W. Porter. 2009. "Poleward shifts in breeding bird distributions in New York State," *Global Change Biology*, 15:1866-188.

