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## Dynamics of Boreal Birds at the Edge of Their Range in the Adirondack Park, NY

Michale J. Glennon\*

**Abstract** - The Adirondack Park in northern New York is located at the southern range extent for several bird species that inhabit lowland boreal forest habitats, which in the Adirondacks are naturally fragmented and intermixed with eastern temperate forest types. I examined occupancy dynamics of 8 bird species in lowland boreal forest wetlands, evaluating the influence of variables associated with climate change and habitat fragmentation, including wetland size and connectivity, on colonization and extinction dynamics for the period 2007–2011. Occurrence data from point-count surveys conformed to predictions of metapopulation theory with respect to extinction, with most species more likely to experience local extinction from smaller, more isolated wetlands. Responses to latitude and elevation were variable. Proximity of human infrastructure was the most consistent driver of short-term dynamics across species, with two-thirds more likely to colonize low-impact sites and become locally extinct from more-impacted sites. Evidence for metapopulation structure suggests that improved connectivity among wetlands and reduction of human impact near wetlands should be conservation goals for these species in the park.

### Introduction

The Adirondack Park in northern New York State represents the southern range extent for several species of boreal forest birds within eastern North America. These populations are subject to the stresses imposed by conditions at the periphery of a species' range, and they are also geographically isolated from conspecific populations found further north. These birds are thought to be vulnerable to climate change because they prefer northern boreal habitat types expected to be sensitive to warming temperatures (Moore 2002, Niemi et al. 1998, Pastor et al. 1998). Habitats in the Adirondacks are naturally fragmented and less continuous than the Canadian boreal to the North, with patches of boreal wetland habitat surrounded by temperate forest habitat types (Jenkins 2010). Additionally, habitats within the Adirondack landscape are further fragmented by small amounts of agriculture and developed land uses.

Little is known about the population status of these boreal specialists in this region of the US. The North American Breeding Bird Survey (BBS; Sauer et al. 2012) provides information on long-term trends in abundance of avian species, but trend information is often rated as deficient in credibility for these peatland-associated species. The roadside nature of BBS routes, combined with the rarity of species and habitats such as these, often means that marginal populations of birds near the edges of their ranges are not well sampled (Sauer et al. 1995). Mountain Birdwatch

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(Scarl 2012) is a land-bird monitoring program for montane species in the northeastern US, but the targets of the program and the species for which published trend information is available do not overlap with the low-elevation boreal species described here. New York State Breeding Bird Atlas data (Andrle and Carroll 1988, McGowan and Corwin 2008) provide the best information on the distribution of low-elevation boreal species in New York, but are limited as a source of information on trends. Comparisons between atlas surveys conducted 20 years apart reveal declines in occupancy across the state for some boreal bird species, and increases for others (McGowan and Corwin 2008). Because of these limitations, scientists at the Wildlife Conservation Society, Adirondack Program (hereafter WCS), have been monitoring a suite of 12 species in lowland boreal habitats of the Adirondacks, including an intensive period of data collection between 2007 and 2011. In this paper, I use occupancy data from this survey to explore short-term trends in and potential drivers of boreal bird dynamics at their southern range extent in this part of the northeast US.

Given the fragmentation of habitats for boreal forest birds in the northeast, one might expect that these species follow the predictions of metapopulation theory, which generally apply to any species inhabiting a patchy habitat or any spatially structured population (Akçakaya et al. 2006, Hanski 1998). Sjögren-Gulve and Hanski (2000) suggest that metapopulation models are best applied to systems of relatively small habitat patches that are highly fragmented and cover maximally some 20% of the landscape. Lowland boreal habitats in the Adirondacks cover approximately 11% of the landscape and are scattered throughout the 19,700-km<sup>2</sup> park (Jenkins 2010). According to metapopulation theory, long-term population dynamics should be driven by size and connectivity of habitat patches. Therefore, boreal birds should be more likely to colonize large, well-connected habitat patches and to experience local extinction in smaller, more isolated patches (Hames et al. 2001, Hanski 1998, Pulliam 1988).

In addition to habitat patch size and connectivity, habitat degradation from climate change and anthropogenic development may also affect population dynamics of boreal birds in this region. Because these species are on the edge of their range and at the southern fringe of a northern habitat, climate change may be influencing long-term population trends in the Adirondacks. As such, they may be moving up in either latitude or elevation or both (Parmesan 2006). Several authors have noted actual or predicted changes in the ranges of boreal bird species as a result of climate change (Brommer 2004, La Sorte and Thompson 2007, Parmesan 2006, Thomas and Lennon 1999, Zuckenberg et al. 2009). Zuckenberg et al. (2009) found that southern range boundaries of New York birds shifted northward 11.4 km in the time between the 1985 and 2005 atlases of breeding birds in New York State (Andrle and Carroll 1988, McGowan and Corwin 2008). Though occurring over a longer time interval than the dataset described here, such observed shifts in patterns of bird occupancy suggest that range boundaries may be changing rapidly for some species. Thomas and Lennon (1999) found that the northern range margins of British birds shifted northwards by 18.9 km in a 20-year period, and similarly,

Brommer (2004) identified poleward shifts of 19 km in the range margins of Finish birds in only a 12-year period of time. A meta-analysis of range-boundary changes for more than 1700 species in the Northern Hemisphere estimated that northern and upper-elevational boundaries had shifted, on average, 6.1 km per decade northward or 6.1 m per decade upward (Parmesan and Yohe 2003). The rapidity of these shifts suggests that the influence of elevation or latitude on colonization and extinction probabilities of boreal birds over the 5-year time scale of the current study may be detectable. Other potential impacts of climate change, and therefore mechanisms through which bird abundance or occupancy patterns may shift, include peat loss, bog contraction, and tree invasion resulting from increased summer drought created by higher temperatures and lower rainfall (Moore 2002). Information on the current occurrence of such changes in the peatlands of the Adirondacks is not available. Multiseason occupancy data, however, when paired with covariate information, allow for an opportunity to test whether dynamic processes of avian species in these habitats are related to latitudinal or elevational patterns.

In addition to the potential impacts of habitat fragmentation and climate change, there also exists the possibility that, because these are very specialized species in the Adirondacks associated with a limited habitat type, they may be particularly sensitive to human alteration and general habitat degradation or subject to competition with more generalist species that often thrive in human-dominated environments (DeVictor et al. 2007, Glennon and Porter 2005). The Adirondack Park is unique in its mix of public and private land uses in a state park setting, with approximately 50% of its landscape in state ownership or conservation easement, and the other 50% providing for a variety of uses by its 130,000 year-round residents and multitudes of visitors. Dynamics of lowland boreal birds here may also be influenced by proximity and activities of humans in relation to their habitats. As such, they may be more likely to colonize sites with low human impact and abandon sites with high human impact.

Using the 5-year intensive survey dataset from WCS, I examined the mechanistic processes underlying patterns of occupancy change for 8 of 12 monitored species. Specifically, I tested underlying assumptions of metapopulation dynamics, and then examined the effects of wetland size, connectivity, latitude, elevation, and development on short-term dynamics using a multi-year occupancy modeling approach. I used a model-selection framework and multi-model inference to draw conclusions about the status and trends of these 8 species in the Adirondacks and to identify those drivers that may have the strongest influence on observed patterns.

### **Field-Site Description**

The Adirondack Park is located in the northern part of New York State and encompasses an area of 19,700 km<sup>2</sup>. Elevations range from 30 to 1600 m, and the dominant vegetation is a mixture of boreal and northern hardwood forest types (Glennon and Porter 2005). The predominant habitat type in the park is Northern Hardwood and Conifer Forest, followed by Boreal Upland Forest and Northern Swamp (Anderson et al. 2013). The boreal habitats that are the subject of this study consist

of bogs, fens, wooded wetlands, and open river corridors in the Adirondack Park. Though the Adirondacks as a whole lie in the transition zone between the temperate and boreal regions, there are extensive areas in the park that have summer temperatures characteristic of the south edge of the true boreal and are characterized by boreal community types that are maintained by boreal processes such as ice build-up on river shores (Jenkins 2010). Boreal habitats are distributed in small patches throughout the Adirondacks but are most concentrated in a band running from the north-central part of the park to the southwestern edge. These habitats contain both high- and low-elevation components; this paper deals solely with low-elevation boreal communities and does not address the montane boreal. As recently characterized by Anderson et al. (2013), these boreal communities fall primarily into Northern Swamp and Northern Peatland macrogroups, with dominant habitat types within those macrogroups including Northern Appalachian Acadian Conifer Hardwood Acid Swamp, Boreal Laurentian-Acadian Acidic Basin Fen, and Boreal Laurentian Bog. **These are wet, acid, carbon-accumulating habitats with mean summer temperature <18 °C (64° F) and predominantly coniferous vegetation.** Dominant tree species include *Picea mariana* (Mill.) Britton, Sterns, & Poggenburg (Black Spruce), *Picea glauca* (Moench) Voss (White Spruce), and *Larix laricina* (Du Roi) K. Koch (Tamarack), and dominant shrubs include *Andromeda polifolia* L. (Bog Rosemary), *Ledum groenlandicum* Oeder (Labrador Tea), and *Kalmia polifolia* Wengen. (Bog Laurel). Study sites ranged in latitude from 43°40'8.141" to 44°41'39.559"N and in elevation from 397 to 594 m (Table 1).

Table 1. Study sites at which a suite of 12 boreal bird species were monitored in the Adirondack Park, NY, 2007–2011, including wetland area, location, and ownership at the time of the study. New York State Forest Preserve ownership includes state land designations of Wilderness, Wild Forest, and Primitive Area, recreational uses of which are described in the New York State Land Master Plan (Adirondack Park Agency 1987). Wilderness is the most restrictive designation.

Name	Area (km <sup>2</sup> )	Latitude (N)	Longitude (W)	Ownership
Barnum Bog	0.63	44°27'13"	74°15'46"	Private
Beaver Brook Bog	0.78	43°48'48"	74°42'45"	NYS: Wilderness
Beaver Brook Fen East	0.69	43°49'49"	74°40'18"	NYS: Wild Forest
Beaver Brook Fen West	0.69	43°49'43"	74°41'3"	NYS: Wild Forest
Bigelow Road	5.47	44°25'18"	74°5'57"	NYS: Wild Forest
Black Brook North	4.19	44°21'7"	74°31'45"	Private
Black Pond Swamp	3.75	44°19'50"	74°17'27"	NYS: Wild Forest
Bloomington Bog	5.45	44°22'44"	74°8'32"	NYS: Wild Forest
Bloomington Bog II	3.34	44°24'23"	74°7'33"	NYS: Wild Forest
Bloomington Bog III	5.47	44°25'13"	74°7'2"	NYS: Wild Forest
Blue Mountain Road	0.10	44°29'5"	74°25'49"	NYS: Wild Forest
Bog Stream	0.82	44°3'34"	74°33'1"	Private
California Road	5.85	44°41'39"	74°12'36"	NYS: Wild Forest
Chubb River	0.26	44°15'21"	74°1'11"	NYS: Wilderness
Chubb River II	2.50	44°14'35"	74°1'36"	NYS: Wilderness
Dexter Road Bog	0.83	44°37'17"	74°27'43"	NYS: Wild Forest
Eastern Brown's Tract Inlet Fen	1.62	43°48'29"	74°39'54"	NYS: Wild Forest
Ferd's Bog	0.59	43°47'18"	74°44'58"	NYS: Wilderness
Helldiver	0.55	43°40'8"	74°41'38"	NYS: Wild Forest

## Methods

### Bird data collection

*Focal species.* The bird data analyzed for this paper are the result of a long-term monitoring program run by the Adirondack Program of the WCS for the purpose of understanding the distribution, abundance, and population trends of a suite of boreal birds in the park. All of the focal species are at or close to the southern extent of their eastern North American range in the Adirondack Park and all are known to occur in the Canadian boreal. A set of species was selected from those deemed

Table 1, continued.

Name	Area (km <sup>2</sup> )	Latitude (N)	Longitude (W)	Ownership
Hitchens Bog	1.04	44°6'34"	74°39'17"	NYS: Primitive Area
Horseshoe Bog	1.55	44°7'57"	74°38'46"	NYS: Primitive Area
Jones Pond Bog	0.20	44°27'8"	74°32'18"	NYS: Wild Forest
Jones Pond Outlet	0.19	44°27'4"	74°12'41"	NYS: Wild Forest
Jones Pond Road	0.20	44°27'7"	74°11'59"	NYS: Wild Forest
Kildare Bear Creek	5.23	44°19'30"	74°33'38"	Private
Kildare Bog	0.42	44°19'55"	74°32'33"	Private
Last Gasp Fen	1.54	43°51'14"	74°36'57"	NYS: Wild Forest
Little Cherry Patch Pond	0.07	44°18'0"	73°56'22"	NYS: Wild Forest
Lost Ponds	0.04	43°41'9"	74°40'19"	NYS: Wild Forest
Lower St. Regis	0.19	44°26'2"	74°14'16"	Private: easement
Madawaska	1.50	44°30'27"	74°24'38"	NYS: Primitive Area
Marion River Fen Central	2.43	43°50'2"	74°34'37"	NYS: Wild Forest
Marion River Fen East	2.43	43°50'12"	74°33'8"	Private
Marion River Fen West	2.43	43°49'56"	74°35'26"	NYS: Wild Forest
Massawepie Mire	6.06	44°13'31"	74°40'40"	Private: easement
Meachum Lake Swamp	1.86	44°32'41"	74°17'48"	NYS: Wild Forest
Meno Bog	0.50	44°30'55"	74°28'0"	NYS: Wild Forest
Moose Pond Road	0.37	44°22'25"	74°8'43"	NYS: Wild Forest
Osgood River	3.84	44°28'1"	74°13'42"	NYS: Wild Forest
Paul Smiths Bog Complex	0.38	44°25'20"	74°14'37"	Private: easement
Quebec Brook	2.05	44°29'40"	74°20'34"	NYS: Primitive Area
Red River	0.12	43°41'2"	74°44'52"	Private: easement
Regis-Spitfire	0.63	44°25'20"	74°15'28"	Private: easement
Rock Pond	1.31	44°21'56"	74°33'14"	Private: easement
Round Lake Bog	1.08	44°3'24"	74°34'18"	Private
Route 55 Bloomingdale	3.34	44°24'49"	74°7'46"	NYS: Wild Forest
Sabattis Circle Road	0.32	44°4'13"	74°32'30"	Private: easement
Sevey Bog	2.14	44°15'29"	74°41'49"	Private
Silver Lake Bog	0.57	44°28'50"	73°53'18"	Private: easement
Slush Pond	0.51	44°28'10"	74°18'37"	NYS: Wild Forest
South Inlet Fen North	0.76	43°47'58"	74°37'3"	NYS: Wilderness
South Inlet Fen South	0.76	43°47'17"	74°37'48"	NYS: Wilderness
Spring Pond Bog	4.19	44°22'12"	74°30'10"	Private: easement
Spring Pond Bog South	4.19	44°21'37"	74°30'57"	Private: easement
Sumner Stillwater	0.06	43°41'19"	74°39'42"	NYS: Wild Forest
Ton-Da-Lay	2.08	44°22'41"	74°28'30"	Private: easement
Twin Brook Bog	0.81	44°34'58"	74°29'33"	Private: easement
Western Brown's Tract Inlet Fen	1.62	43°48'12"	74°41'17"	NYS: Wild Forest

to best represent the lowland boreal habitats of the Adirondacks and to be best sampled with a point-count methodology. Those species are *Picoides dorsalis* Baird (American Three-toed Woodpecker), *Picoides arcticus* Swainson (Black-backed Woodpecker), *Contopus cooperi* Swainson (Olive-sided Flycatcher), *Empidonax flaviventris* Baird and Girard (Yellow-bellied Flycatcher), *Perisoreus canadensis* L. (Gray Jay), *Poecile hudsonicus* Forster (Boreal Chickadee), *Oreothlypis peregrina* Wilson (Tennessee Warbler), *Setophaga tigrina* Gmelin (Cape May Warbler), *Setophaga castanea* Wilson (Bay-breasted Warbler), *Setophaga palmarum* Gmelin (Palm Warbler), *Melospiza lincolni* Audubon (Lincoln's Sparrow), and *Euphagus carolinus* Müller (Rusty Blackbird).

*Site selection.* An initial list of potential field sites was compiled by consulting a variety of data sources including Adirondack Park Agency wetlands inventory data, New York State Breeding Bird Atlas data (Andrle and Carroll 1988, McGowan and Corwin 2008), postings to the Northern New York Breeding Bird Listserv, and local expert opinion. The final list of study sites was then determined by selecting from within the potential list to include a number of the major well-known boreal wetlands of the Adirondack Park and a random sample of smaller, less-known locations. Because the lowland boreal habitats of the Adirondacks are relatively disjunct and many are located in remote and roadless areas, our design precluded a completely random selection of study sites. The best possible effort was made to include a mix of known boreal wetlands in which some of these species had been documented in the past and numerous sites that had never been surveyed.

*Avian monitoring.* WCS conducted unlimited-distance point counts to assess presence/absence of our target species along transects of 5 points spaced at least 250 m apart within boreal wetland habitats (Ralph et al. 1995). In a small number of particularly large wetlands or wetland complexes, multiple transects were placed in order to adequately represent the bird community present, but spaced with a minimal distance separation of 300 m to maintain independence. All points were surveyed for 10-minutes between the hours of 5:00 and 9:00 am. Survey start and end dates for each year varied with weather conditions and song activity. All sampling occurred during the primary breeding season on survey dates ranging from the last week of May to the third week of July, with the majority of sites sampled in June. At each sample point, birds were recorded by species, time period of detection (i.e., 0–3 minutes, 3–5 minutes, 5–10 minutes), and activity (i.e., singing, calling, individual seen). Point counts were conducted by trained observers, the majority of whom conducted counts at the same locations for 3 or more of the project years. During counts, we recorded the date, start and end time for each survey, ambient temperature, and sky and wind conditions. We measured sky conditions on a scale from 0 to 6 ranging from clear or a few clouds to rain, and wind on a Beaufort scale from 0 to 5 ranging from calm to small trees swaying. Surveys were halted in the event of wind or sky conditions that affected behavior or precluded detection of birds (e.g., 5 or 6 on the sky scale and 4 or 5 on the wind scale). Surveys in boreal river corridors were conducted by boat. We employed spatial replication of sample points rather than temporal replication, to reduce costs and allow for the calculation of detection probabilities (MacKenzie et al. 2006). The sites themselves, and not the five points within each site, serve as

the experimental units for the purposes of analysis. Estimation of parameters from spatial, rather than temporal replication is also employed by the BBS (Hines et al. 2010). In most cases, the sites were large and uniform enough to accommodate a linear transect of 5 points, but in some cases points were placed in a nonlinear fashion, maintaining a minimal distance separation of 250 m. We have sampled more than 80 locations over the course of the project; 58 of those were sampled consistently for the period between 2007 and 2011 and are the subject of the current analysis (Table 1).

### Analysis

*GIS datasets.* I used 3 primary GIS datasets to calculate variables of hypothesized importance to boreal bird dynamics: wetland cover-type maps, a regional human-footprint layer (Woolmer et al. 2008), and a digital elevation model. Area and connectivity of study wetlands were calculated from wetland cover-type data provided by the Adirondack Park Agency (APA) and made available as a layer on their Shared Adirondack Park Geographic Information CD-ROM ver 1.0. These maps were produced by APA staff and exist for all watersheds in the Adirondacks. Polygon vector files are provided in which all park wetlands are classified by system, which describes the complex of wetlands and deepwater habitats that share the influence of similar hydrologic, geomorphologic, chemical, or biological factors (e.g., palustrine, lower perennial riverine), and by class, which describes the general appearance of the habitat in terms of either the dominant life form of the vegetation or the physiography and composition of the substrate (e.g., forested/evergreen, broad-leaved deciduous scrub/shrub; Cowardin et al. 1979). I consulted with local wetland ecologists to determine which of the class types within the cover-type wetlands corresponded to the boreal habitat types in which our sampling was conducted and used those cover-type polygons to calculate the area of each wetland sampled. In order to assess wetland connectivity, I used the cluster and outlier analysis tool in ArcMap 10, which identifies spatial clusters of features with high or low value based on an analysis field. I ran the tool on the wetland polygons described above, with wetland area as the analysis field. The tool calculates a Moran's *I* value, which is positive when the feature is part of a cluster and negative when the feature represents an outlier. I used a fixed-distance band of 5 km in order to evaluate the statistical properties of the wetland area data at a specific spatial scale. I chose this distance because it is representative of landscape scale for birds and comparable to other studies that have investigated the impacts of habitat size and isolation on various avian species (Brown and Dinsmore 1986, Hames et al. 2001, Smith and Chow-Fraser 2010). Calculated Moran's *I* values for each study wetland were used as an index of habitat connectivity.

I used a regional human-footprint dataset to characterize the relative human influence at each of the study wetlands. The human footprint is a representation of the magnitude of human transformation of the landscape and was originated at a global scale by Sanderson et al. (2002). Woolmer et al. (2008) used an adaptation of Sanderson's methodology to map the human footprint at the Northern Appalachian ecoregional scale. GIS Layers from Woolmer et al.'s (2008) analysis were made available through the Two Countries One Forest Northern Appalachian online atlas ([www.2c1forest.org](http://www.2c1forest.org)). Scores range from 0 to 100 and represent the relative impact

associated with human settlement, access, land-use change, and electrical power infrastructure. This dataset provides a relative measurement of human transformation of the natural landscape across the park. I used the average human-footprint score across each of the 5 points along each study transect to characterize human impact at each study wetland.

I obtained information on elevation of study wetlands from a digital elevation model also provided by the Adirondack Park Agency, and calculated a latitude for each transect by mapping their UTM coordinates and using ArcMap 10 to determine the latitude of the centroid for each transect. Together, these datasets resulted in 5 variables used in occupancy models to characterize study wetlands: area (wetarea), connectivity (connect), latitude (utmy), elevation (elev), and human footprint (HF).

*Occupancy modeling.* To investigate dynamics of boreal birds in the Adirondacks, I used the multi-season model implemented in program Presence (Hines 2006) to calculate detection ( $p$ ), occupancy ( $\psi$ ), colonization ( $\gamma$ ), and extinction ( $\epsilon$ ) probabilities for 2007–2011 for each of the species for which adequate data were obtained (detections at 15% or more of study locations; George and Zack 2008). Those included Black-backed Woodpecker, Olive-sided Flycatcher, Yellow-bellied Flycatcher, Gray Jay, Boreal Chickadee, Palm Warbler, Lincoln's Sparrow, and Rusty Blackbird. Data for the other 4 target species (Three-toed Woodpecker, Tennessee Warbler, Cape May Warbler, and Bay-breasted Warbler) constituted  $\leq 12$  detections of each species in the entire 5-year dataset and therefore could not be used in an occupancy-modeling framework.

Occupancy probability is defined as the probability of a site being occupied within a given season, while detection probability denotes the probability of a species being detected, given its presence. Colonization probability is defined as the probability that an unoccupied site in season  $t$  is occupied by the species in season  $t + 1$ , and extinction probability denotes the probability that a site occupied in season  $t$  is unoccupied by the species in season  $t + 1$  (MacKenzie et al. 2006). Program Presence uses the logit link and a maximum-likelihood approach to linearize the relationships among covariates and probabilities of detection, occupancy, colonization, and extinction (Glennon and Kretser 2013, Hines 2006). I used Akaike's information criterion (AIC) to select among competing models calculated in Presence (Akaike 1974, Burnam and Anderson 2002).

I first modeled detection for each species while holding other parameters constant and tested 6 variables for their influence on detection probability including wind, sky (relative cloud cover), date, time, temperature, and observer. Here, I used the default parameterization of the multi-season model, which estimates initial occupancy, colonization, and extinction probabilities directly, and is the most numerically stable (MacKenzie et al. 2006). Upon determining the best single predictor of detection probability, I ran a set of 9 models (Table 2) incorporating best-detection variables to first establish the appropriateness of the assumption of Markovian changes in occupancy and metapopulation structure for these birds, as well as to determine the evidence for stable or dynamic populations. This initial phase of the analysis addressed whether for each species (1) occupancy is static or dynamic, (2) changes in occupancy are random or Markovian, (3) populations are

at equilibrium, and (4) probability of occupancy and local extinction are dependent on patch size, as predicted by metapopulation theory.

Using support for metapopulation dynamics and Markovian changes in occupancy from the initial model set, I next modeled the impacts of 5 covariates (wetland area, connectivity, latitude, elevation, and human footprint) on extinction and colonization dynamics for each species over the 5-year period between 2007 and 2011, incorporating the best predictor for detection. This model set also included 2 equilibrium models for comparison against dynamic models: one in which equilibrium was defined in terms of constant occupancy probability (Stationary Markov) and one in which it was defined in terms of constant colonization and extinction probabilities (MacKenzie et al. 2006). I did not place any covariates on occupancy itself, assuming it to be reflective of past dynamics (Sjögren-Gulve and Hanski 2000) and adequately captured by covariates placed on colonization and extinction. Finer-scale habitat quality is also likely to impact occupancy dynamics of these species, but past analyses of these data have demonstrated much greater support for large-scale factors in controlling occupancy (M.J. Glennon, unpubl. data). The purpose of the second part of the analysis was specifically to assess the impact of landscape-scale drivers on short-term dynamics of these birds in the Adirondacks.

In this second phase of the analysis, I tested a set of models whereby I asked if (1) occupancy and/or rates of colonization and extinction are constant, (2) colonization dynamics depend on wetland area, connectivity, latitude, elevation, and human infrastructure, and (3) extinction dynamics depend on wetland area, connectivity, latitude, elevation, and human infrastructure. I did not have plausible biological explanations for modeling every possible combination of covariates and chose, for simplicity, to hold one rate constant and vary the other within the model set, resulting in a set of 12 models for each species (Table 3). It is possible, of course, that both colonization and extinction rates vary at the same time and, as such, I draw inferences from the betas and model-averaged estimates of  $\gamma$  and  $\epsilon$  for all models. My predictions were that (1) wetland area and connectivity would positively influence colonization and negatively influence extinction—bigger, more-connected wetlands are expected to be of higher quality for birds than smaller, more-isolated sites, (2) latitude and elevation would positively influence colonization and negatively

Table 2. Nine models of occupancy ( $\psi$ ), colonization ( $\gamma$ ), and extinction ( $\epsilon$ ) probability used to examine metapopulation structure and equilibrium assumptions for 8 bird species in boreal wetlands of the Adirondack Park, NY, 2007–2011. Covariates are explained in Methods.

Model	Predicted dynamics reflective of
$\psi$ (.)	Static occupancy
$\psi$ (2007), $\gamma$ (year), $\epsilon = 1 - \gamma$	Random changes, population not at equilibrium
$\psi$ (2007), $\gamma$ (.), $\epsilon = 1 - \gamma$	Random changes, population at equilibrium
$\psi$ (.), $\gamma$ (.), $\epsilon$ (.)	Markovian changes, population at equilibrium
$\psi$ (.), $\gamma$ (year), $\epsilon$ (year)	Markovian changes, population not at equilibrium
$\psi$ (.), $\gamma$ (.)	Stationary Markov process
$\psi$ (.), $\epsilon$ (wetarea)	Constant occupancy, area-driven extinction
$\psi$ (.), $\gamma$ (.), $\epsilon$ (wetarea)	Markovian changes, area-driven extinction
$\psi$ (wetarea), $\gamma$ (.), $\epsilon$ (wetarea)	Markovian changes, area-driven occupancy and extinction

influence extinction—given their location at the southern range extent, it is expected that these birds may move northward and up in elevation over time given climate change, and (3) human infrastructure would negatively influence colonization, and positively influence extinction—these specialist birds will generally avoid human habitats and/or be outcompeted by more abundant, generalist species near human-influenced areas. I used model-averaged estimates of colonization and extinction to calculate occupancy rates for each of the years between 2007 and 2011 in order to examine trends over time. The default model parameterization calculates colonization and extinction probabilities, as well as occupancy for year 1 ( $\psi_1$ ); occupancy for each subsequent season is calculated as:

$$\psi_{t+1} = \psi_t(1 - \epsilon_t) + (1 - \psi_t)\gamma_t,$$

where  $\psi$  represents occupancy probability, and  $\gamma$  and  $\epsilon$  represent colonization and extinction probabilities, respectively (MacKenzie et al. 2006).

## Results

A total of 1305 detections were made for all species over the 5-year time frame, with the majority of detections occurring for Yellow-bellied Flycatcher (30%), Lincoln's Sparrow (23%), and Yellow Palm Warbler (20%), and far fewer detections made of Black-backed Woodpecker (8%), Gray Jay (8%), Olive-sided Flycatcher (6%), Boreal Chickadee (3%), and Rusty Blackbird (2%). Wetland area ranged from 0.04–6 km<sup>2</sup> (mean = 1.77 km<sup>2</sup>), elevation ranged from 397–594 m (mean = 512 m), and latitude ranged from 43°40'8"N–44°41'40"N. Most wetlands (90%) were associated with positive values for Moran's *I*, indicating that they were within clusters. *Z* scores calculated from Moran's *I* values for these wetlands indicated that the majority of them (83%) were large wetlands within clusters of other large wetlands ( $P < 0.05$ ). Human-footprint values for individual wetlands ranged from 3.8–47.5 (mean = 20), and these values generally did not vary greatly among points within wetlands (mean coefficient of variation = 23%).

Table 3. Twelve models used to predict probability of occupancy ( $\psi$ ), colonization ( $\gamma$ ), and extinction ( $\epsilon$ ) for 8 bird species in boreal wetlands of the Adirondack Park, NY, 2007–2011. Covariates are explained in Methods.

Model	Predicted dynamics dependent on
$\psi$ (.), $\gamma$ (.), $\epsilon$ (.)	Markovian changes in yearly occupancy of wetlands.
$\psi$ (.), $\gamma$ (.)	Stationary Markov process.
$\psi$ (.), $\gamma$ (wetarea), $\epsilon$ (.)	Area-driven colonization rates.
$\psi$ (.), $\gamma$ (connect), $\epsilon$ (.)	Connectivity-driven colonization rates.
$\psi$ (.), $\gamma$ (utmy), $\epsilon$ (.)	Latitude-driven colonization rates.
$\psi$ (.), $\gamma$ (elev), $\epsilon$ (.)	Elevation-driven colonization rates.
$\psi$ (.), $\gamma$ (HF), $\epsilon$ (.)	Human impact-driven colonization rates.
$\psi$ (.), $\gamma$ (.), $\epsilon$ (wetarea)	Area-driven extinction rates.
$\psi$ (.), $\gamma$ (.), $\epsilon$ (connect)	Connectivity-driven extinction rates.
$\psi$ (.), $\gamma$ (.), $\epsilon$ (utmy)	Latitude-driven extinction rates.
$\psi$ (.), $\gamma$ (.), $\epsilon$ (elev)	Elevation-driven extinction rates.
$\psi$ (.), $\gamma$ (.), $\epsilon$ (HF)	Human impact-driven extinction rates.

I found that no single variable best predicted detection probability for all boreal species. Time of day and observer were the best predictors of detection probability for 2 species each, while detection probabilities for the 4 remaining species were best predicted by wind, sky, date, and temperature, respectively (Table 4). The results of top models in the first model set indicated that changes in occupancy were driven by Markovian, rather than random changes. Though constant-occupancy models were supported for some species, the majority of models supported for 6 of 8 species were dynamic models, indicating that occupancy was not constant over the 5-year period. Most species also demonstrated some support for area-driven extinction, as predicted by metapopulation theory (Table 4). These results provided justification for the structure of the second phase of the analysis, which explicitly examined drivers of colonization and extinction, and which assumed Markovian changes in occupancy.

Results of the second model set indicated that most species were controlled more strongly by extinction rather than colonization dynamics (Table 5). Among drivers of extinction and colonization dynamics, the strongest predictors by total model weight across all species were the effect of elevation on colonization and latitude

Table 4. Summary of model selection results from analysis of underlying dynamics for 8 bird species monitored in boreal wetlands in the Adirondack Park, NY, 2007–2011. Covariates are explained in Methods; only the results of top models are shown ( $\Delta\text{AIC} \leq 2.0$ ). L = likelihood; # = number of parameters. Species: B-b W = Black-backed Woodpecker, O-s F = Olive-sided Flycatcher, Y-b F = Yellow-bellied Flycatcher, G J = Gray Jay, B C = Boreal Chickadee, P W = Palm Warbler, L S = Lincoln's Sparrow.

Species	Model	AIC	$\Delta\text{AIC}$	AIC wt	L	#	-2LogLike
B-b W	$\psi(\text{wetarea}), \gamma(\cdot), \varepsilon(\text{wetarea}), p(\text{wind})$	713.23	0.00	0.4754	1.0000	7	699.23
	$\psi(\cdot), \gamma(\cdot), \varepsilon(\text{wetarea}), p(\text{wind})$	713.27	0.04	0.4660	0.9802	6	701.27
O-s F	$\psi(\cdot), \gamma(\cdot), p(\text{time})$	571.9	0.00	0.3448	1.0000	4	563.90
	$\psi(\cdot), \gamma(\cdot), \varepsilon(\cdot), p(\text{time})$	572.18	0.28	0.2998	0.8694	5	562.18
	$\psi(\cdot), \gamma(\cdot), \varepsilon(\text{wetarea}), p(\text{time})$	573.39	1.49	0.1637	0.4747	6	561.39
Y-b F	$\psi(\cdot), \gamma(\cdot), p(\text{date})$	1461.88	0.00	0.4878	1.0000	4	1453.88
	$\psi(\cdot), \gamma(\cdot), \varepsilon(\cdot), p(\text{date})$	1463.68	1.80	0.1983	0.4066	5	1453.68
G J	$\psi(\cdot), \gamma(\cdot), \varepsilon(\text{wetarea}), p(\text{obs})$	687.78	0.00	0.298	1.0000	6	675.78
	$\psi(\text{wetarea}), \gamma(\cdot), \varepsilon(\text{wetarea}), p(\text{obs})$	688.21	0.43	0.2404	0.8065	7	674.21
	$\psi(\cdot), \gamma(\cdot), p(\text{obs})$	688.41	0.63	0.2175	0.7298	4	680.41
	$\psi(\cdot), \gamma(\cdot), \varepsilon(\cdot), p(\text{obs})$	689.49	1.71	0.1267	0.4253	5	679.49
B C	$\psi(\text{wetarea}), \gamma(\cdot), \varepsilon(\text{wetarea}), p(\text{obs})$	364.37	0.00	0.8125	1.0000	7	350.37
	$\psi(\text{wetarea}), \gamma(\cdot), \varepsilon(\text{wetarea}), p(\text{temp})$	998.42	0.00	0.2811	1.0000	7	984.42
	$\psi(\cdot), \gamma(\cdot), \varepsilon(\text{wetarea}), p(\text{temp})$	998.7	0.28	0.2444	0.8694	6	986.70
	$\psi(\cdot), \gamma(\cdot), \varepsilon(\cdot), p(\text{temp})$	999.39	0.97	0.1731	0.6157	5	989.39
	$\psi(\cdot), \varepsilon(\text{wetarea}), p(\text{temp})$	999.46	1.04	0.1671	0.5945	5	989.46
L S	$\psi(\cdot), \gamma(\cdot), p(\text{temp})$	999.97	1.55	0.1295	0.4607	4	991.97
	$\psi(\cdot), \gamma(\text{year}), \varepsilon(\text{year}), p(\text{time})$	1240.98	0.00	0.7285	1.0000	11	1218.98
R B	$\psi(\cdot), \gamma(\cdot), p(\text{sky})$	235.16	0.00	0.3972	1.0000	4	227.16
	$\psi(\cdot), \varepsilon(\text{wetarea}), p(\text{sky})$	236.16	1.00	0.2409	0.6065	5	226.16
	$\psi(\cdot), \gamma(\cdot), \varepsilon(\cdot), p(\text{sky})$	236.85	1.69	0.1706	0.4296	5	226.85

on extinction processes. In both cases, however, agreement with predictions was mixed (Table 6). In general, no single covariate had strong effects on colonization or extinction dynamics across species, and there was high variability among species in their response to individual covariates. With respect to colonization, the strongest responses by species were as follows: Black-backed Woodpecker to wetland area; the 2 flycatcher species to human footprint; Gray Jay, Rusty Blackbird, and Palm Warbler to elevation; and Boreal Chickadee and Lincoln's Sparrow to latitude. In terms of extinction probability, the different species were most strongly influenced as follows: Black-backed Woodpecker and Rusty Blackbird by connectivity; Olive-sided Flycatcher, Boreal Chickadee, and Lincoln's Sparrow by latitude; Gray Jay by elevation; Yellow-bellied Flycatcher by human footprint; and Palm Warbler by wetland area (Table 6).

In addition to examining model weights, it is also of value to examine signs of the betas to determine the degree of consistency with which species responded to covariates and the degree of agreement with predictions. Human footprint and wetland area were the most consistent predictors of colonization probability across species, and size and connectivity of wetlands—as well as human footprint—were the most consistent predictors of extinction probability (Table 6).

Trends calculated from modeled colonization and extinction probabilities indicated that 4 of the 8 species modeled are demonstrating a pattern of declining occupancy in boreal wetlands in the Adirondacks, although the relative rate of decline is variable among them (Table 7). Rusty Blackbird and Yellow-bellied Flycatcher occupancy remained stable over the 5-year period, while only Lincoln's Sparrow and Palm Warbler demonstrated a pattern of increasing occupancy. In no

Table 5. Summary of model selection results from analysis of drivers of dynamics for 8 bird species monitored in boreal wetlands in the Adirondack Park, NY, 2007–2011. Covariates are explained in Methods; only the results of top models are shown ( $\Delta AIC \leq 2.0$ ). L = likelihood; # = number of parameters. Species: B-b W = Black-backed Woodpecker, O-s F = Olive-sided Flycatcher, Y-b F = Yellow-bellied Flycatcher, G J = Gray Jay, B C = Boreal Chickadee, P W = Palm Warbler, L S = Lincoln's Sparrow.

Species	Model	AIC	$\Delta AIC$	AIC wt	L	#	-2LogLike
B-b W	$\psi(\cdot), \gamma(\cdot), \varepsilon(\text{connect}), p(\text{wind})$	711.25	0.00	0.5411	1.0000	6	699.25
O-s F	$\psi(\cdot), \gamma(\cdot), \varepsilon(\text{utmy}), p(\text{time})$	569.46	0.00	0.3420	1.0000	6	557.46
Y-b F	$\psi(\cdot), \gamma(\cdot), \varepsilon(\text{HF}), p(\text{date})$	1454.08	0.00	0.6826	1.0000	6	1442.08
	$\psi(\cdot), \gamma(\text{HF}), \varepsilon(\cdot), p(\text{date})$	1455.96	1.88	0.2666	0.3906	6	1443.96
G J	$\psi(\cdot), \gamma(\text{elev}), \varepsilon(\cdot), p(\text{obs})$	682.37	0.00	0.5231	1.0000	6	670.37
B C	$\psi(\cdot), \gamma(\cdot), \varepsilon(\text{utmy}), p(\cdot)$	362.14	0.00	0.7605	1.0000	5	352.14
P W	$\psi(\cdot), \gamma(\text{elev}), \varepsilon(\cdot), p(\text{temp})$	997.63	0.00	0.2513	1.0000	6	985.63
	$\psi(\cdot), \gamma(\cdot), \varepsilon(\text{wetarea}), p(\text{temp})$	998.70	1.07	0.1472	0.5857	6	987.60
	$\psi(\cdot), \gamma(\cdot), \varepsilon(\cdot), p(\text{temp})$	999.39	1.76	0.1042	0.4148	5	989.39
L S	$\psi(\cdot), \gamma(\cdot), \varepsilon(\text{utmy}), p(\text{time})$	1274.74	0.00	0.5422	1.0000	6	1228.74
R B	$\psi(\cdot), \gamma(\text{elev}), \varepsilon(\cdot), p(\text{sky})$	232.86	0.00	0.2714	1.0000	6	220.86
	$\psi(\cdot), \gamma(\text{wetarea}), \varepsilon(\cdot), p(\text{sky})$	233.02	0.16	0.2505	0.9231	6	221.02
	$\psi(\cdot), \gamma(\text{utmy}), \varepsilon(\cdot), p(\text{sky})$	233.63	0.77	0.1847	0.6805	6	221.63

Table 6. Model weights for single-covariate models used to predict colonization and extinction rates of 8 boreal bird species in the Adirondack Park, NY, 2007–2011. Prediction indicates the direction of the expected relationship between predictor variables and colonization and extinction rates; asterisks denote that the effect of the variable on colonization or extinction was as predicted (i.e., the sign of the betas matched predictions). Covariates are explained in Methods.

Covariates	Prediction	Black-backed Woodpecker	Olive-sided Flycatcher	Yellow-bellied Flycatcher	Gray Jay	Boreal Chickadee	Palm Warbler	Lincoln's Sparrow	Rusty Blackbird	Total wt
Colonization										
wetarea	+	0.15	0.03*	0.00*	0.02*	0.02*	0.04	0.02	0.25*	0.55
connect	+	0.01	0.05	0.00	0.16*	0.00*	0.04	0.02	0.02*	0.29
utmy	+	0.03	0.04*	0.01	0.07*	0.03*	0.09*	0.11	0.18	0.55
elev	+	0.03*	0.04	0.01*	0.52	0.01	0.25	0.01*	0.27*	1.14
HF	-	0.00*	0.08	0.27*	0.01*	0.02*	0.05	0.02*	0.03*	0.47
Extinction										
wetarea	-	0.20	0.05*	0.00*	0.04*	0.01*	0.15*	0.01*	0.01*	0.46
connect	-	0.54	0.03	0.00*	0.02*	0.09*	0.07*	0.01*	0.06*	0.84
utmy	-	0.01	0.34*	0.00	0.02*	0.76*	0.04*	0.54*	0.02	1.72
elev	-	0.01*	0.12	0.00	0.06	0.00	0.05	0.14	0.01	0.41
HF	+	0.00*	0.03	0.68*	0.04*	0.02*	0.04	0.01*	0.02*	0.84

Table 7. Model-averaged parameter estimates of occupancy ( $\psi$ ), colonization ( $\gamma$ ), and extinction ( $\epsilon$ ) for 8 bird species in boreal wetlands in the Adirondack Park, NY, 2007–2011.

Parameter	Black-backed Woodpecker	Olive-sided Flycatcher	Yellow-bellied Flycatcher	Gray Jay	Boreal Chickadee	Palm Warbler	Lincoln's Sparrow	Rusty Blackbird
$\psi_{2007}$	0.71 ± 0.12	0.55 ± 0.12	0.77 ± 0.08	0.71 ± 0.13	0.36 ± 0.11	0.39 ± 0.07	0.63 ± 0.09	0.22 ± 0.11
$\psi_{2008}$	0.64 ± 0.12	0.49 ± 0.12	0.75 ± 0.08	0.68 ± 0.13	0.32 ± 0.11	0.44 ± 0.07	0.65 ± 0.09	0.22 ± 0.11
$\psi_{2009}$	0.58 ± 0.12	0.45 ± 0.12	0.75 ± 0.08	0.67 ± 0.13	0.29 ± 0.11	0.48 ± 0.07	0.67 ± 0.09	0.23 ± 0.11
$\psi_{2010}$	0.54 ± 0.12	0.43 ± 0.12	0.75 ± 0.08	0.67 ± 0.13	0.27 ± 0.11	0.51 ± 0.07	0.68 ± 0.09	0.23 ± 0.11
$\psi_{2011}$	0.50 ± 0.12	0.42 ± 0.12	0.75 ± 0.08	0.66 ± 0.13	0.26 ± 0.11	0.53 ± 0.07	0.69 ± 0.09	0.23 ± 0.11
$\gamma$	0.08 ± 0.12	0.14 ± 0.09	0.44 ± 0.14	0.37 ± 0.29	0.09 ± 0.08	0.13 ± 0.05	0.17 ± 0.10	0.10 ± 0.11
$\epsilon$	0.13 ± 0.10	0.22 ± 0.14	0.15 ± 0.07	0.19 ± 0.10	0.28 ± 0.28	0.07 ± 0.04	0.07 ± 0.04	0.34 ± 0.25

case was the stationary occupancy model included in the top model set ( $\Delta AIC < 2.0$ ) for any species (Table 5).

## Discussion

The geography of the Adirondack boreal region, the location of these species at their southern range extent within eastern North America, and the patterns identified here suggest that boreal bird populations in the Adirondack Park are dynamic. This analysis also demonstrates that occupancy by several species appears to be in decline. Understanding the processes that drive their dynamics can enhance the ability of land managers to influence their long-term conservation (MacKenzie et al. 2006). For species occurring in the patchy habitats of the Adirondack boreal region, metapopulation biology and the lessons that arise from it are also valuable to conservation planning. I predicted that wetland size and connectivity would positively influence colonization and negatively influence extinction of birds in boreal wetlands in the Adirondack Park. Patterns in boreal bird dynamics matched these expectations of metapopulation theory strongly for extinction but not for colonization. Seven of the 8 species modeled were more likely to disappear from smaller, isolated wetlands, but only 5 of 8 were more likely to colonize larger wetlands, and only 3 of 8 were more likely to colonize more connected wetlands. As suggested by Hames et al. (2001) and others, the effect of isolation must be measured in comparison to the dispersal abilities of the organism under study. It is possible that these effects were inconsistent across species and stronger with respect to extinction dynamics because birds are highly vagile and thus less sensitive to isolation of their habitats than other vertebrate taxa. Opdam (1991) and others have suggested, however, that the effects of isolation on birds should not be dismissed a priori (Hames et al. 2001, Villard et al. 1995). Hames et al. (2001) also state that resident birds are expected to be more affected by isolation of habitat patches than are long-distance migrants. I did find a greater influence of wetland connectivity on resident birds than on migrants (Table 6), but the direction of the influence was as predicted for only 2 of the 3 resident species. In general, I found stronger evidence for the influence of wetland size and connectivity on extinction rather than colonization dynamics, and uneven support among species, with some (e.g., Black-backed Woodpecker, Rusty Blackbird) much more highly influenced by size and connectivity of boreal wetlands than others and not necessarily in the ways predicted. Most investigations of boreal birds elsewhere have not employed a metapopulation framework because such an approach may be less appropriate in more continuous boreal habitats in northern regions. Support for birds exhibiting metapopulation dynamics has been found for other species, however, including the work of Hames et al. (2001) in investigations of *Piranga olivacea* Gmelin (Scarlet Tanager) breeding in fragmented habitats in eastern North America, and Smith and Chow-Fraser (2010) who examined the influence of isolation on marsh bird communities in southern Ontario.

I also predicted that latitude and elevation would positively influence colonization and negatively influence extinction for these bird species. Because they are

largely at their southern range extent in the Adirondacks, I expected that these birds may move northward and up in elevation over time given observed and predicted changes in distribution and abundance of other northern bird species across the globe in response to climate change (Virkkala and Rajasärkkä 2011, Virkkala et al. 2008, Waite and Strickland 2006, Zuckerberg et al. 2009). Both latitude and elevation were strong predictors of colonization and extinction dynamics, but only for a few species, and with inconsistent results. Some species did have higher probability of extinction at southern sites and at sites of lower elevation, while others demonstrated opposite patterns. The inconsistency of responses among species to these 2 predictor variables suggests that other factors may be playing a larger role in controlling these species' dynamics than does climate change over this small window of time, and that the responses of individual species to climate change are not likely to be uniform or highly predictable. Though these species are at their southern range extent and expected to be sensitive to climate change, the short duration of the dataset in comparison to climate-driven processes may preclude detection of changes driven solely by warming. Zuckerberg et al. (2011) pointed out the importance of urbanization and behavioral adaptation in modifying the impact of climate change on birds. Human land use—in particular, residential and commercial development—along with other stressors are likely interacting with any impacts of climate change on these birds in the Adirondacks.

I predicted that proximity of human infrastructure would impact these highly specialized species by negatively influencing colonization and positively influencing extinction rates. Although these boreal wetlands are, in general, not in close proximity to roads and development in the Adirondacks, our previous research in the region, as well as that of others, has demonstrated that the impacts of development can permeate significant distances within undeveloped areas (Bock et al. 1999, Glennon and Kretser 2013, Odell and Knight 2001, Smith and Chow-Fraser 2010) and that development tends to benefit more generalist species at the expense of habitat specialists in this landscape and elsewhere (DeVictor et al. 2007, Glennon and Kretser 2013, Glennon and Porter 2005, Hansen et al. 2005, Maestas et al. 2001, Smith and Chow-Fraser 2010). When considering both colonization and extinction, human footprint was the most consistent predictor of boreal bird dynamics across species, with 6 of 8 modeled species more likely to colonize areas of low human infrastructure and more likely to experience local extinction from highly impacted areas. It is likely that human infrastructure, in the form of roads and houses, is close enough to boreal wetlands in some places that the negative consequences that can accompany human development are apparent. In the case of these highly specialized bird species, it is possible that the influx of more cosmopolitan species, those better able to exploit a variety of habitats and food sources, may result in competition through which these boreal specialists ultimately lose out. Such processes have been documented for marsh birds in areas proximal to urbanization (Smith and Chow-Fraser 2010) and for the songbird community in upland forested habitats of the Adirondacks (Glennon and Porter 2005). They have also been hypothesized as a potential driver of the alarming decline in Rusty Blackbird

abundance (Greenberg and Matsuoka 2010). It is possible that competitive interactions around food or other resources between several of these species and more widespread family members (e.g., Gray Jay and *Cyanocitta cristata* L. [Blue Jay], Boreal Chickadee and *Poecile atricapillus* L. [Black-capped Chickadee]) may impact their success in wetlands more proximal to human-dominated areas; such species are commonly detected in the study wetlands described here (M.J. Glennon, unpubl. data). Niemi et al. (1998) identified a need for a better understanding of interactions with predators and competitors and effects to population variability as a critical knowledge gap for boreal bird species.

I suspect that isolated wetland populations of boreal birds are functioning as metapopulations in the Adirondack Park, but that their dynamics with respect to response to wetland size and connectivity are tempered by other factors such as warming temperatures and adjacent human infrastructure. Modeled occupancy rates for 4 of the 8 study species demonstrate declining patterns; 2 appear stable, and only Lincoln's Sparrow and Palm Warbler appear to be increasing in the Adirondack landscape. Colonization and extinction rates among these species are highly variable, with 4 species demonstrating higher colonization rates than extinction rates, and the other 4 species demonstrating the opposite pattern. Several of the species for which I observed declining occupancy in the Adirondacks do not appear to show declining abundance across North America from the large-scale monitoring effort of the North American Breeding Bird Survey, including Black-backed Woodpecker, Boreal Chickadee, and Gray Jay, though Boreal Chickadee does appear to be declining in the Atlantic Northern Forest. These data may be deficient for this species and Black-backed Woodpecker (BBS; Sauer et al. 2012). Contrastingly, Lincoln's Sparrow, which increased in occupancy between 2007 and 2011 in the Adirondacks, shows no significant survey-wide trend (Sauer et al. 2012). Rates of colonization and extinction among the 8 modeled species are modest for the most part, but there are notable exceptions.

Three species may warrant particular attention in the Adirondacks. Boreal Chickadee, Olive-sided Flycatcher, and Rusty Blackbird showed high extinction probabilities in Adirondack wetlands, and Boreal Chickadee and Olive-sided Flycatcher appear to demonstrate declining trends in New York as well as on some larger scales. All 3 species declined in occupancy across New York State in the period between 1985 and 2005 (McGowan and Corwin 2008). Rusty Blackbird did not show declines in the short-term period described here, but its occupancy rate is so low that large changes may be difficult to detect. All three of these birds were more likely to experience local extinction from smaller, more isolated wetlands, and both Boreal Chickadee and Rusty Blackbird appeared sensitive to human infrastructure in close proximity to wetland sites. Rusty Blackbird is known to be declining at alarming rates and is the subject of much current effort to elucidate causes and mechanisms for its decline (Greenberg and Matsuoka 2010). Olive-sided Flycatcher is also experiencing declines and is listed as a species of concern by several management entities (Altman and Sallabanks 2012). Boreal Chickadee has not generated widespread concern, and its status is unknown in the high-elevation

boreal habitats it also uses in the Adirondacks, but its high probability of extinction, coupled with low colonization rates and declining occupancy, may indicate an ongoing decline in this landscape.

Several of the predictor variables I tested for their influence on boreal bird dynamics are, unfortunately, confounded to a large degree by the geography of the Adirondack boreal region. The majority of the large and highly connected wetland complexes in the Adirondacks are located in the northwest part of the park, and boreal habitats at more southern latitudes in the southwest region are generally smaller and more isolated. As such, it is difficult to separate the effects of wetland size and connectivity from the effects of latitude. The interrelatedness of these factors presents both opportunities and challenges for conservation, however. Larger, more connected wetlands are more likely to retain birds, but most wetlands in the Adirondacks (and everywhere) are small (Semlitsch and Bodie 1998). Smaller wetlands are also more likely to be nearby and impacted by human infrastructure and smaller, more isolated wetlands in the Adirondacks are generally located at higher elevations. Because these birds probably function in metapopulations across this landscape, all boreal wetlands probably have some importance to them, and smaller, isolated wetlands may serve as sink habitats that are of lesser quality but important to long-term maintenance of these species on the landscape as a whole. This conclusion presents a challenge to conservation in the form of protecting both large and small wetlands across the landscape. Searching for a lower area threshold for occupancy by boreal birds is probably not a relevant exercise (Opdam 1991), and conservationists and land managers in the Adirondacks must strive to make the case for the maintenance of a complex of boreal wetlands across the park rather than assuming that we can safely ignore the small ones. Semlitsch and Bodie (1998) point out the importance of small, isolated wetlands as critical for maintaining regional biodiversity because they harbor very large numbers of species. This is the case in the Adirondacks. The total number of species detected at least once in point counts at boreal wetlands is 136—roughly 70% of the total known breeding bird species richness for the park—in comparison to an average species richness of 70 on counts conducted in upland forest sites (M.J. Glennon, unpubl. data). The majority of small boreal wetlands may be of lower quality to birds, but they are likely to contain a large fraction of the total individuals in a population (Pulliam 1988) simply because there are many more of them than larger ones. These potential sink habitats can be critical in maintaining long-term viability of populations (Davis and Howe 1992, Doak 1995, Howe et al. 1991, Pulliam 1988, Pulliam and Danielson 1991).

Although maintaining a complex of large and small wetlands across the park is challenging, there are also opportunities for conservation. Several of the variables demonstrated here to be important in controlling bird dynamics in the Adirondacks are unlikely to change in the near future. Area of the large peatlands is likely to remain relatively consistent in the near future because a large proportion of these “charismatic megawetlands” are protected in the park. Their elevation and latitude will not change. What will change, and what land managers have the greatest potential to influence, is human footprint and connectivity. Decreasing the likelihood

of human impacts nearby to boreal wetlands, and maintaining the smaller, isolated fringe habitats that probably provide important stepping stones for boreal birds in this landscape will probably best serve their long-term maintenance. Minimizing human infrastructure in and near these areas will have the added benefit of reducing the likelihood of invasion by synanthropic species with which these birds may compete. Climate change may render the long-term persistence of these species in the park uncertain. On shorter time scales, however, additional research to understand the importance of specific human impacts, coupled with efforts to buffer these habitats and to maintain their functional connectivity through protection and management will benefit this iconic community of birds found nowhere else in the state.

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