The Use of Terrestrial and Airspace Habitat by Migratory Land Birds during Autumn Migration along a Coastal Ecological Barrier

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Dedication

I dedicate this dissertation to the millions of boreal birds traveling thousands of miles every year just to survive. May you always have a safe journey home.

Abstract

During fall migration, the northern coastline of Lake Superior acts as an ecological barrier for migrating land birds that breed across the boreal forests of Canada and Alaska. This area provides an opportunity to examine the distribution of migrating birds during stopover and use of airspace during active migration in a relatively intact coastal environment. I conducted stopover habitat surveys for birds during two fall migration seasons (Aug-Oct, 2009-2010) and assessed diurnal migratory bird movements during three seasons (Sept – Oct, 2008-2010) within Lake Superior's coastal region of Minnesota, USA.

Land cover and topographic features only weakly explained some migratory species distributions during stopover. Selection of migratory habitats was strongest among permanent resident species, representing the importance of coniferous forests for foraging and cover. The strongest habitat association for a migratory species was the use of near shore areas and high ridgelines by Swainson's Thrushes. I also detected a difference in the scale of topographic features between long- and short-distance migrants: Neotropical migratory passerines were associated with broad-scale features, while shorter distance migratory passerines were associated with local-scale features. My results suggest that within forested coastal areas, migratory birds are less confined to the shoreline, specific habitat types, or topographic features as reported for other coastal landscapes.

A total of 13,702 raptors (2008-2010) and 151,550 non-raptors (of which 90% were passerines; 2009-2010) were recorded using airspace during migration within the coastal region of Lake Superior. Several raptors showed patterns in airspace associated with topographic features such as proximity to the shore and presence of ridgelines. However, the funneling movement that is commonly used to describe raptor behavior along migratory diversion lines occurred only among Bald and Golden eagles, suggesting a "leaky" migration funnel for most migratory raptors. Seventy percent of passerines were observed during the first two hours after sunrise and many participated in morning flights inland, not in the migratory direction. In addition, more passerines than raptors showed spatial and temporal structure in airspace distribution, including a funneling movement and association with airspace near the shore. I conclude that a) using raptor counts from single migration sites at the "tips" of presumed migration funnels to account for total raptor abundance within a concentration area greatly underestimates true numbers of raptors, b) the diurnal spatial and temporal movement patterns of migrating passerines along ecological barriers have been largely overlooked, and c) the airspace associated with anthropogenic development (e.g., buildings, towers, wind turbines) is heavily utilized by both raptors and non-raptors during diurnal migratory periods.

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Preface

Habitat fragmentation, degradation, and loss are major contributors to declines in animal populations and diversity. Migrating animals worldwide are encountering an increasing number of human hazards in their movements between seasonal use areas. Migratory birds have especially complex and dynamic habitat needs that vary from summer breeding sites, wintering grounds, and stopover areas *en route* between these areas. Until recently, scientific efforts investigating bird habitat conservation have focused almost exclusively on summer breeding habitat, and to a lesser extent on wintering areas; much less are known about the habitats birds use while migrating (Mehlman *et al.* 2005).

As earth-bound creatures, it is more natural for us to focus on the protection and enhancement of terrestrial habitats, yet migratory birds' airspace "habitat" is equally as important and threatened by fragmentation, degradation, and loss. Rapid construction of communication and renewable energy infrastructure, such as communication towers and wind turbines, has the potential to compound the effects of terrestrial bird habitat loss by introducing potential hazards and fragmenting the airspace through which birds travel.

Migratory birds are vulnerable to alterations in both terrestrial and airspace habitat when resource availability, geographic constraints, and habitat loss concentrate their movement into relatively small migration corridors. Habitat alteration within migration corridors can lead to disproportionately negative outcomes for migratory species, as alternative habitats may not exist. The North Shore of Lake Superior (hereafter north shore) is a major migration corridor for birds that breed in the boreal forests of northern Minnesota, Canada, and Alaska.

Each autumn, an estimated 3-5 billion birds, and 90% of boreal bird species participate in one of the world’s largest migration events as they travel to wintering grounds as far away as South America (Rich *et al.* 2004, Wells and Blancher 2011). Rather than heading due south, many of these forest birds begin their autumn migration by heading in an east or southeasterly direction, presumably to avoid the unforested prairies of central Canada and the U.S. and aided by the prevailing westerly winds to reach over-wintering areas in the southern US, Central America, and South America. As a result of this trajectory, a significant proportion of these migrants encounter the Great Lakes region. The Great Lakes act as “barriers” to migrating birds because they are devoid of safe places to land and require extra energy to cross. Dominant ridges and valleys paralleling Lake Superior’s inhospitable waters act as topographical cues that direct birds down the 210 km long north shore.

Coastlines often face increased pressure from development due to concentrated human population density and abundant natural resources. The north shore is experiencing increased urban, exurban, and recreational development (MNDNR 2006), increases in communication towers, windows with urban and commercial development, and wind energy is in the assessment and planning phases. To improve our understanding on the extent and magnitude of terrestrial and airspace use of migratory corridors, this dissertation research used the north shore as an experimental area to assess how autumn migrating birds use such corridors. This information can be useful to improve conservation and planning development specifically for the north shore, but also provides a framework for other migratory corridors.

Development of renewable energy sources is currently a national and international priority; leading to the rapid siting and construction of wind turbines across the U.S. and worldwide. Despite the potential to reduce dependence upon non-renewable energy sources, wind energy development may result in other environmental impacts, including hazards to birds. This investigation is timely because wind turbines are being considered or planned along most major coastlines worldwide, including coastlines of the Great Lakes (Mageau *et al.* 2008, GLWC 2011). Data on how birds use airspace and terrestrial habitats during migration are currently lacking, and guidelines to minimize conflicts between structures, such as wind turbines, and birds presently rely on professional judgment (USFWS 2003, USFWS 2013). My research contributes much-needed information about migratory bird airspace and terrestrial habitat use in migration corridors that can be used to guide potential development of such structures.

My research goals for this dissertation were to bring attention to, and help protect, migratory birds traveling through coastal migration corridors, and guide development of structures, such as wind turbines and associated infrastructure, to minimize impacts on migratory birds. To achieve these goals, my dissertation objectives were to 1) identify patterns in the use of terrestrial habitat by migratory birds, 2) identify patterns in the use of airspace by migratory birds, and 3) emphasize the importance of airspace as habitat for flying animals. This is the first study to use a ground observation and transect sampling approach over a large area (>2000 km^2). Similar methodology and the results from this investigation can provide a framework for improving our understanding of migratory bird terrestrial and airspace habitat use along coastal ecological barriers.

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CHAPTER 1.

MECHANISMS OF STOPOVER HABITAT SELECTION IN A RELATIVELY INTACT COASTAL ENVIRONMENT

ABSTRACT.- During fall migration, the northern coastline of Lake Superior acts as an ecological barrier for migrating land birds that breed across the boreal forests of Canada and Alaska. The coastal area of Lake Superior is heavily forested and less fragmented by human development than many other coastal stopover areas. This area provides an opportunity to examine the distribution of migrating birds during stopover in a relatively intact coastal environment. I conducted transect surveys for birds during two fall migration seasons (Aug-Oct, 2009-2010) at 114 sites within Lake Superior’s coastal region of Minnesota, USA. Land cover and topographic features only weakly explained some migratory species distributions. Selection of migratory habitats was strongest among permanent resident species, representing the importance of coniferous forests for foraging and cover. The strongest habitat association for a migratory species was Swainson’s Thrush use of near shore areas and high ridgelines. I also detected a difference in the scale of topographic features between long- and short-distance migrants: Neotropical migratory passerines were associated with broad-scale features, while shorter distance migratory passerines were associated with local-scale features. My results suggest that within forested coastal areas, migratory birds are less confined to the shoreline and specific habitat types as reported for other coastal landscapes.

INTRODUCTION

For many bird species, migration periods constitute a critical life-stage that may have profound effects on species survivorship (Sillett and Holmes 2002, Newton 2006). While many factors influence survival during the alternating active flight and stoppage of migratory movement (Hutto 2000, Petit 2000, Moore et al. 2005b, Buler et al. 2007), the quality and quantity of ‘stopover’ habitats available for migrants to obtain food and cover for rest are particularly limiting factors in successful completion of the migratory journey (Hutto 2000, Tankersley 2004, Buler and Moore 2011). Therefore, strategies aimed at the protection of migratory birds must consider stopover habitat preservation to be complete (Petit 2000, Mehlman et al. 2005, Faaborg et al. 2010a, Ewert et al. 2012).

During migratory periods, birds concentrate in disproportionately high numbers adjacent to ecological barriers, topographic features that act as barriers to migratory movement such as deserts and large bodies of water, to either circumvent the barrier, prepare to cross it, or to find refuge after crossing (Buler et al. 2007, Deppe and Rotenberry 2008, Buler and Moore 2011). Habitats adjacent to ecological barriers are particularly critical for migration success so have been the focus of many studies to gain knowledge of migrant habitat use for conservation planning (Ewert et al. 2006, Bonter 2009, Buler and Moore 2011, Ewert et al. 2012). These studies suggest that stopover habitat use is nonrandom (Hutto 2000, Petit 2000, Buler et al. 2007) and influenced by features at various landscape scales (Buler and Moore 2011, Taylor et al. 2011). In particular, migratory birds are often associated with the presence and amount of forest cover, especially in proximity to coastal ecological barriers (Buler et al. 2007, Bonter et al. 2009, Ewert et al. 2006, Buler and Moore 2011).

Greater than 90% of the three to five billion land birds that breed in the boreal regions of North America migrate (Green 1995, Rich et al. 2004, Wells and Blancher 2011). A substantial number of these species are unique to the boreal forest and are experiencing population declines (Niemi et al. 1998, Rich et al. 2004, Sauer et al. 2011). During fall migration periods, the movement direction of many boreal land birds is southeast, a trajectory that results in a large proportion of these birds intersecting the Great Lakes region (Fig. 1; Moore et al. 1995, Williams and Webb 1996, Faaborg et al. 2010b, Leppold and Mulvihill 2011). The coastlines of the Great Lakes are heavily utilized by land birds during fall migration, and Lake Superior’s north shore is the first coastline encountered by a number of these migrants (Diehl et al. 2003, MNDNR 2006, Smith et al. 2007; Bonter et al. 2007, 2009).

Nearly 40% of the U.S. population (123 million people) lives in a county adjacent to a major U.S. coastline, resulting in coastal areas experiencing disproportionately high pressures from industrial, urban, and exurban development (NOAA 2013b). The coastal region along the north shore of Lake Superior is continuously experiencing alteration and pressure from forestry and urban, exurban, and energy development pressure. Development is the greatest threat to the biodiversity of the region (TNC 1999, 2002), but over 93% of the landscape is still undeveloped (MNDNR 2006). The forested land in this region is largely privately owned; therefore several strategies are on-going to guide future development and conservation along this coastline (TNC 2002, Ewert et al. 2011a, NOAA 2013a).

Stopover habitat selection characteristics documented in previous coastal studies, such as the amount of hardwood forest in the landscape (Buler et al. 2007, Buler and Moore 2011), do not provide adequate management or conservation information for areas such as the Lake Superior coastal region because of differences in land cover type and abundance, topography, and the potential that suitable habitat is readily available. Therefore, the Lake Superior coastal area provides an opportunity to examine mechanisms of stopover habitat selection in a forested coastal environment heavily used by boreal land birds during migration.

The objective of this study was to examine the influence of topography and land cover features on bird distribution during migratory stopover in a 160 kilometer long and 6 kilometer wide forested area adjacent to a coastal ecological barrier. As shown in previous coastal studies, I predicted that migratory bird stopover use would be associated with proximity to the shoreline and particular land cover types in the coastal region of Lake Superior.

METHODS

Study region and sites.- My study region lies in far northeastern Minnesota along the northern shore (oriented northeast-southwest) of Lake Superior within a broad coastal area stretching from the city of Duluth, Minnesota to the US-Canada border (Fig. 2). The region is mostly forested (72%), consisting of a matrix of aspen-birch (e.g. *Populus tremuloides, Betula papyrifera*), sugar maple (*Acer saccharum*), pine (e.g. *Pinus resinosa, Pinus strobus*), spruce (e.g. *Picea glauca*), tamarack (*Larix laricina*), and balsam fir (*Abies balsamea*), intermixed with wetlands and lakes (21%). Pasture and cropland (3%) and human development (4%) constitute the major remaining land use types (MNDNR 2006). A ridge and valley topography dominates the region with elevations between 150 meters near the Lake Superior coastline to near 700 meters on prominent northeast-southwest oriented ridgelines. The elevation of the landscape gradually increases from the coastline moving inland. Major ridgelines begin to appear between 1.5 and 2 kilometers inland from the coastline with the most prominent ridgelines and highest elevations in my study area occurring at distances 4-5 kilometers inland.

I established 114 trail-transects, each 500 meters in length, within the Lake Superior coastal region. Each transect was separated by, at minimum, a 50 meter buffer (following Hanowski et al. 1990) and within 6 kilometers of the Lake Superior coastline (Fig. 2). Surveys occurred on recreational trails (e.g., hiking, skiing, and snowmobile) with a minimum of 50% closed canopy.

Bird surveys.- For two fall migration seasons (August – October, 2009 and 2010), surveys occurred from sunrise to 4 hours after sunrise following the Hanowski et al. (1990) transect survey protocol. Surveys were conducted at each trail-transect using GPS units for position and to maintain a consistent travel rate of 1km/hour, resulting in each 500-meter transect survey lasting for 30 minutes. A six-minute time buffer was applied between transects that were adjacent to one another. All birds heard or observed inside and outside 50-meters on either side of the transect trail were identified to the lowest taxonomic group possible and recorded at the location where first detected. Identification to species was difficult during fall migration, as birds rarely sing and many species lack distinctive breeding plumage. Individuals were identified to species when clear views, identifiable chip notes, or distinctive flight and behavior patterns were recognizable. When recording birds, I made a distinction between those in contact with the ground or in vegetation, and those flying over the survey transect. Transects were visited two to four times during each season by randomly selecting survey dates to assure all sites had an equal probability of being surveyed during peak and low migration episodes.

Data analysis.- Birds were analyzed as groups on the basis of migration timing (e.g., early season warblers), family group (e.g., thrushes), and as individual species. Analyses included only those birds recorded as making contact with the ground or vegetation (i.e., flyovers removed) and within 50 meters of the trail because the majority of birds were recorded and identified to species within this distance. As surveys were balanced across various seasonal patterns and weather conditions (minus days of high winds or rain when surveys were not conducted), bird groups and species were averaged (mean) for each 500 meter transect. I included in subsequent analysis only bird groups and species that were represented by ≥ 100 total individual observations.

To assign unidentified warblers and passerines to a migration group, I examined the proportion and timing of identified long- and short-distance migrant species. Yellow-rumped Warblers (*Dendroica coronata*), the second most common identified warbler after American Redstart (*Setophaga ruticilla*), were a short-distance warbler migrant observed in this study (Appendix A, Niemi et al. 2014). From early August to mid-September, Yellow-rumped Warblers comprised only 2% of the total identified warblers, compared to 83% of the total identified warblers from September 15th through the completion of surveys in October. A mid-September shift from predominately long to short-distance warbler and other passerine species was also observed in a companion migratory bird study at Hawk Ridge Bird Observatory, Duluth, Minnesota (Bardon 2012). I therefore assigned unidentified warblers and passerines observed from mid-August through 14 September to an early season warbler group (WAREarly; both identified and unidentified warblers) and an early season passerine group (PASSEarly; unidentified warblers, unidentified passerines, and all other identified passerine migrants). Because my surveys concluded at the end of September, I did not include late season groups in analysis due to a small sample size resulting from only 2.5 weeks of potential survey time.

Birds retained for analyses (n ≥ 100 individuals) included seven groups and 18 species (Chapter 1 Appendix). Groups based on migratory group and taxonomy retained for analysis included early season migratory passerines (PASSEarly), semi-permanent and permanent residents (PERMAll), early season warblers (WAREarly), all thrushes minus American Robin (*Turdus migratorius,* THRAll), all flycatchers (FLYAll), all migratory woodpeckers (excludes resident species, WPRAll), and all migratory passerines across the entire survey season (MIGPASSALL). Because American Robins and Cedar Waxwings (*Bombycilla cedrorum*) are known diurnal migrants that actively move in the migration direction throughout the study period (Bardon 2012), these two species were excluded from the thrush and passerine groups and analyzed separately.

I used ArcGIS 10 software (ESRI 2010) to create polygons for each 500 meter long by 100 meter wide transect survey area (i.e., 50 meters on either side of trail, hereafter ‘transect polygon’). The change in slope (ChngSlp) and average elevation (Elev) for each transect polygon were obtained using digital elevation models. Distance from shore (DistShr) and distance from Duluth, Minnesota were also obtained using ArcGIS 10. The presence of a major ridgeline (RdgLn) within each polygon was recorded as binary presence/absence (1/0) data. During preliminary analyses, some birds showed nonlinear relationships with distance from shore and elevation, so quadratic terms for these variables were included in analyses. Distance from shore and elevation were positively correlated ($R^2 = 0.90$, $P \leq 0.001$), but both were retained as explanatory variables. An illustrated distribution of mean bird abundance by site (bubble plot) was also examined to inform the influence of broad-scale topographic features on bird distribution. Land cover types developed by Wolter and White (2002) were obtained as the number of pixels within each transect polygon at a 30-meter resolution. Land cover types that constituted <1.0% of the total types were excluded from analyses. To assess the importance of landscape features on bird distribution during stopover, explanatory variables were divided into ‘topographic’ and ‘land cover’ variables and analyzed separately. All variables used to obtain best-fitting models are listed in Table 1.

For each transect polygon, I obtained a mean bird abundance for each bird group and species (n=114). Residuals met assumptions of normality (Johnson 1995), so linear models were used. Species richness was not evaluated due to the high proportion of birds that were not identified to species. Several bird groups showed a relationship with the time after sunrise, distance from Duluth (southwestern terminus of the coastline), and the interaction of these two variables. I was primarily interested in the effects topography and land cover variables to I eliminated the influence of time and distance from Duluth by using residuals from models that included these variables in lieu of bird means for analyses.

Variable selection.- To determine the topographic and land cover variables that were most influential in describing the distribution of birds in the landscape, I used a tiered independent variable selection process with a cross-validation technique. For final model development for each bird group, I retained explanatory variables that appeared in ≥ two training models. Selected variables for each bird group were then developed as a best-fitting model using linear regression and subjected to an internal three-fold cross-validation technique to check for model robustness (CVlm procedure in R, package DAAG).

RESULTS

A total of 21,406 individual birds of 95 species were recorded during 582 transect surveys (Chapter 1 Appendix). Unidentified warblers and unidentified passerines comprised 44% of the observations. These birds likely represented a high proportion of long-distance boreal migrants because many were observed earlier in the season coinciding with the known passage of these birds (Bardon 2012). In addition, a larger proportion of short-distance migrants and local residents retain identifiable species characteristics year-round. The most common species identified were the short-distance migrant White-throated Sparrow (*Zonotrichia albicollis,* 10% of total), semi-permanent resident Red-breasted Nuthatch (*Sitta Canadensis,* 9%), and permanent residents Black-capped Chickadee (*Poecile atricapillus,* 7%) and Downy Woodpecker (*Picoides* *pubescens*, 3%).

Topography and birds.- Models based on topographic features were developed for 13 of the 25 bird groups and species with each possible topographic variables included in at least one model (Table 2, Fig. 4). The highest-ranking models were developed for Swainson's Thrushes (R^2 adj. = 0.19, $P \leq 0.001$), Downy Woodpeckers (R^2 adj. = 0.13, $P \leq 0.001$) and the thrush group (R^2 adj. = 0.14, $P \leq 0.001$). Distance from shore, elevation, or a combination of these variables and their quadratic forms were common explanatory variables in these highest-ranking models. The two thrush models revealed these birds were associated with near shore areas of low elevation and inland areas of high elevation. Downy Woodpeckers were associated with areas closer to shore and areas of higher elevation. The remaining models that involved the broad-scale variables distance from shore and elevation were for either permanent residents (e.g., permanent resident group, R^2 adj. = 0.08, $P \leq 0.01$ and Black-capped Chickadees, R^2 adj. = 0.09, $P \leq 0.01$), or long-distant migrant species (e.g., Nashville Warblers, *Vermivora ruficapilla,* R^2 adj. = 0.08, $P \leq 0.01$and Ovenbirds (*Seiurus aurocapilla,* R^2 adj. = 0.06, $P \leq 0.05$).

All of the best-fitting, albeit weak, models that involved the local-scale variables proximity to a major ridgeline and a change in the slope were for short-distance migrant species and groups. Migratory woodpeckers (R^2 adj. = 0.06, $P \leq 0.01$), Northern Flickers (*Colaptes auratus*, R^2 adj. = 0.02, $P \leq 0.05$), and Cedar Waxwings (R^2 adj. = 0.05, $P \leq 0.01$) were associated with the presence of a ridgeline. American Robins (R^2 adj. = 0.03, $P \leq 0.05$) and Yellow-rumped Warblers (R^2 adj. = 0.10, $P \leq 0.001$) were associated with local change in the percent slope. American Robins were associated with flatter areas (little change in slope) while Yellow-rumped Warblers were associated with areas containing high change in slope.

Land cover and birds.- Fifteen land cover types comprised at least 1.0% of the total habitat surveyed (Table 2). The most common land cover types were stands of aspen-birch, a mixture of aspen-birch and conifer species, and northern hardwood (predominately sugar maple, M. White, TNC pers. comm., A. Peterson pers. obs), reflecting dominant land cover for the region (MNDNR 2006). Significant land cover models were obtained for 11 of the 25 bird groups and species, and included 7 of the 15 land cover types (Table 2). Spruce-fir, aspen-birch, and northern hardwood were the most common land cover types among best-fitting models. Highest ranking models were for resident birds and included models developed for the permanent resident group (R^2 adj. = 0.30, $P \leq 0.001$), Red-Breasted Nuthatches (R^2 adj. = 0.32, $P \leq 0.001$), and Black-Capped Chickadees (R^2 adj. = 0.24, $P \leq 0.001$). All of these birds were associated with areas of spruce-fir that lacked northern hardwood land cover types.

Migratory bird associations with land cover were not as strong as those with permanent residents and model correlation coefficients were relatively weak. Among the highest ranking models I found associations between areas containing aspen-birch stands and American Redstarts (R^2 adj. = 0.10, $P \leq 0.001$) and the early season passerine group (R^2 adj. = 0.11, $p \leq 0.001$). Of the remaining models, the migratory passerine group and American Robins were also associated with aspen-birch stands (R^2 adj. = 0.06, $p \leq 0.01$, R^2 adj. = 0.04, $p \leq 0.05$), Red-eyed Vireos (*Vireo olivaceus)* were associated with areas that lacked stands of spruce-fir ($R^2 = 0.08$, $P \leq 0.01$), Brown Creepers (*Certhia* *americana*) were associated with a mixture of hardwood and conifer stands (R^2 adj. = 0.08, $P \leq 0.01$) and Northern Flickers were associated with areas containing stands of jack pine (R^2 adj. = 0.06, $P \leq 0.01$). Yellow-rumped Warblers were associated with areas of open water which included Lake Superior, and other lakes, rivers, or ponds (R^2 adj. = 0.04, $P \leq 0.05$).

DISCUSSION

In contrast to previous stopover studies in coastal habitats, as well as my own predictions, I found most migratory birds were unassociated or showed only weak relationships to landscape features in the coastal region of Lake Superior. Migratory birds were less confined to the shoreline, specific habitat types, or topographic features compared with observations that have been made in other coastal environments. I am unaware of any other stopover habitat study that has occurred along such a broad expanse of habitat (160 km) adjacent to an ecological barrier with similar large numbers of migratory land birds recorded. In addition to a large sample size, my finding that permanent resident species were associated with landscape variables (both topography and land cover) in this region validates the robustness of my analytical methods. While most relationships among migrant abundance, topography, and land cover were weak or absent, my data did reveal a difference in the scale of topographic features influencing long- and short-distance migrant groups discussed below.

Broad-scale topography.- Distance from shore and elevation were common topographic variables in some long-distance migrant models (e.g., Black-and-white Warblers, Nashville Warblers, and Ovenbirds), and especially influenced Swainson’s

Thrush distribution. Swainson’s Thrushes were primarily associated with areas in close proximity to the coast and inland areas of high elevation. Although long-distance migrants commonly move in broad-fronts during nocturnal flights, concentrated nocturnal movements have been found to occur along ecological barriers (Åkesson 1993, Gagnon et al. 2011). The contrast of land and water, or high and low elevation (ridgelines) that act as navigation cues during nocturnal flight may also act as cues for initial stoppage. Although nocturnal movement was outside my study timeframe, this movement behavior likely played an important role in explaining broad-scale topographic stopover selection exhibited by some long-distance migrants in forested habitats.

Local-scale topography.- In contrast to the broad-scale topographic features that influenced some long-distance migrants, short-distance migrant distribution was influenced by fine-scale or “local” topographic features such as ridgelines and change in slope. Diurnal migrants were the most common short-distance migrant species observed in this study (e.g., American Robin, Cedar Waxwing, Yellow-rumped Warbler) and were observed using a fly-and-forage migration strategy – stopping to forage within the habitat during active movement in the migration direction (Alerstam 2009, Bardon 2012, A. Peterson pers. obs.). Local topographic features provide shelter from winds during migratory movements and provide guide-lines in the direction of migration (Williams et al. 2001). Therefore, just as for long-distance migrant species, patterns in active migratory movement may also influence short-distance migrant distribution during stopover.

Stopover in a coastal forested landscape.- During migration periods, migratory birds are essentially “forced” into habitats adjacent to ecological barriers in relatively high numbers at a time when they are in need of both food and cover to survive their migratory journey. In the Lake Superior coastal region, I found land cover and topographic features did not reasonably explain migratory bird distribution and that many migrants were altogether unassociated with land cover type or topography. Several factors may explain these observations. Upon reaching the coastal region, migrants are exposed to continuous tracts of forest that likely provide the necessary resources of food and cover – what Mehlman et al. (2005) refer to as a ‘full service hotel’ – resulting in little need to “select” habitat. In addition, nocturnal relocation flights and morning redistribution flights within this stopover area, to maximize the efficient use of space for foraging, to minimize competition, and to avoid predation or inclement weather by seeking cover (Petit 2000, Faaborg et al. 2010a), would allow for broad dispersal over the landscape (Chernetsov 2006, Mills et al. 2011, Taylor et al. 2011). Furthermore, the orientation of Lake Superior’s north shore (northeast to southwest) allows for migrating birds to participate in a fly-and-forage strategy – a strategy of continued movement in the migration direction and distribution through the forested area of this coastal region.

Conservation implications and future directions.- Unlike the forested coastal area of Lake Superior where migrants exhibit relatively even distributions during stopover, fragmented coastal areas likely present a much greater challenge as migrants must make selections of suitable habitat. Patches of forest in fragmented coastal landscapes, although heavily used by migratory birds (Buler et al. 2007, Bonter et al. 2009), are in danger of becoming crowded, depleted of resources, and especially inviting for predators, making for suboptimal stopover habitat. In addition, relocation and fly-and-forage migration strategies that likely occur in more intact habitats are much more challenging in fragmented landscapes, because migrant movement may be confined to patches of habitat or migrants may be forced to travel through inhospitable areas.

A challenge for future efforts to conserve migratory bird stopover habitat is to establish the amount and location of forests that should be conserved so as to not disrupt migratory stopover, migratory movements, and breeding or wintering bird survival (Faaborg et al. 2010a). Ecological barriers to migratory movement often lie at the convergence of ecological transition zones, contain unique topographic and vegetative landscape patterns, act as migratory bottlenecks, and contain critical habitat with the potential to have disproportionate impacts on species survival during migration and other times of the year (Mehlman et al. 2005, Newton 2006). For instance, in addition to the >190 bird species (36 of conservation concern, MNDNR 2006) that use the Lake Superior coastal region during migratory periods, the region has one of the richest diversities of breeding birds in the nation (>170 species, 50 species of conservation concern; Green 1995, Rich et al. 2004, MNDNR 2006). The unique landscape features that characterize areas adjacent to ecological barriers often result in these areas being more heavily affected by human factors that have known impacts on avian survival, such as communication and transmission towers, wind turbines, windowed structures, loss of habitat due to development, and both natural and unnatural predators (Schaub 2012, Bracey 2013, Longcore et al. 2013, NOAA 2013b). Many of the long-distance migrants that have been declining both regionally and continent wide (Sauer et al. 2011, Niemi et al. 2014) experience some of the highest mortality rates from collisions with windows and other structures during migration (Mack and Young 2000, Bracey et al. 2013) – such as warblers in the family Parulidae (Arnold and Zink 2011) – creating the potential for coastline or ridgeline development to disproportionately impact these species during migratory periods.

I, along with others, emphasize the need to restore large and/or well-connected tracts of forested habitat along fragmented ecological barriers for use by migratory land birds (Petit 2000, Faaborg et al. 2010a). Additional information from advanced movement technologies to discover how and where migratory birds utilize stopover habitat (Robinson et al. 2010, McKinnon et al. 2013), in conjunction with studies of avian use of intact environments, will be necessary to identify priority areas for protection or restoration. As climate change is expected to put additional pressure on coastal areas in the form of increased human population as well as increased energy infrastructure (NOAA 2013b), there is an urgent need to provide comprehensive conservation strategies in areas that support significant habitat for migratory land birds.

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TABLE 1. Topographic and land cover variables used in determining influence of landscape features on bird distribution during migratory stopover. Land cover type followed in parentheses by proportion of the total land cover surveyed.

Variable Code	**Type**	**Description (land cover proportion of total)**
ChngSlp	Topographic	Average change in the slope of transect polygon
DistShr	Topographic	Average distance to Lake Superior coastline
DistShr2	Topographic	Quadratic distance to Lake Superior coastline
Elev	Topographic	Average elevation of transect polygon
Elev2	Topographic	Quadratic elevation of transect polygon
RdgLn	Topographic	Presence of a ridgeline in the transect polygon
AspnBrch	Land Cover	Aspen-birch (32.1%)
AspnBrchConif	Land Cover	Aspen-birch - Conifer (16.3%)
NHrd	Land Cover	Northern Hardwoods (14.7%)
AspnBrchConifUnd	Land Cover	Aspen-birch - Conifer Understory (13.2%)
NatvGrss	Land Cover	Native Grass (2.9%)
SprcFrHrd	Land Cover	Spruce-fir - Hardwood (2.4%)
HrdRgn	Land Cover	Hardwood Regeneration (2.4%)
BrshMisc	Land Cover	Miscellaneous Brush Spp. (2.4%)
JckPn	Land Cover	Jack Pine (1.7%)
SprcFr	Land Cover	Spruce-fir (1.5%)
Rds	Land Cover	Roads (1.1%)
Wtr	Land Cover	Water (1.1%); lake shore, ponds, rivers
BrGrnd	Land Cover	Bare Ground (1.1%)
BrshAldr	Land Cover	Brush-alder (1.1%)
Dvlpd	Land Cover	Developed (1.0%)

TABLE 2. Linear models developed using topographic and land cover variables to describe migratory bird distribution in the landscape ($p<0.05$*, $p<0.01$**, $p<0.001$***). The migratory passerine group, early season passerine group, early season warbler group, flycatcher group, American Redstarts, Blue Jays (*Cyanocitta cristata*), Brown Creepers (*Certhia americana*), Golden-crowned Kinglets (R*egulus satrapa*), Purple Finches (*Carpodacus purpureus*), Red-breasted Nuthatches, Red-eyed Vireos, and White-throated Sparrows were not associated with any topographic variables used in this study. The early season warbler group, flycatcher group, thrush group, migratory woodpecker group, Black-and-white Warblers, Blue Jays, Cedar Waxwings, Downy Woodpeckers, Golden-crowned Kinglets, Nashville Warblers, Ovenbirds, Purple Finches, Swainson’s Thrushes, and White-throated Sparrows were not associated with any land cover variables used in this study.

	Best Topographic Model					Best Land Cover Model				
	Variable	**Estimate**	**p-value**	**Adj r2 (p-value)**		**Variable**	**Estimate**	**p-value**	**Adj r2 (p-value)**	
Migratory Passerines (entire season)	-					*(Intercept)*	*-1.95*	*0.04*	*0.06*	**
						AspnBrch	*0.10*	*0.01*		
Permanent Residents	*(Intercept)*	*1.33*	*0.01*	*0.08*	**	*(Intercept)*	*-0.14*	*0.74*	*0.30*	***
	DistShr	*0.00*	*0.00*			*SprcFrHrd*	*0.22*	*0.12*		
						SprcFr	*0.53*	*0.00*		
						NHrd	*-0.08*	*0.00*		
Migratory Passerines (early season)	-					*(Intercept)*	*-2.81*	*0.00*	*0.11*	***
						AspnBrch	*0.15*	*0.00*		
Thrush Spp. (minus American Robin)	*(Intercept)*	*5.00*	*0.00*	*0.13*	***	-				
	DistShr	*0.00*	*0.00*							
	DistShr2	*0.00*	*0.00*							
	Elev	*-0.04*	*0.00*							
	Elev2	*0.00*	*0.00*							
Migratory Woodpeckers	*(Intercept)*	*-0.04*	*0.30*	*0.06*	**	-				
	RdgLn[T.y]	*0.32*	*0.00*							
American Redstart	-					*(Intercept)*	*-0.27*	*0.01*	*0.10*	***
						AspnBrch	*0.01*	*0.00*		
American Robin	*(Intercept)*	*0.20*	*0.07*	*0.03*	*	*(Intercept)*	*-0.19*	*0.06*	*0.04*	*
	ChngSlp	*-0.01*	*0.03*			*AspnBrch*	*0.01*	*0.01*		
Black and White Warbler	(Intercept)	-0.10	0.05	0.09	**	-				
	DistShr	0.00	0.39							
	DistShr2	0.00	0.93							
Black-capped Chickadee	(Intercept)	0.19	0.94	0.09	**	*(Intercept)*	*0.11*	*0.56*	*0.24*	***
	Elev	0.01	0.70			*SprcFr*	*0.27*	*0.00*		
	Elev2	0.00	0.41			*NHrd*	*-0.04*	*0.00*		
Brown Creeper	-					*(Intercept)*	*-0.11*	*0.02*	*0.08*	**
						NHrd	*0.01*	*0.00*		
						AspnBrchConifUnd	*0.00*	*0.05*		
						SprcFr	*0.03*	*0.07*		
Cedar Waxwing	*(Intercept)*	*-0.11*	*0.35*	*0.05*	**	-				
	RdgLn[T.y]	*0.91*	*0.01*							
Downy Woodpecker	*(Intercept)*	*-0.90*	*0.01*	*0.14*	***	-				
	DistShr	*0.00*	*0.00*							
	Elev	*0.00*	*0.00*							
Nashville Warbler	*(Intercept)*	*1.61*	*0.00*	*0.08*	**	-				
	Elev	*-0.01*	*0.00*							
	Elev2	*0.00*	*0.00*							
Northern Flicker	*(Intercept)*	*-0.02*	*0.48*	*0.03*	*	*(Intercept)*	*-0.02*	*0.47*	*0.06*	**
	RdgLn[T.y]	*0.15*	*0.04*			*JckPn*	*0.02*	*0.00*		
Ovenbird	(Intercept)	0.17	0.68	0.06	*	-				
	Elev	0.00	0.43							
	Elev2	0.00	0.26							
Red-breasted Nuthatch	-					*(Intercept)*	*-0.80*	*0.43*	*0.32*	***
						SprcFrHrd	*2.15*	*0.03*		
						SprcFr	*4.22*	*0.00*		
						NHrd	*-3.79*	*0.00*		
Red-eyed Vireo	-					*(Intercept)*	*0.05*	*0.24*	*0.08*	**
						SprcFr	*-0.05*	*0.00*		
Swainson's Thrush	*(Intercept)*	*3.23*	*0.00*	*0.19*	***	-				
	DistShr	*0.00*	*0.00*							
	DistShr2	*0.00*	*0.01*							
	Elev	*-0.02*	*0.00*							
	Elev2	*0.00*	*0.00*							
Yellow-rumped Warbler	*(Intercept)*	*-0.77*	*0.00*	*0.10*	***	*(Intercept)*	*-0.08*	*0.61*	*0.04*	*
	ChngSlp	*0.04*	*0.00*			*Wtr*	*0.12*	*0.02*		

Fig.1. Fall migratory movement of boreal land birds in relationship to the Great Lakes and Lake Superior.

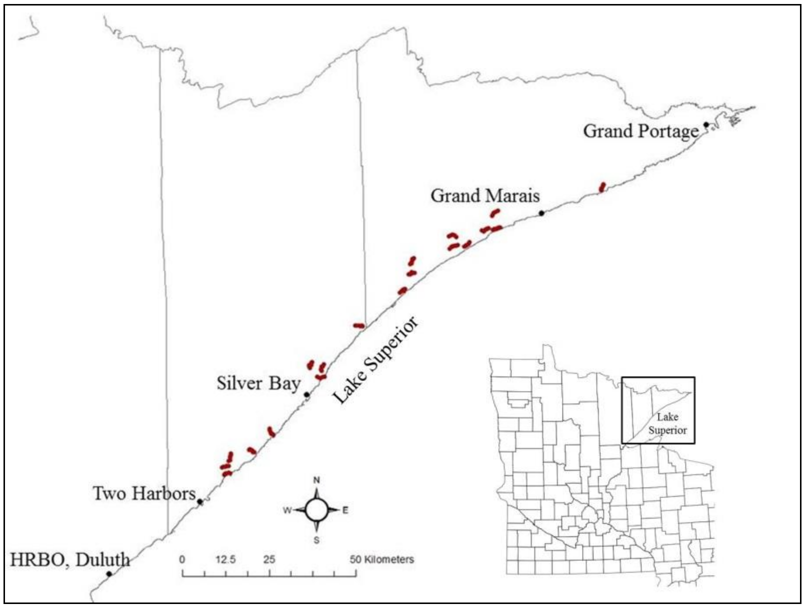

Fig. 2. General locations of survey transects (red) and major towns along Lake Superior's north shore in Minnesota, USA.

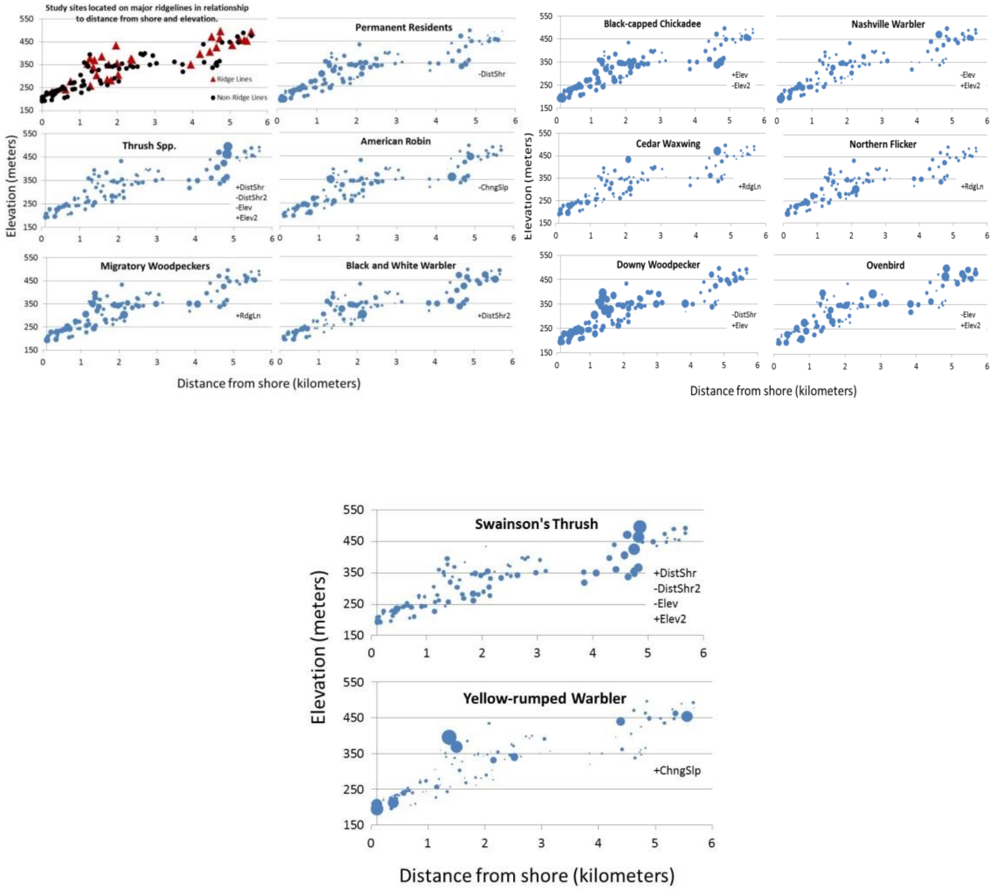

Figure 3.Relative mean bird abundance (indicated by bubble size) across study sites for best-fitting topographic models distributed by the variables distance from shore and elevation. Sites that intersect major ridgelines are indicated by red triangles (upper left graph). Important variables and direction of relationship are listed on graph. Bubble sizes represent relative abundance within individual graphs only. A gap in study sites at approximately 3.5 kilometers from shore reflects the lack of accessible and suitable trails at this distance.

(This manuscript is formatted for submission to the Journal Ecological Applications)

Chapter 2.

Migratory bird use of airspace along an ecological barrier

Abstract: During autumn migration, the northern coastline of Lake Superior acts as an ecological barrier for migrating land birds that breed across the boreal forests of Canada and Alaska. From a series of observation points, I assessed diurnal migratory bird movements during autumn migration, 2008-2010, along this coastal migration barrier. A total of 13,702 raptors (2008-2010) and 151,550 non-raptors (of which 90% were passerines; 2009-2010) were recorded during surveys that began within 1-2 hours of sunrise. Several raptor species or groups showed patterns in airspace associated with topographic features such as proximity to the shore and presence of ridgelines. However, the funneling movement that is commonly used to describe raptor behavior along migratory diversion lines occurred only among Bald and Golden eagles, suggesting a "leaky" migration funnel for most migratory raptors. Seventy percent of passerines were observed during the first two hours after sunrise and many participated in morning flights inland, not in the migratory direction. In addition, more passerines than raptors showed spatial and temporal structure in airspace distribution, including a funneling movement and association with airspace near the shore. I conclude that a) using raptor counts from single migration sites at the "tips" of presumed migration funnels to account for total raptor abundance and population trends greatly underestimates true numbers of raptors and affects estimated population trends, b) the diurnal spatial and temporal movement

patterns of migrating passerines along ecological barriers have been largely overlooked, and c) the airspace associated with anthropogenic development (e.g., buildings, towers, wind turbines) is heavily utilized by both raptors and non-raptors during diurnal migratory periods.

INTRODUCTION

For migratory land birds, the migration phase of the annual-cycle is a critical time that may have profound effects on individual survivorship and populations (Sillett and Holmes 2002, Newton 2006, Klaassen et al. 2013). Migratory bird conservation efforts aimed at migration periods generally focus on the identification and protection of stopover habitats and staging areas (Mehlman et al. 2005, Ewert et al. 2012). Although stopover areas are a limiting factor in migration success, the aerial environment through which migrants move is heavily utilized and subject to anthropogenic development pressures and other changes that potentially impact avian populations (Loss et al. 2012, Schaub 2012, Longcore et al. 2013). Therefore, strategies aimed at the protection of migratory land birds are incomplete without understanding how birds utilize airspace during periods of migratory movement.

Three to five billion landbirds (> 90%) that breed in the boreal regions of North America will annually migrate to areas from the southern United States to Central or South America (Green 1995, Wells and Blancher 2011). A substantial number of these birds are unique to the boreal forest and are species of conservation concern due to population declines (Rich et al. 2004, Sauer et al. 2007, Niemi et al. 2014). During autumn migration, the southeastern movement trajectory of boreal landbirds results in a large proportion of these birds intersecting the Great Lakes region, and Lake Superior's southwest – northeast oriented northern shore (hereafter "north shore", Fig. 1, Diehl et al. 2003, Bonter et al. 2009, Leppold and Mulvihill 2011, Evans et al. 2012). Hawk Ridge in Duluth, Minnesota (hereafter 'HR', Fig. 2) is located at the extreme southwestern tip of Lake Superior.

HR is one of the premier autumn raptor migration observation sites in North America, both in terms of sheer abundance of raptors and number of raptor species (Hofslund 1966, Farmer et al. 2008, Evans et al. 2012). During migratory movements, birds concentrate adjacent to ecological barriers, geographical features that act to change, hinder, or obstruct migratory movement such large bodies of water (Berthold 2001). The landscape features that define the Lake Superior coastal region northeast of HR include the coastline and a series of ridgelines parallel to the coast that are broken by broad valleys. The presence of these topographic features, coupled with an overall migratory movement towards the western Great Lakes region, results in a concentration of migratory birds adjacent to Lake Superior's north shore (Hofslund 1966, Goodrich and Smith 2008).

In addition to raptors, many non-raptors participate in diurnal migratory movements and respond to topographic cues such as coastlines and ridgelines (Alerstam and Pettersson 1977, Bingman 1980, Williams et al. 2001, Berthold 2001, Alerstam 2009). The diurnal movements of non-raptors (e.g., passerines) during autumn migration recently have been systematically recorded from the southwestern tip of Lake Superior (Bardon 2012) in abundances that compare to, or rival, nationally known migration sites (e.g., Cape May, Wiedner et al. 1992). Although this study was originally intended to study raptors (Seeland et al. 2012), during the 2008 migration season I observed migratory movements of non-raptors that greatly outnumbered that of raptors. I expanded my study in 2009-2010 to include these birds.

Nearly 40% of the U.S. human population lives within 50 miles of a major coastline, a percentage expected to rise (NOAA, 2013). As human need for renewable energy (e.g., wind power), communication technology (e.g., towers), and living space expands, so does the fragmentation of airspace within these coastal areas. Because many coastal areas act as bird migration bottlenecks and corridors, there is a need to understand migratory bird movement in airspace to mitigate disruptions in migratory routes and timing, and prevent direct mortality from development.

The objective of my study was to characterize the spatial and temporal patterns that define the aerial distribution of diurnal migratory birds. I explored this objective within a migration concentration area that spanned 210 kilometers (130 mile) - an area of >2000 kilometers^2 - along a coastal ecological barrier, Lake Superior. I expected that diurnal timing patterns in raptor abundance would be consistent with patterns in raptor movements observed during other regional studies (HRBO 2013, Seeland 2012) where raptor abundance increased throughout the day. Because many raptors are reluctant to cross large bodies of water (Goodrich and Smith 2008), and use coastlines and ridgelines as ‘lead-lines’ in the migration direction, I expected raptors to be spatially associated with ridgelines and the shore. I also expected raptors to exhibit an increase in abundance in the migration direction toward the southwestern tip of Lake Superior (Duluth, Minnesota) due to a “funneling movement” along a diversion line created by the north shore of Lake Superior (Hofslund 1966, Goodrich and Smith 2008). Lastly, I anticipated an overall even distribution of raptors vertically in the airspace. Because information about the diurnal movement of non-raptors in this region was lacking and in other regions assumed to be “broad-front” (Faaborg et al. 2010), I expected non-raptors to exhibit even temporal and spatial distributions in airspace during diurnal migratory movements.

METHODS

Site Selection. I used a study design developed by Seeland et al. (2012) that used a series of observation points to assess migratory bird movements within a large geographical area (Fig. 2). Twenty-four survey sites (three sites in each of eight regions) were established between Duluth and Grand Portage, Minnesota at locations with either naturally broad views of the surrounding landscape or aided views with the help of structures such as tree stands. The three sites per region were located at various distances inland from the shore of Lake Superior. Sites nearest the shore ranged from 0.4 to 2.0 kilometers inland, sites furthest from shore ranged from 5.4 to 12.0 kilometers inland. Two survey sites used during the Seeland et al. (2012) study (sites 1c and 6a) were replaced in 2009 due to inaccessibility and an increased landscape viewing potential; thus they were excluded from my data set.

Bird Surveys. Migratory bird survey methods followed those of Seeland et al. (2012). Surveys involved trained observers simultaneously recording birds at the three sites within a region. Each region was visited 3-4 times during autumn migration (late August – early November), 2008-2010. Only raptors were recorded in 2008; all birds were recorded in 2009 and 2010. During 2008, observations began 1-2 hours after sunrise and continued for 7 hours. During 2009-2010, observations began as close to sunrise as possible and continued for 7-8 hours to account for the large numbers of non-raptors moving during the early morning hours. Observers rotated among sites to minimize bias, and surveys generally followed an “up shore” (northeast) direction to avoid double-counting birds. When observations moved to a “down shore” location, a 1-2 day buffer without sampling was applied. During every observation hour, all actively moving birds were recorded as a point on a topographic map where first detected above the landscape, and identified to the lowest taxonomic identification possible. Birds were defined as “moving” when passing through the observation area without landing. Estimates of flight height and flight direction were also recorded for each bird observation.

Data Analysis. All bird observations and associated flight data were entered into a GIS (ArcGIS 10 software) to identify the corresponding geographic coordinate locations and obtain distance from shore and distance from Duluth measurements. A 30-meter digital elevation model (DEM) was used to obtain ridgeline data. Ridgelines were defined as ridges with > 20% rise from the surrounding landscape within the viewing area, and having an orientation parallel to the Lake Superior shore. Data from weather stations in proximity to each site were used to develop an average wind direction and speed for each survey date during observation hours.

Analyses included only bird species or groups represented by ≥ 200 individuals. Birds were grouped by order or family, and for landscape analyses, passerines (Order Passeriformes) were grouped by season (e.g., early season and late season) to better represent unidentified individuals that were more likely long- (early season) or short- (late season) distance migrants. Only birds recorded within a maximum distance of 1600 meters (one mile) from the observer were retained in analyses. More than 85% of observations occurred within this distance, beyond which the majority of birds were unidentifiable to species or group. Bird species and groups were averaged (mean) for each site by hour after sunrise and by all visits across all years, so normal distribution assumptions were met (Johnson 1995). To balance the difference in the amount of airspace that was viewable among survey sites, the viewing area for each site was defined as the spatial area that contained 99% of bird observations and obtained in the GIS. The resulting viewing areas were applied as weights to mean bird observations for each site, resulting in mean birds per square kilometer as the unit of analysis. For ease of interpretation, raptors were separated from other migrants (non-raptors) for analyses and discussion.

Timing. To assess the daily timing of bird movement, mean bird abundance for each of the major bird species or groups was calculated for each full hour after sunrise (e.g., hour one = sunrise to one hour after sunrise, etc.). For surveys that did not start at sunrise or at the exact start of the one hour interval after sunrise, bird abundance was split by the proportion of survey time spent during each survey hour according to sunrise time. For example, if sunrise occurred at 0700 and the first hour of a survey occurred from 0730-0830 yielding 4 Merlins, 50% (n = 2 Merlins) would be assigned to hour 1 (0700-0800), and 50% (n = 2 Merlins) assigned to hour 2 (0800-0900). I then used one-way Analysis of Variance (ANOVA) to determine if there were any differences in mean bird abundance per kilometer^2 among each hour after sunrise.

Flight Height and Wind Speed. Birds were assigned a flight height category relative to the height of the tree canopy (averaged 20 meters in height) at the point where the bird was first observed by using the topography of the landscape in relation to the height of the observer. Each bird observation was assigned one of the following flight height categories: below the tree canopy, between the canopy and 100 meters above the canopy, 100 meters to 500 meters above the canopy, and over 500 meters above the canopy. Due to limited visibility of bird movement below the tree canopy at some sites, I examined only the three categories of flight height above the canopy. Because wind speed may affect raptor height in the airspace, I also assessed the effect of wind speed on flight height when wind speeds were ≤ 6 knots (category 2 on the Beaufort wind scale) and > 6 knots by assigning a numeric flight altitude to each flight height category (50m, 300m, and 700m, respectively) and calculating the relative average flight altitude of raptors at each site. Wind speeds were averaged for each day using the on-site wind speed (Beaufort wind scale) recorded by observers and average wind speed recorded at the closest weather station. I used a t-test to assess any differences in flight height between high (> 6 knots) and low (≤ 6 knots) wind speeds among different flight altitudes for each raptor species or group. The majority of non-raptors were observed at low flight altitudes during both low and high wind speeds, so I did not examine differences between low and high wind days for non-raptor species or groups in this analysis.

Influence of landscape. To determine the landscape variables that were most influential in describing the distribution of birds in airspace, I used a step-wise multiple regression using backward/forward elimination and BIC selection criterion in R (stepwise procedure from R software package Rcmdr). Bird species and groups were the dependent variables and explanatory variables included distance from shore (DistShr), distance from Duluth, MN (DistD), the presence of a major ridgeline parallel to the Lake Superior shore (RdgLn), and the interaction of these variables. Best fit models were cross-validated using the CVlm procedure (3-fold, CVlm procedure) in R to test for model fit and robustness. For this analysis, the warbler and passerine groups were divided into early and late season migration guilds using the process detailed in Peterson et al. (Chapter 1). Because raptors were shown to concentrate within my survey area on days with no wind or when winds were from the west and north (Seeland et al. 2012), I divided survey days into two categories based on wind information from the closest weather station: days with no wind or winds with a west and/or north component and days winds with a south and/or east component. I applied wind direction analysis only to raptors because wind direction did not influence the abundance of most non-raptors in my study. Bubble plots were used to illustrate landscape relationships among the best models for raptors and non-raptors.

Because many non-raptors observed during my study were participating in morning flights not exclusively in the migration direction, I assessed the impact of the shoreline on non-raptor movement by comparing early- and late-season passerine flight direction to the angle of the nearest section of shore. Passerines were divided into flight direction categories based on the difference in flight angle from the shore angle: flights inland from shore (difference angles $\geq 6^o$), flights parallel to the coastline (difference angles between -5^o and 5^o), and flights towards the shore (difference angles $\leq -6^o$). An ANOVA was used to determine flight direction differences at the 2 sites within each region closest to the shore during the first 3 hours after sunrise, the time period when most passerine movement occurred.

RESULTS

A total of 13,702 raptors (2008-2010) and 151,550 non-raptors (2009-2010, of which 104,308 were migratory passerines) were recorded during 89 days (2008-2010) and 66 days (2009-2010) of surveys (Appendix A). During the early-season time period (on or before September 14th), I counted over 23,000 passerines, 53% of which were identified as warblers. Baltimore Orioles (*Icteris galbula*), Chimney Swifts (*Chaetura pelagica*), Ruby-throated Hummingbirds (*Archilochus colubris*), and all identified long-distance

(Neotropical) warbler species (Appendix A), were observed during the early season only. During the late-season (after September 14th), I counted over 57,000 late season passerines, 16% of which were identified as warblers and likely consisted of mostly Yellow-rumped Warblers (*Dendroica coronata;* Bardon 2012).

Seven raptor species were retained in analyses (n ≥ 200 individuals). Because Broad-winged Hawks (*Buteo platypterus*) migrate in pulses of relatively short duration but high abundance (Farmer et al. 2008), I compared my study dates to migratory pulses that occurred at HR (HRBO 2013) during corresponding survey years. I found my study dates did not consistently correspond to Broad-winged Hawk migratory pulses at HR (Seeland et al. 2012, HRBO 2013); therefore I excluded this species from analyses. In addition to species, I grouped raptors based on families with similar life histories and migratory behavior (e.g., accipiter, buteo, and falcon groups). Bald and Golden Eagles have different natural histories and migratory behavior, so were not grouped. Twenty-five species of non-raptors were retained for analyses along with 3 groups based on life similar histories and migratory behavior (e.g., blackbird, finch, warbler, and passerine groups, Chapter 2 Appendix).

Daily Timing. Two raptor groups and 5 species showed significant changes in the hourly timing of active movement (Fig. 3). The overall pattern for raptors that exhibited significant differences in hourly abundance was a small number of raptors moving during the first two hours after sunrise, then an increase in hour 3. Sharp-shinned Hawks, and to lesser extent American Kestrels, were the exception as a large number of these birds were active earlier in the morning, between hours 1 and 2 after sunrise. The falcon group, Bald Eagles and Rough-legged Hawks showed no difference in the mean number of birds actively moving during each hour after sunrise. Of the 28 non-raptor groups and species analyzed, 15 showed significant changes in the hourly timing of active movement (Fig. 4). The majority of these birds moved during the first 3 hours after sunrise with a decrease in active movement throughout the day. Seventy percent of passerines moved during the first 2-hours after sunrise.

Flight Height. Only one species, Turkey Vultures, showed a significant difference in flight height between low and high wind days ($t = -2.48$, $df = 23$, p-value ≤ 0.05), where more Turkey Vultures flew at lower altitudes on high wind days. The flight height of other raptor groups and species varied and did not significantly change between low and high wind days (Fig. 5). Most American Kestrels (77%) and Sharp-shinned Hawks (63%), as well the accipiters and falcons, were observed in the airspace between the tree canopy and 100 meters above the canopy. Bald and Golden Eagles were relatively equal in their use of airspace between tree canopy to 100 meters above the canopy, and 100 meters to 500 meters above the canopy. Bald Eagles more heavily used the airspace above 500 meters than Golden Eagles ($t = 6.25$, $df = 23$, p-value ≤ 0.001). In general, the Buteo group (47%) and Red-tailed Hawks (49%) were more often observed between 100 meters and 500 meters above the canopy, but Rough-legged Hawks (52%) were most often observed at lower altitudes. The Buteo group (25%), Bald Eagles (11%), and Red-tailed Hawks (11%) were the most common raptors observed $\geq$ 500 meters above the tree canopy. Non-raptor groups were mostly observed flying between the tree canopy and 100 meters above the canopy. Blackbirds were the only group observed $\geq$ 500 meters above the canopy.

Raptors and Landscape Effects. During days with winds conducive to raptors concentrating near the Lake Superior coastline (no wind or north and west wind), several groups and species were utilizing airspace associated with topographic landscape variables (Table 2, Fig. 6). Turkey Vultures, exhibiting the best fit model, were associated with proximity to the shore near Duluth, and major ridgelines near Duluth (adj. $r^2 = 0.45$, $p \leq 0.01$). Bald Eagles (adj. $r^2 = 0.27$, $p \leq 0.05$) and Golden Eagles (adj. $r^2 = 0.30$, $p \leq 0.01$) were associated with proximity to the shore and proximity to Duluth. The accipiter group, falcon group, and Sharp-shinned Hawks were associated with proximity to the shore (adj. $r^2 = 0.18$, $p \leq 0.05$, adj. $r^2 = 0.22$, $p \leq 0.05$, adj. $r^2 = 0.18$, $p \leq 0.05$ respectively). American Kestrels were associated with the presence of a major ridgeline (adj. $r^2 = 0.14$, $p \leq 0.05$). During days with winds not conducive for raptor concentration near the coastline (south and east winds), Bald Eagles and the falcon group were associated with proximity to the shore (adj. $r^2 = 0.24$, $p \leq 0.01$, adj. $r^2 = 0.27$, $p \leq 0.01$ respectively), and the accipiter group and Sharp-shinned Hawks were associated with proximity to the shore and the absence of major ridgelines (adj. $r^2 = 0.27$, $p \leq 0.05$, adj. $r^2 = 0.26$ $p \leq 0.05$ respectively). American Kestrels, Golden Eagles, and Turkey Vultures, showed no associations to landscape features on days with south or east winds.

The Buteo group, Red-tailed Hawks and Rough-legged Hawks showed no association with landscape features in either wind direction scenarios.

Nonraptors and Landscape Effects. I found no significant differences in the number of early season passerines participating in either morning flights inland, following the shore, or towards the shore (35%, 40%, 25% of total respectively). However, when comparing early and late season migrants, significantly higher proportions of early season migrants flew at angles inland from shore during the first hour after sunrise ($t = 3.59$, $df = 15$, $p\text{-value} \leq 0.001$). During the late season time period, I observed a significantly higher numbers of birds flying at angles towards Lake Superior than at angles inland during both hours 1 and 2 ($t = -2.47$, $df = 15$, $p\text{-value} \leq 0.05$, $t = -2.95$, $df = 15$, $p\text{-value} \leq 0.01$, respectively).

Movements of early season passerines and early season warblers were unassociated with topographic variables. In contrast, proximity to the shore and Duluth accounted for a substantial amount of the variability in late season passerine (adj. $r^2 = 0.70$, $p \leq 0.001$) and late season warbler (adj. $r^2 = 0.48$ $p \leq 0.001$) aerial distribution (DistShr, Table 3, Fig.7). The blackbird group (adj. $r^2 = 0.24$, $p \leq 0.05$), Blue Jays (adj. $r^2 = 0.23$, $p \leq 0.05$), and Cedar Waxwings (adj. $r^2 = 0.20$, $p \leq 0.05$) were also associated with proximity to the shore. American Robins (adj. $r^2 = 0.40$, $p \leq 0.01$) and Rusty Blackbirds (adj. $r^2 = 0.30$, $p \leq 0.05$) were associated with an increase in proximity to the shore and Duluth. Dark-eyed Juncos (adj. $r^2 = 0.56$, $p \leq 0.001$) were associated with the presence of ridgelines near

Duluth, whereas Pine Siskins (adj. $r^2 = 0.53$, $p \leq 0.001$), Myrtle Warblers (adj. $r^2 = 0.43$, $p \leq 0.01$), and the finch group (adj. $r^2 = 0.32$, $p \leq 0.05$) were associated with ridgelines near shore. American Goldfinches (adj. $r^2 = 0.38$, $p \leq 0.05$) were associated with proximity to the shore at sites farther from Duluth, but associated with ridgelines near Duluth.

DISCUSSION

I introduce, with Seeland et al. (2012), the first study to examine diurnal avian movements along 210 kilometers (130 miles) of a coastal ecological barrier that concentrates land birds during autumn migratory movements from breeding grounds to wintering areas. I found patterns related to time of day, height in the air-column, and landscape that described diurnal raptor and passerine use of airspace during migratory movements, and many patterns were unique to specific groups or species of migrants. I discuss here how these findings illustrate that a) counts from single raptor migration sites (e.g., HR) used to account for total movement abundance in a concentration area do not accurately represent and likely underestimate the number of raptors within a specific flyway, b) the migratory movement patterns of passerines have been overlooked along ecological barriers, and c) the airspace associated with anthropogenic development (e.g., buildings, towers, turbines) is heavily utilized by both raptors and non-raptors alike, many of which are species of concern and/or legally protected (e.g., Chimney Swifts, Golden Eagles, Rusty Blackbirds, Kochert and Steenhof 2002, Nebel 2010, Greenberg et al. 2011).

Underestimation and misinterpretation of raptor movement. Migratory “funneling” is commonly used to describe the raptor movement along topographic diversion lines, including the north shore of Lake Superior (Hofslund 1966, Goodrich and Smith 2008, Seeland et al. 2012). The funneling effect is the idea that, if an ecological barrier prevents or a diversion line enhances the preferred migration direction, birds accumulate and travel along the barrier or diversion line until they reach a dispersal point. Because south - southeasterly movements of raptors result in flight paths intersecting the coastline of Lake Superior – and because raptors often exhibit reluctance to cross this body of water – many of these birds travel adjacent to the shore, circumventing Lake Superior around its southwestern tip. The large numbers of migrating raptors that are counted seasonally at HR, and other migration sites, have been used as evidence for such funneling movement (Hofslund 1966, Kerlinger 1989, Farmer et al. 2008, Hussell and Ruelas Inzunza 2008, Seeland et al. 2012, HRBO 2013).

My results reveal that, for raptors, the funneling effect applies only to eagles. I suggest two explanations for the large number of migrating raptors concentrating along the shore but not increasing in abundance when approaching the southwestern tip of Lake Superior. First, it is possible that many of these boreal breeding raptors enter the Lake Superior coastal region farther north along the coastline than the boundary of my study (e.g., Canada). Therefore, few to no additional raptors enter the coastal area once they reach the Lake Superior shore in Minnesota. This scenario is unlikely because there is no natural diversion line separating the Canadian and U.S. shores.

The second and more-likely scenario is that concentration areas along large ecological barriers such as Lake Superior are “leaky.” For instance, several of the raptor species recorded in my study (e.g., *Falco* spp.) readily fly over water during migration, including over the Great Lakes (Perkins 1964, Bildstein and Zalles 2005). In addition to possible “leakage” over Lake Superior, raptors may encounter Lake Superior and move inland, exiting the coastal region in a barrier-avoidance migration strategy. This behavior may be learned and facilitated by natural selection as raptors repeatedly make the same autumn migration trip through the region (Goodrich and Smith 2008) thus resulting in experienced migrants avoiding the coastal region altogether. Further evidence of leakage includes a study of Sharp-shinned Hawk movement in the Lake Superior coastal area where radio-telemetry signals were consistently lost within 30 kilometers of the original capture site (170 km NE of Duluth), and not detected by a receiver placed at HR or during reconnaissance flights of the region (Peterson and Niemi 2011). The lack of funneling evidence indicates that observation counts at strategically placed research sites at the “tip” of these assumed migration funnels (e.g., HR) do not adequately represent the total number of birds traveling within a migration corridor along a migratory diversion line. I suggest the abundance of raptors migrating along coastal barriers are therefore, underestimated. I also suggest that using counts from migration sites such as HR may be inaccurate and inappropriate to develop raptor population trends over time (Farmer et al. 2008).

Passerines and overlooked movement patterns. Migratory passerines were the most abundant group of diurnal migrants observed along the north shore of Lake Superior and many revealed spatial and temporal movement patterns in airspace. In general, the movement of these birds during migration has been described as nocturnal and broad-front (Gauthreaux et al. 2003, Faaborg et al. 2010). However, many birds also participate in migratory movements during daylight hours in an uneven distribution over the landscape (Alerstam and Pettersson 1977, Bingman 1980, Williams et al. 2001, Berthold 2001, Alerstam 2009). Furthermore, studies of non-raptor movement using Doppler radar provide important broad-scale nocturnal movement information (Diehl et al. 2003, Dokter et al. 2011), but fine-scale nocturnal and diurnal movement patterns are hard to decipher and are undetectable in areas such as the Lake Superior coastal region where, due to topography and radar beam angle, birds literally 'fly under the radar' (Diehl et al. 2003, Newton 2008, Robinson et al. 2010, D. Miller pers. comm.).

Within the coastal area of Lake Superior, nearly all migratory passerines moved at low altitudes (< 100 meters above the canopy) and were observed during the first several hours after sunrise. Individuals were largely unaffected by the direction of wind during surveys; however, the low altitude flight of these birds may reflect a general wind avoidance as small birds often succumb to wind-drift and winds tend to be less pronounced at lower altitudes during daylight hours (Åkesson 1993, Newton 2008).

Early season passerine migrants were unassociated with topography, used airspace almost exclusively during the first few hours after sunrise, and compared with late season passerines, often traveled in a direction inland, away from the coastline. Because all the Neotropical migrants identified in my study were present during the early season only, it is likely my early season migrant group consisted of many nocturnal migrants that participated in nocturnal migratory movements during my study. Although the mechanism for my observed “morning flights” was unknown, studies of passerine migrants along similar ecological barriers suggest I were observing one or a combination of migration strategies that represented a reorientation flight response to errors during nocturnal movements (e.g., orientation, wind drift), an intentional flight away from a water barrier (Åkesson et al. 1996, Diehl et al. 2003), movements to locate stopover habitats before crossing Lake Superior (Wiedner et al. 1992), or relocation movements to suitable stopovers after an initial stop during the night (Mills et al. 2011, Taylor et al. 2011). Whatever the mechanism, my results suggest these migrants were not exclusively engaged in movement in the migration direction. Thus, the topographic features that influenced the migratory movement of other diurnal migrants, such as short-distance migrants, were not as important for these birds. In addition, a companion study showed that some long-distance migrants were associated with stopover locations at high elevations inland from shore (Chapter 1), suggesting some of my observed morning flights by long-distance migrants were a broad movement from over the water of Lake Superior or the coastline, to areas further inland to forage and/or find cover.

In contrast to the early season passerine migrants, the late season migrants exhibited a “funneling” movement (increased abundance near shore and Duluth), a pattern of migratory movement commonly reserved to describe the movements of migrating raptors (Hofslund 1966, Goodrich and Smith 2008) that I found exhibited by only two raptor species, Bald and Golden Eagles. Many of these late season species were short-distance migrants that are known to participate in diurnal migratory movements (Berthold 2001, Bardon 2012). A companion study provided evidence that many of these same species utilized stopover habitat during the same daily time period (Chapter 1). The combination of these observations suggests that not only do these birds show structure in airspace use but also used a ‘fly and forage’ migration strategy (Alerstam 2009, Chapter 1), seeking foraging opportunities during periods of active movement.

Implications for anthropogenic development of airspace. During migratory movements, the use of airspace by many land birds is patterned in space and time. Many studies that focus on the potential effects of human airspace development (e.g., wind turbines) during diurnal migration events specifically target raptors (e.g., Seeland et al. 2012, Schaub 2012). However, I show that passerine movements were more structured in airspace and greatly outnumbered raptors. I therefore suggest passerine movements have been overlooked in the context of human use and development of airspace. Furthermore, the seven or so hours of diurnal migratory bird movement information obtained through my study represents only a fraction of the 24-hour period of avian movement that occurs every autumn within the Lake Superior coastal region, and along other ecological barriers. For instance, large movements of Common Nighthawks (*Chordeiles minor*; 43,690 on 26 August 1990) are regular occurrences in August and large numbers of Saw-whet Owls (*Aegolius acadicus*; average 544/season) are banded each autumn migration period at Hawk Ridge (Bardon 2012, Evans et al. 2012). In addition, the information elicited from my study, a companion study (Bardon 2012), and a regional radar study (Diehl et al. 2003) suggest a predawn movement of passerine migrants in airspace related to stopover habitat choice that has yet to be documented and understood. These examples illustrate bird use of airspace outside the window of my study of which there is little to no migratory movement information available. This implies that the full magnitude of bird migration along Lake Superior's north shore and similar coastal ecological barriers likely greatly exceed current estimates.

Many birds of conservation concern displayed selective use of airspace within the coastal region of Lake Superior. For instance, Neotropical migrants were generally confined to airspace between the forest canopy and 100 meters above the canopy, and were most active during the first two hours after sunrise. Rusty Blackbirds, a species of continental concern (Greenberg et al. 2011), utilized the same airspace as Neotropical migrants, but also exhibited a funneling movement towards the shore of Lake Superior and Duluth. Funneling was also exhibited by Golden Eagles, a focal species of concern in the context of wind energy development (USFWS 2013), which were most often found at altitudes less than 500 meters in airspace, beginning the third hour after sunrise.

As structures such as tall windowed buildings, communication towers, and wind turbines continue to fragment airspace, it is imperative to understand how flying animals, such as birds, utilize airspace during their life-cycle. Recent studies that show how structures may impact avian populations emphasize the need to understand avian use of aerial environments (Schaub 2012, Longcore et al. 2013). It is also important to understand the patterns in which movement occurs – not only the diurnal patterns I illustrate here, but also nocturnal patterns that may be influenced by spatial and temporal cues (Perkins 1964, Gagnon et al. 2012). As human population continues to grow more quickly along coastlines in comparison with in any other landscape (NOAA 2013), so too will the infrastructure needed to support this growth. There is a need to understand the role and importance of airspace as an element of habitat for flying animals (Chapter 3), guide human development of coastal areas, and integrate this information into conservation strategies.

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Table 1. The proportion of total birds, mean birds per kilometer^2, standard deviation, and significance test (t-test) comparing raptor group and species abundance on favorable (N-W, zero) and unfavorable (S-E) wind days ($p<0.05$*, $p<0.01$**, $p<0.001$***).

	Favorable Wind			**Unfavorable Wind**				
Raptor Group/Spp.	**Proportion**	**mean**	**SD**	**Proportion**	**mean**	**SD**	**t-value**	
Accipiter	70%	4.87	4.11	30%	3.17	2.93	1.83	
Buteo	86%	3.16	2.81	14%	0.76	0.60	4.06	***
Falcon	67%	1.35	0.99	33%	0.95	1.01	1.33	
American Kestrel	69%	2.45	2.30	31%	1.38	1.43	1.70	
Bald Eagle	79%	6.50	3.67	21%	2.73	1.81	5.45	***
Golden Eagle	94%	0.97	0.96	6%	0.07	0.15	4.42	***
Rough-legged Hawk	89%	1.93	1.72	11%	0.30	0.38	4.57	***
Red-tailed Hawk	89%	4.82	4.29	11%	0.94	0.68	4.53	***
Sharp-shinned Hawk	69%	7.61	5.74	31%	5.35	4.87	1.51	
Turkey Vulture	70%	3.79	2.29	30%	2.05	1.41	3.19	**

Table 2. Parameter estimates of intercept, landscape explanatory variables, and variable interaction (denoted by ':') from stepwise models describing raptor distribution in airspace on favorable (no wind, winds from north and west) and unfavorable (winds from south and east) wind days. Landscape variables include distance from shore (DistShr), distance from Duluth (DistD), and the presence of a major ridgeline (RdgLn), and p-values include $p<0.05$*, $p<0.01$**, $p<0.001$***. Buteo groups were unassociated with landscape variables in this study.

	North and West Winds / No wind					South and East Winds				
Bird Group/Spp.	**Variable**	**Estimate**	**p-value**	**Adj r2 (p-value)**		**Variable**	**Estimate**	**p-value**	**Adj r2 (p-value)**	
Accipiter	(Intercept)	7.62	0.00	0.18	*	(Intercept)	6.46	0.00	0.27	*
	DistShr	-0.56	0.02			DistShr	-0.47	0.01		
						RdgLn	-2.00	0.07		
Falcon	(Intercept)	2.07	0.00	0.22	*	(Intercept)	1.75	0.00	0.27	**
	DistShr	-0.15	0.01			DistShr	-0.16	0.01		
American Kestrel	(Intercept)	1.50	0.02	0.14	*	-				
	RdgLn	1.89	0.04							
Bald Eagle	(Intercept)	11.24	0.00	0.27	*	(Intercept)	4.10	0.00	0.24	**
	DistD	-0.02	0.09			DistShr	-0.28	0.01		
	DistShr	-0.53	0.01							
Golden Eagle	(Intercept)	2.33	0.00	0.30	**	-				
	DistD	-0.01	0.02							
	DistShr	-0.12	0.02							
Sharp-shinned Hawk	(Intercept)	11.42	0.00	0.18	*	(Intercept)	10.80	0.00	0.26	*
	DistShr	-0.78	0.02			DistShr	-0.73	0.01		
						RdgLn	-3.72	0.05		
Turkey Vulture	(Intercept)	3.38	0.11	0.45	**	-				
	DistD	0.02	0.15							
	DistShr	0.01	0.98							
	RdgLn	2.35	0.18							
	DistD:DistShr	0.00	0.06							
	DistD:RdgLn	-0.02	0.08							

Table 3. Parameter estimates of intercept, landscape explanatory variables, and variable interaction (denoted by ‘:’) from stepwise models describing migratory non-raptor distribution in airspace. Only significant models ($\alpha = 0.05$) are shown. Landscape variables include distance from shore (DistShr), distance from Duluth (DistD), and the presence of a major ridgeline (RdgLn). P-values include $p<0.05$*, $p<0.01$**, $p<0.001$***. Bird species or groups not associated ($\alpha=0.05$) with landscape variables in this study included the early season passerines and warblers, American Crows, American Pipits (*Anthus rubescens*), Black-capped Chickadees, Canada Geese, Common Grackles, Common Loons, Common Ravens, Common Redpolls, Eastern Bluebirds (*Sialia sialis*), Horned Larks (*Eremophila alpestris*), Lapland Longspurs, Purple Finches, Red-winged Blackbirds, Sandhill Cranes, Snow Buntings, White-throated Sparrows (*Zonotrichia albicollis*), and White-winged Crossbills.

Bird/Variable	**Estimate**	**p-value**	**Adj r2 (p-value)**		**Bird/Variable**	**Estimate**	**p-value**	**Adj r2 (p-value)**	
Late Season Passerines					Blue Jay				
Intercept)	47.02	0.00	0.70	***	(Intercept)	11.76	0.00	0.23	*
DistD	-0.20	0.00			DistShr	-1.32	0.01		
DistShr	-3.61	0.00							
DistD:DistShr	0.02	0.02			Cedar Waxwing				
					(Intercept)	7.10	0.00	0.20	*
Late Season Warblers					DistShr	-0.69	0.02		
(Intercept)	10.40	0.00	0.48	***					
DistD	-0.06	0.00			Dark-eyed Junco				
DistShr	-0.96	0.00			(Intercept)	-0.02	0.98	0.56	***
DistD:DistShr	0.01	0.02			DistD	0.00	0.88		
					DistShr	0.18	0.00		
Blackbird spp.					RdgLn	2.11	0.01		
(Intercept)	5.62	0.00	0.24	**	DistD:RdgLn	-0.01	0.01		
DistShr	-0.63	0.01							
					Pine Siskin				
Finch spp.					(Intercept)	2.42	0.00	0.53	***
(Intercept)	2.36	0.02	0.32	*	DistD	-0.01	0.08		
DistShr	-0.12	0.39			DistShr	-0.10	0.20		
RdgLn	2.52	0.05			RdgLn	1.75	0.02		
DistShr:RdgLn	-0.36	0.10			DistShr:RdgLn	-0.27	0.03		
American Goldfinch					Rusty Blackbird				
(Intercept)	-0.41	0.45	0.38	*	(Intercept)	7.78	0.00	0.30	*
DistD	0.01	0.01			DistD	-0.04	0.02		
DistShr	0.12	0.07			DistShr	-0.82	0.02		
RdgLn	0.99	0.04			DistD:DistShr	0.00	0.11		
DistD:DistShr	0.00	0.01							
DistD:RdgLn	-0.01	0.00			Yellow-rumped Warbler				
					(Intercept)	2.59	0.01	0.43	**
American Robin					DistD	-0.01	0.01		
(Intercept)	28.81	0.00	0.40	**	DistShr	0.03	0.80		
DistD	-0.14	0.00			RdgLn	2.27	0.03		
DistShr	-2.82	0.01			DistShr:RdgLn	-0.36	0.03		
DistD:DistShr	0.02	0.05							

Figure 1. Overall movements of boreal landbirds during autumn migration in relationship to the Great Lakes and Lake Superior.

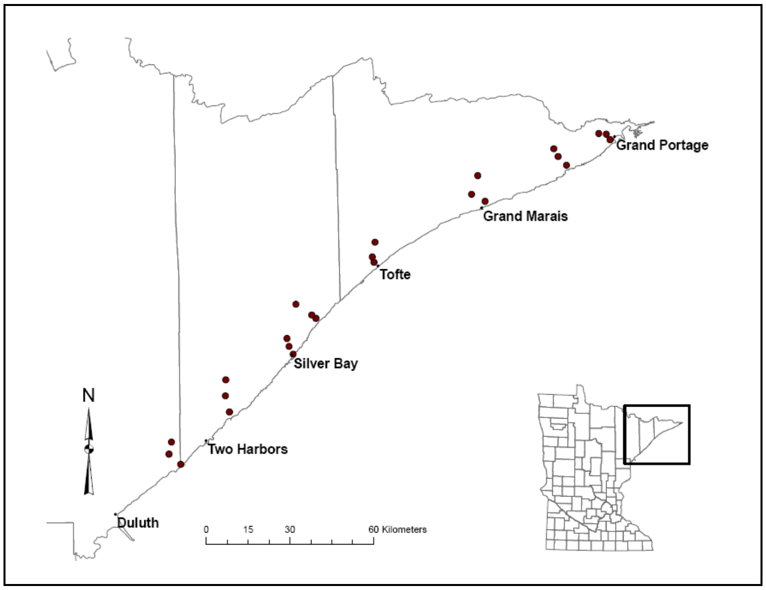

Figure 2. Locations of migration observation sites along the northern shore of Lake Superior, Minnesota, USA. Hawk Ridge (HR) is located in Duluth (printed with permission from Seeland et al. 2012).

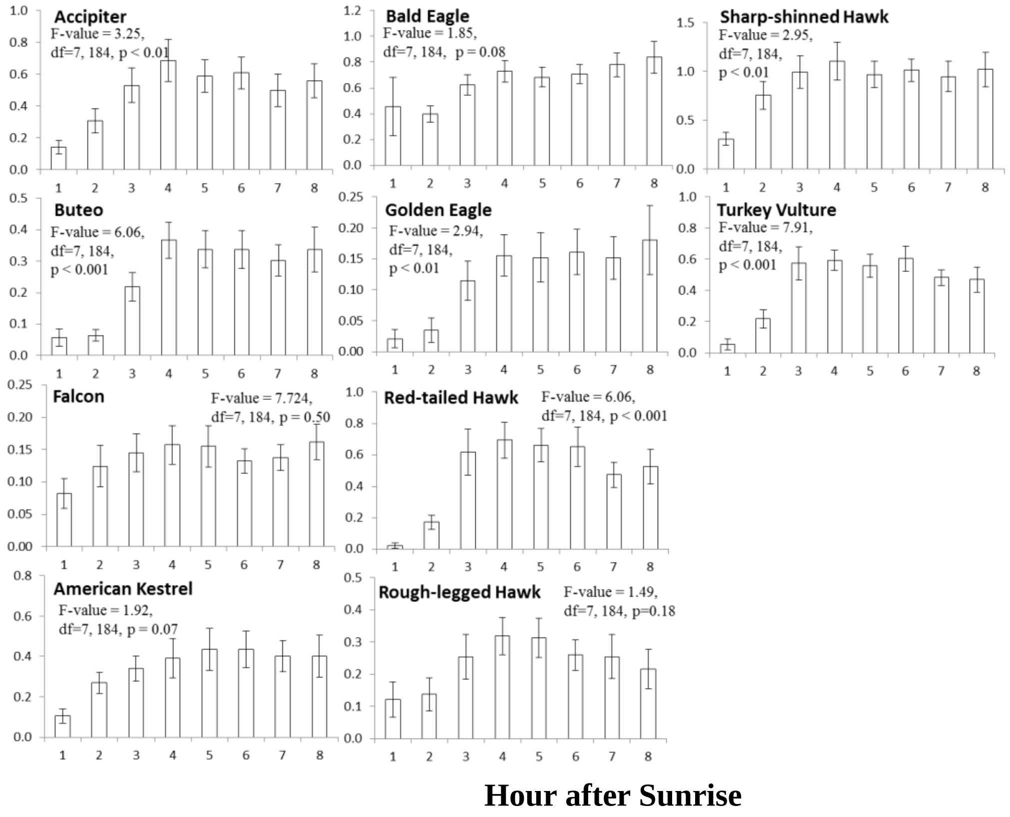

Figure 3. ANOVA analyses and mean (SE) of birds per kilometer^2 (y-axis) for raptor species and groups at consecutive hours after sunrise, during autumn migration along the north shore of Lake Superior, 2008-2010.

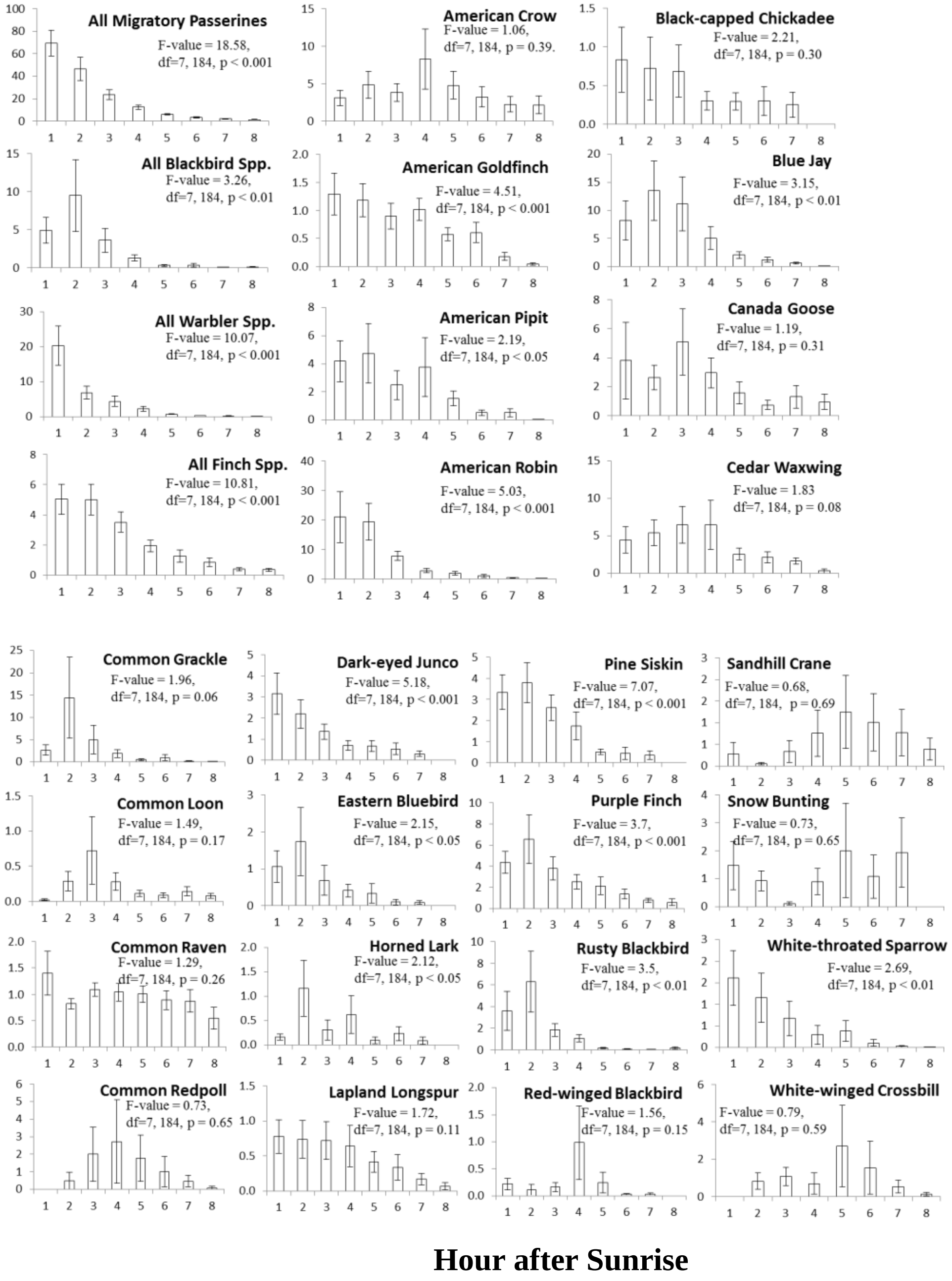

Figure 4. ANOVA analyses and mean (SE) observed birds per kilometer^2 (y-axis) for non-raptor species and groups at consecutive hours after sunrise, during autumn migration along the north shore of Lake Superior, 2009-2010. The non-raptors that did not show significant differences (α = 0.05) in time after sunrise included American Crow,

Black-capped Chickadee (*Poecile atricapillus*), Canada Goose, Cedar Waxwing, Common Grackle, Common Loon (*Gavia immer*), Common Raven (*Corvus corax*), Common Redpoll (*Carduelis flammea*), Lapland Longspur (*Calcarius lapponicus*), Red-winged Blackbird, Sandhill Crane, Snow Bunting, and White-winged Crossbill.

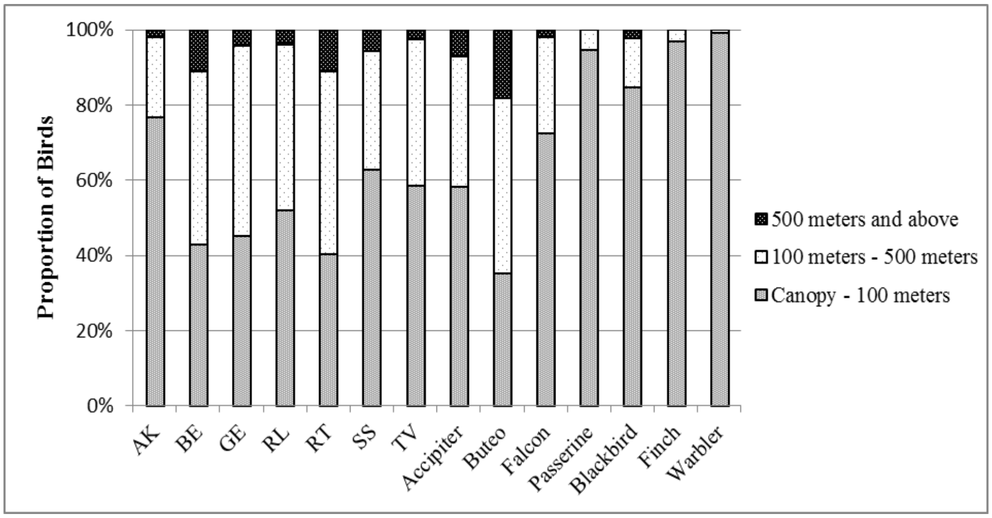

Figure 5. Proportions of the raptor species and groups, and non-raptor groups in each flight height category recorded during autumn migration surveys (raptors: 2008-2010; non-raptors 2009-2010) not separated for different wind speeds. AK = American Kestrels, BE = Bald Eagles, GE = Golden Eagles, RL = Rough-legged Hawks, RT = Red-tailed Hawks, SS = Sharp-shinned Hawks, TV = Turkey Vultures.

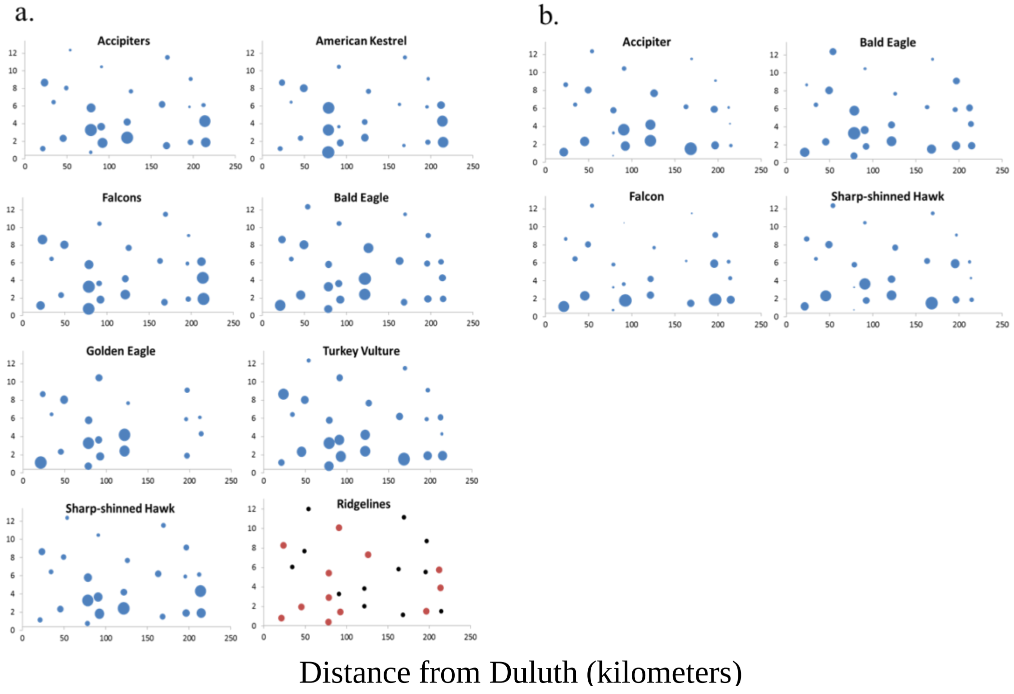

Figure 6. Bubble plots illustrating the distribution of raptors (mean by site) for best models during days with (a.) no wind or north and west winds and (b.) south and east winds, by distance from Duluth and distance from shore (y-axis). Sites with major ridgelines parallel to the Lake Superior shore shown in red.

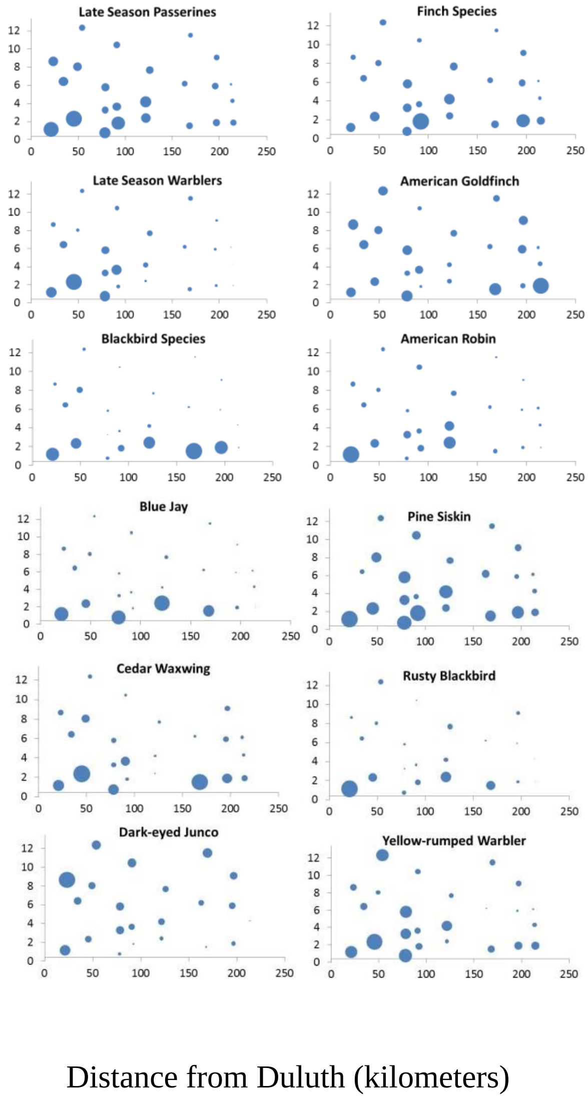

Figure 7. Relative mean bird abundance (indicated by bubble size) across study sites for best fit models distributed by the variables distance from Duluth and distance from shore (y-axis). Bubble sizes represent relative abundance within individual graphs only. See figure 6 for location of ridgelines.

(This manuscript is formatted for submission to the journal BioScience.)

Chapter 3.

Airspace as Habitat

“Habitat” is a fundamental unifying concept in ecology and evolutionary biology (Block and Brennen 1993, Hall et al. 1997). Scientists in these fields often seek to understand how species’ survival and reproductive strategies are shaped in relationship to the habitats on which they depend. The habitat concept is also foundational to conservation and policy strategies that address human impacts on species’ survival. Currently, the role of environmental factors in shaping species’ life history strategies is viewed almost entirely in terms of terrestrial and aquatic habitat. For many of the 1000 bat, 9000 bird, and 900,000 insect species on Earth, the focus on land and water environments considers only part of the full suite of habitat requirements. Technological and methodological innovations are enabling scientists to better observe how these animals use *airspace* to perform many critical life tasks. These advances coincide with a growing urgency to understand animal use of the aerial environment as human use and development of this same airspace is rapidly increasing (Kunz et al. 2008). Here I show that the intersection of scientific innovation and human modification of the aerial environment necessitate broadening the habitat concept to include airspace.

In Western culture, animal-habitat observations first appear in the writings of Aristotle (384-322 BCE). Centuries later, Charles Darwin’s (1809-1882) observations and theory of natural selection became the impetus for naturalists such as Joseph Grinnell (1877-1939) to investigate the evolutionary underpinnings of animal distributions and for ecologists such as Aldo Leopold (1887-1948) to associate animal presence with particular environments. Such seminal contributions to the ecology of animal-environment relationships built the foundation for the current, general description of habitat: a geographic space with characteristics that facilitate occupancy and survival of a species (Block and Brennen 1993, Hall et al. 1997).

In recent decades, human understanding of animal-habitat relationships has broadened dramatically as technology illuminates patterns of habitat use beyond what is readily observed. For instance, radio and satellite telemetry provide information on use of habitat in areas nearly impossible for humans to access and by species whose size or behavior prevents direct observation (Robinson et al. 2010). As advanced technological tools continue to provide information about the spatial relationships between flying animals and their terrestrial or aquatic habitats, information is also gained about movement patterns in the airspace near, and during travel between, these same habitats. Increasingly, methodologies are being developed to apply advanced technology specifically to the study of the aerial environment. As a result, emerging disciplines such as movement ecology and aeroecology (Kunz et al. 2008, Nathan 2008) are showing animal use of airspace to be more complex and nuanced than once thought. Aerial patterns are shaped by physiological constraints and adaptive behaviors in combination with physiographical features and weather events (Gauthreaux and Belser 2003, Wikelski et al. 2006, Kunz et al. 2008, Katzner et al. 2012). Moreover, technologies enable the characterization of airspace use by four dimensions: latitude, longitude, altitude, and time.

For example, thermal cameras and radar show that species of “high flying” migratory bats forage at surprisingly low altitudes above the ocean surface to prey upon crustaceans, but tall structures on the ocean (e.g., wind turbines) cause bats to dramatically ascend from this foraging altitude (Ahlén et al. 2009). Miniature transmitters on dragonflies reveal that these insects time their migrational movements in relation to weather patterns, aggregate in airspace along topographic features, and display distinct periods of flight and rest (Wikelski et al. 2006). Weather radar stations record broadly distributed and high-altitude mass movements of nocturnally migrating birds (Gauthreaux and Belser 2003), yet more focused use of radar reveals these same migrants concentrate at unexpectedly low altitudes adjacent to features such as coastlines (Gagnon et al. 2011). With photosensitive geolocator technology, scientists are discovering extraordinary avian migration routes and lengths, rethinking migration strategies, and for the first time producing maps of complete life-cycle geographic “connectivity” of small-bodied birds (McKinnen et al. 2013).

Understanding animal use of airspace has important implications for identifying and mediating conflicts that arise as humans alter (e.g., with pollution, lights), move through (e.g., with aircraft, automobiles), and develop (e.g., with fences, transmission lines, communication towers, wind turbines, buildings, oil rigs) this same airspace. The potential effects on flying animals from this global increase in modifications to the aerial environment are being recognized and addressed by scientists and decision makers (Katzner et al. 2012, USFWS 2012, Longcore et al. 2013). For example, studies indicate that constructing highway underpasses at the precise locations where bat commuting routes intersect major highways may help preserve bat movement patterns amid the threat of vehicle collision (Berthinussen and Altringham 2012). Scientists show that simply removing the steady-burning lights that attract nocturnally migrating birds to communication towers could reduce the annual collision mortality of 6.8 million birds at these towers in the United States and Canada (Gehring et al. 2009, Longcore et al. 2013). Despite enhanced understanding of animal-airspace interaction, current investigations are largely reactive, addressing issues posed on a site-by-site basis and lacking methodological and theoretical intersection with a larger scientific context (Loss et al. 2012, Schaub 2012). This narrow and conflict-centric approach limits the integration of important research into a broader framework of flying-animal ecology. For instance, policy guidelines addressing wind power development might suggest site-specific strategies to mitigate conflicts with birds or bats (USFWS 2012), but such voluntary guidelines may not be followed, or the results of research and mitigation efforts remain uncertain (Loss et al. 2012). In addition, although human-induced airspace modifications affect flying animal populations (Schaub 2012, Voigt et al. 2012, Longcore et al. 2013), conservation programs rarely include airspace as a measureable and potentially limiting resource.

Expanding the habitat concept to incorporate the aerial environment more accurately describes behaviors and life history strategies of flying animals, and has important implications for how humans utilize and manage airspace. Just as understanding species' terrestrial and aquatic habitat requirements has played a unifying role in science, technology, conservation, and policy, the acknowledgment of airspace as an important component for maintaining animal fitness will unify research across these disciplines. Greater scientific clarity about the dimensions of species- or population-specific aerial habitat will also facilitate accessibility of information in developing robust and comprehensive policy and management strategies that address human-animal airspace use conflicts. Furthermore, knowledge of animal airspace use under current climate conditions will provide current and future science and conservation programs a better capacity to deal with effects of climate change. As technological advances enable more detailed understanding of the dependence of flying animals on the aerial environment, and as human modification of this same environment continues to increase exponentially, it is time to broaden the habitat concept skyward: airspace is habitat.

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Appendices

Chapter 1

Appendix A. Bird species, migration group (Group), and number of species observed (Count) at below canopy sites during fall migration surveys along Lake Superior's north shore 2008-2010. (Group: LONG = Long-distance migrant, SHRT = Short-distance migrant, PERM = Permanent resident, MIG = General migrant (Long or Short), NA = Not enough information to determine migration group).

English Name	**Taxonomic Name**	**Migration Group**	**Total**
Alder Flycatcher	*Empidonax alnorum*	LONG	2
American Crow	*Corvus brachyrhynchos*	PERM	60
American Goldfinch	*Carduelis tristis*	SHRT	75
American Kestrel	*Falco sparverius*	SHRT	1
American Redstart	*Setophaga ruticilla*	LONG	395
American Robin	*Turdus migratorius*	SHRT	306
Bald Eagle	*Haliaeetus leucocephalus*	SHRT	4
Black-and-white Warbler	*Mniotilta varia*	LONG	113
Black-backed Woodpecker	*Picoides arcticus*	PERM	4
Black-capped Chickadee	*Poecile atricapillus*	PERM	1603
Belted Kingfisher	*Ceryle alcyon*	LONG	1
Blue-headed Vireo	*Vireo solitarius*	LONG	6
Blackburnian Warbler	*Dendroica fusca*	LONG	12
Blue Jay	*Cyanocitta cristata*	PERM	314
Blackpoll Warbler	*Dendroica castanea*	LONG	10
Boreal Chickadee	*Poecile hudsonica*	PERM	1
Brown Creeper	*Certhia americana*	SHRT	159
Black-throated Blue Warbler	*Dendroica caerulescens*	LONG	9
Black-throated Green Warbler	*Dendroica virens*	LONG	74
Broad-winged Hawk	*Buteo platypterus*	LONG	7
Canada Warbler	*Wilsonia canadensis*	LONG	32
Cedar Waxwing	*Bombycilla cedrorum*	SHRT	514
Chipping Sparrow	*Spizella passerina*	SHRT	12

Cape May Warbler	*Dendroica tigrina*	LONG	1
Common Grackle	*Quiscalus quiscula*	SHRT	1
Cooper's Hawk	*Accipiter cooperii*	SHRT	1
Common Merganser	*Mergus merganser*	SHRT	17
Common Raven	*Corvus corax*	PERM	15
Common Redpoll	*Carduelis flammea*	SHRT	2
Connecticut Warbler	*Oporornis agilis*	LONG	1
Common Yellowthroat	*Geothlypis trichas*	SHRT	59
Chestnut-sided Warbler	*Dendroica pensylvanica*	LONG	64
Dark-eyed Junco	*Junco hyemalis*	SHRT	90
Downy Woodpecker	*Picoides pubescens*	PERM	548
Eastern Bluebird	*Sialia sialis*	SHRT	5
Eastern Kingbird	*Tyrannus tyrannus*	LONG	1
Eastern Phoebe	*Sayornis phoebe*	SHRT	6
Eastern Wood-pewee	*Contopus virens*	LONG	17
Evening Grosbeak	*Coccothraustes vespertinis*	PERM	5
Fox Sparrow	*Passerella iliaca*	SHRT	2
Great Crested Flycatcher	*Myiarchus crinitus*	LONG	2
Golden-crowned Kinglet	*Regulus satrapa*	SHRT	321
Gray-checked Thrush	*Catharus minimus*	LONG	3
Gray Jay	*Perisoreus canadensis*	PERM	1
Gray Catbird	*Dumetella carolinensis*	LONG	1
Hairy Woodpecker	*Picoides villosus*	PERM	91
Hermit Thrush	*Catharus guttatus*	SHRT	39
House Wren	*Troglodytes aedon*	SHRT	2
Indigo Bunting	*Passerina cyanea*	LONG	1
Lapland Longspur	*Calcarius lapponicus*	SHRT	1
Least Flycatcher	*Empidonax minimus*	LONG	98
Lincoln's Sparrow	*Melospiza lincolnii*	SHRT	2
Magnolia Warbler	*Dendroica magnolia*	LONG	37
Merlin	*Falco columbarius*	SHRT	12
Mourning Warbler	*Oporornis philadelphi*	LONG	67
Nashville Warbler	*Vermivora ruficapilla*	LONG	146
Northern Flicker	*Colaptes auratus*	SHRT	100
Northern Goshawk	*Accipiter gentilis*	SHRT	1
Baltimore Oriole	*Icteris galbula*	LONG	1
Northern Parula	*Parula americana*	LONG	12
Northern Waterthrush	*Seiurus noveboracensis*	LONG	8
Olive-sided Flycatcher	*Contopus cooperi*	LONG	7
Ovenbird	*Seiurus aurocapilla*	LONG	138

Peregrine Falcon	*Falco peregrines*	LONG	1
Pine Siskin	*Carduelis pinus*	PERM	15
Pileated Woodpecker	*Dryocopus pileatus*	PERM	30
Purple Finch	*Carpodacus purpureus*	PERM	121
Rose-breasted Grosbeak	*Pheuctuicus ludovicia*	LONG	46
Red-breasted Nuthatch	*Sitta canadensis*	PERM	1891
Ruby-crowned Kinglet	*Regulus calendula*	SHRT	97
Red Crossbill	*Loxia curvirostra*	PERM	18
Red-eyed Vireo	*Vireo olivaceus*	LONG	255
Ruby-throated Hummingbird	*Archilochus colubris*	LONG	34
Ruffed Grouse	*Bonasa umbellus*	PERM	61
Savannah Sparrow	*Passerculus sandwichensis*	SHRT	1
Scarlet Tanager	*Piranga olivacea*	LONG	2
Song Sparrow	*Melospiza melodia*	SHRT	21
Spotted Sandpiper	*Actitis macularia*	LONG	1
Sharp-shinned Hawk	*Accipiter striatus*	SHRT	13
Swamp Sparrow	*Melospiza georgiana*	SHRT	6
Swainson's Thrush	*Catharus ustulatus*	LONG	124
Tennessee Warbler	*Vermivora peregrina*	LONG	50
Veery	*Catharus fuscescens*	LONG	14
White-breasted Nuthatch	*Sitta carolinensis*	PERM	13
White-crowned Sparrow	*Zonotrichia leucophrys*	SHRT	4
Wilson's Warbler	*Wilsonia pusilla*	LONG	8
Winter Wren	*Troglodytes troglodytes*	SHRT	87
Palm Warbler	*Dendroica palmarum*	LONG	8
White-throated Sparrow	*Zonotrichia albicollis*	SHRT	2235
White-winged Crossbill	*Loxia leucoptera*	PERM	3
Yellow-bellied Flycatcher	*Emipdonax flaviventris*	LONG	12
Yellow-bellied Sapsucker	*Sphyrapicus varius*	SHRT	40
Yellow-rumped Warbler	*Dendroica coronata*	LONG	358
Yellow-throated Vireo	*Vireo flavifrons*	LONG	1
Yellow Warbler	*Dendroica petechia*	LONG	3
Unidentified Blackbird		NA	2
Unidentified Finch		NA	84
Unidentified Flycatcher		NA	92
Unidentified Goose		NA	1
Unidentified Kinglet		NA	130
Unidentified Non-passerine		NA	15

Unidentified Passerine		NA	4694
Unidentified Raptor		NA	4
Unidentified Shorebird		NA	1
Unidentified Sparrow		NA	153
Unidentified Thrush		NA	98
Unidentified Vireo		NA	6
Unidentified Warbler		NA	4793
Unidentified Woodpecker		NA	119
Unidentified Wren		NA	1
TOTAL			**21406**

Chapter 2.

Appendix A. Bird species, migration guild (Guild) and number of species observed (Count) during autumn migration surveys along Lake Superior’s north shore 2008-2010. (Guild: LONG = Long distance migrant, SHRT = Short distance migrant, PERM = Permanent resident, MIG = General migrant (Long or Short), NA = Not enough information to determine migration guild).

English Name	**Taxonomic Name**	**Migration Guild**	**Abundance**
American Blackduck	*Anas rubripes*	SHRT	1
American Crow	*Corvus brachyrhynchos*	PERM	10300
American Goldfinch	*Carduelis tristis*	SHRT	1314
American Kestrel	*Falco sparverius*	SHRT	607
American Pipit	*Anthus rubescens*	SHRT	3011
American Redstart	*Setophaga ruticilla*	LONG	37
American Robin	*Turdus migratorius*	SHRT	16373
American Tree Sparrow	*Spizella arborea*	SHRT	3
American White Pelican	*Pelecanus erythrorhynchos*	SHRT	3
American Wigeon	*Anas americana*	SHRT	1
American Woodcock	*Scolopax minor*	SHRT	1
Bald Eagle	*Haliaeetus leucocephalus*	SHRT	2741
Baltimore Oriole	*Icteris galbula*	LONG	1
Belted Kingfisher	*Ceryle alcyon*	LONG	15
Black-backed Woodpecker	*Picoides arcticus*	PERM	46
Black-capped Chickadee	*Poecile atricapillus*	PERM	345
Black-throated Green Warbler	*Dendroica virens*	LONG	1
Blue Jay	*Cyanocitta cristata*	PERM	12809
Bobolink	*Dolichonyx oryzivorus*	LONG	8
Bohemian Waxwing	*Bombycilla garrulus*	SHRT	54
Boreal Chickadee	*Poecile hudsonica*	PERM	1

Broad-winged Hawk	*Buteo platypterus*	LONG	1356
Brown Creeper	*Certhia americana*	SHRT	16
Cackling Goose	*Branta canadensis minima*	SHRT	4
Canada Goose	*Branta canadensis*	SHRT	3124
Cape May Warbler	*Dendroica tigrina*	LONG	4
Cedar Waxwing	*Bombycilla cedrorum*	SHRT	6238
Chimney Swift	*Chaetura pelagica*	LONG	11
Chipping Sparrow	*Spizella passerina*	SHRT	10
Cliff Swallow	*Petrochelidon pyrrhonota*	LONG	4
Common Grackle	*Quiscalus quiscula*	SHRT	5511
Common Loon	*Gavia immer*	SHRT	266
Common Merganser	*Mergus merganser*	SHRT	2
Common Nighthawk	*Chordeiles minor*	LONG	7
Common Raven	*Corvus corax*	PERM	2423
Common Redpoll	*Carduelis flammea*	SHRT	1865
Cooper's Hawk	*Accipiter cooperii*	SHRT	41
Dark-eyed Junco	*Junco hyemalis*	SHRT	1383
Dickcissel	*Spiza americana*	LONG	1
Double-crested Cormorant	*Phalacrocorax auritus*	SHRT	16
Downy Woodpecker	*Picoides pubescens*	PERM	57
Eastern Bluebird	*Sialia sialis*	SHRT	524
Eastern Kingbird	*Tyrannus tyrannus*	LONG	10
European Starling	*Sturnus vulgaris*	PERM	19
Evening Grosbeak	*Coccothraustes vespertinis*	PERM	65
Fox Sparrow	*Passerella iliaca*	SHRT	3
Golden Eagle	*Aquila chrysaetos*	SHRT	120
Golden-crowned Kinglet	*Regulus satrapa*	SHRT	176
Gray Jay	*Perisoreus canadensis*	PERM	4
Great Blue Heron	*Ardea herodias*	SHRT	15
Hairy Woodpecker	*Picoides villosus*	PERM	32
Hermit Thrush	*Catharus guttatus*	SHRT	2
Herring Gull	*Larus argentatus*	SHRT	1
Horned Lark	*Eremophila alpestris*	SHRT	438
Lapland Longspur	*Calcarius lapponicus*	SHRT	574
Least Sandpiper	*Calidris minutilla*	SHRT	1
Magnolia Warbler	*Dendroica magnolia*	LONG	1

Mallard	*Anas platyrhynchos*	SHRT	45
Merlin	*Falco columbarius*	SHRT	139
Mourning Dove	*Zenaida macroura*	SHRT	3
Myrtle Warbler	*Dendroica coronata*	LONG	2352
Northern Flicker	*Colaptes auratus*	SHRT	194
Northern Goshawk	*Accipiter gentilis*	SHRT	50
Northern Harrier	*Circus cyaneus*	SHRT	144
Northern Shrike	*Lanius excubitor*	SHRT	6
Northern Waterthrush	*Seiurus noveboracensis*	LONG	2
Osprey	*Pandion haliaetus*	LONG	101
Palm Warbler	*Dendroica palmarum*	LONG	11
Peregrine Falcon	*Falco peregrines*	LONG	65
Pileated Woodpecker	*Dryocopus pileatus*	PERM	17
Pine Grosbeak	*Pinicola enucleator*	SHRT	88
Pine Siskin	*Carduelis pinus*	PERM	3231
Purple Finch	*Carpodacus purpureus*	PERM	5986
Red Crossbill	*Loxia curvirostra*	PERM	152
Red-bellied Woodpecker	*Melanerpes carolinus*	SHRT	1
Red-breasted Nuthatch	*Sitta canadensis*	PERM	187
Red-eyed Vireo	*Vireo olivaceus*	LONG	11
Red-shouldered Hawk	*Buteo lineatus*	SHRT	1
Red-tailed Hawk	*Buteo jamaicensis*	SHRT	1101
Red-winged Blackbird	*Agelaius phoeniceus*	SHRT	323
Ring-billed Gull	*Larus delawarensis*	SHRT	1
Rock Dove	*Columba livia*	PERM	12
Rose-breasted Grosbeak	*Pheuctuicus ludovicia*	LONG	170
Rough-legged Hawk	*Buteo lagopus*	SHRT	284
Ruby-crowned Kinglet	*Regulus calendula*	SHRT	47
Ruby-throated Hummingbird	*Archilochus colubris*	LONG	14
Rusty Blackbird	*Euphagus carolinus*	SHRT	2365
Sandhill Crane	*Grus canadensis*	SHRT	627
Semipalmated Plover	*Charadrius semipalmatus*	LONG	1
Sharp-shinned Hawk	*Accipiter striatus*	SHRT	3228
Short-eared Owl	*Asio flammeus*	SHRT	1
Snow Bunting	*Plectrophenax nivalis*	SHRT	885
Snow Goose	*Chen caerulescens*	LONG	26

Solitary Sandpiper	*Tringa solitaria*	LONG	2
Song Sparrow	*Melospiza melodia*	SHRT	2
Spotted Sandpiper	*Actitis macularia*	LONG	1
Swainson's Thrush	*Catharus ustulatus*	LONG	170
Townsand's Solitare	*Myadestes townsendi*	SHRT	2
Tree Swallow	*Tachycineta bicolor*	LONG	11
Tundra Swan	*Cygnus columbianus*	SHRT	2
Turkey Vulture	*Cathartes aura*	SHRT	1258
Upland sandpiper	*Bartramia longicauda*	LONG	12
White-breasted Nuthatch	*Sitta carolinensis*	PERM	2
White-crowned Sparrow	*Zonotrichia leucophrys*	SHRT	2
White-throated Sparrow	*Zonotrichia albicollis*	SHRT	431
White-winged Crossbill	*Loxia leucoptera*	PERM	1177
Wilson's Snipe	*Gallinago delicata*	SHRT	4
Yellow Warbler	*Dendroica petechia*	LONG	65
Yellow-bellied Sapsucker	*Sphyrapicus varius*	SHRT	2
Unidentified Accipiter			365
Unidentified Buteo			577
Unidentified Blackbird			6567
Unidentified Corvid			35
Unidentified Duck			475
Unidentified Eagle			103
Unidentified Falcom			211
Unidentified Finch			1105
Unidentified Flycatcher			3
Unidentified Goose			575
Unidentified Gull			211
Unidentified Kinglet			724
Unidentified Loon			1
Unidentified Non-Passerine			470
Unidentified Passerine			36064
Unidentified Raptor			1209
Unidentified Shorebird			47
Unidentified Sparrow			108
Unidentified Swallow			32
Unidentified Thrush			32

Unidentified Vulture			1
Unidentified Vireo			1
Unidentified Warbler			19272
Unidentified Waxwing			30
Unidentified Woodpecker			24