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TRACKING MIGRATORY BIRD MOVEMENTS IN THE GULF OF MAINE WITH AUTOMATED RADIO TELEMETRY AND STABLE HYDROGEN ISOTOPE MARKERS

A Dissertation Presented

by

JENNIFER R. SMETZER

Submitted to the Graduate School of the University of Massachusetts Amherst in partial fulfillment of the requirements for the degree of

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Wildlife, Fish and Conservation Biology
TRACKING MIGRATORY BIRD MOVEMENTS IN THE GULF OF MAINE WITH
AUTOMATED RADIO TELEMETRY AND STABLE HYDROGEN ISOTOPE
MARKERS

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DEDICATION

To Orijah...though you were only here for the last leg of this journey, you sure made life so unbelievably fun and helped me keep everything in perspective. May we continue to find joy and laughter outside together, and have many, many more spontaneous dance parties.
ACKNOWLEDGEMENTS

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Thank you to my dear and loving family. Carrie: you too should be granted a PhD for your constant support, devotion, and good spirits. You are my biggest cheerleader, and always make me feel like my work is important. Thanks to my parents Alan and Judy, and my brother Dan for always believing in me, for inspiring my love of the natural world with many beloved canoe trips and hikes, for urging me to go to college, and supporting me through all the good and bad times. Your generosity and unwavering love is unbelievable. Thanks to Cree, Oly, Turtle and baby for the noisy, often muddy
backdrop of pitter pattering paws and feet, giggles and barks, chaotic rumblings, stolen food, and snuggles. You are my joy.

This work was financially supported by the US Fish and Wildlife Service, the USDA Forest Service, and the NSF-sponsored IGERT: Offshore Wind Energy Engineering, Environmental Science, and Policy (Grant Number 1068864).
Coastal and offshore areas of the eastern United States provide valuable resources for both migratory songbirds and breeding seabirds, but face some of the most drastic rates of habitat alteration and urbanization. Coastal development can result in loss of significant habitats, and in proliferation of collision hazards that can pose a grave threat to birds. Conserving birds that use these coastal and offshore areas requires better information on how coastal stopover habitats are used, what breeding populations visit these regions during migration, how birds move through these landscapes, and how development can be most sensibly and responsibly directed to minimize adverse effects. In the first chapter, I used hydrogen stable isotope analysis of feather samples to identify the likely breeding origin and describe the geographic timing of migration for Blackpoll Warblers (*Setophaga striata*) and Red-eyed Vireos (*Vireo olivaceus*) at a coastal stopover site in the Gulf of Maine, USA. In the second chapter, I made use of a regional-scale...
automated radio telemetry array to study stopover and migratory flights and migratory routes of these species at the same coastal stopover site in the Gulf of Maine. In the third chapter, I used the same automated radio telemetry array and bird sample to test the hypothesis that blackpolls and vireos – which differ markedly in migratory strategy, route, and diet during fall migration – would differ in the degree to which they exhibited prolonged stopover in the Gulf of Maine. In chapter four I turned my attention to seabirds breeding the Gulf of Maine. I used automated VHF radio telemetry to study colony attendance patterns of Common (*Sterna hirundo*) and Arctic Terns (*Sterna paradisaea*) in the Gulf of Maine where both species are facing regional declines in productivity, and compared foraging metrics between incubation and chick rearing. Finally, Appendix A details a publication co-authored with another PhD student, in which we used the foraging metrics derived in chapter 4 to build a Markov movement model that can predict space use of Common and Arctic Terns, and estimate collision mortality under a range of spatially explicit alternative OWED development scenarios.
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CHAPTER 1

INTRINSIC MARKERS REVEAL BREEDING ORIGIN AND GEOGRAPHICALLY-STRUCTURED MIGRATION TIMING OF TWO SONGBIRDS AT A COASTAL STOPOVER SITE

1.1 Introduction

Throughout their annual cycle, migrant songbirds move great distances, and occupy many distinct habitats and environmental conditions, complicating their conservation. Determining the geographic linkage between breeding areas, stopover sites, and wintering grounds for specific populations can aide in the conservation and management of migratory birds, and is an important research priority (Webster et al. 2002, Faaborg et al. 2010b, Hobson et al. 2014). Data on migratory connectivity can help elucidate threats across multiple geographic scales, and thus can aid in identifying where populations are most limited (Myers et al. 1987, Moore et al. 1995, Sherry and Holmes 1995). Migratory connectivity also has important implications for the ability of breeding populations to respond to loss of non-breeding season habitats or other environmental change through phenotypic plasticity or genetic adaptations (Webster and Marra 2005). Though connectivity between breeding and wintering areas has been widely investigated (Chamberlain et al. 1997, Hobson and Wassenaar 1997, Kelly et al. 2005, Boulet et al. 2006), less is known about connectivity between breeding and stopover locations (Laughlin et al. 2013).
Understanding which breeding populations use regional stopover sites can be valuable for the monitoring, conservation, and management of migratory songbirds. For one, identifying links between breeding populations and specific stopover regions can greatly improve migration monitoring efforts by identifying sites that can effectively sample remote breeding populations that are not well represented in breeding-season surveys (Hobson et al. 2015). Information on the breeding origin of migrants is also critical for linking population trends from migration monitoring to specific breeding populations (Wassenaar and Hobson 2001, Webster et al. 2002, Webster and Marra 2005, Dunn et al. 2006) and for subsequently geographically targeting population-level conservation efforts for declining populations (Sherry and Holmes 1995, Norris and Marra 2007, Hobson et al. 2014). Determining links between breeding, wintering and stopover areas for specific breeding populations can also help determine where mortality during the non-breeding period will most heavily affect breeding-season recruitment (i.e. geographically), and which breeding populations may be threatened by anthropogenic factors at different locations along the migratory route (Runge and Marra 2005, Paxton et al. 2007). For instance, data on the geographic composition of migrants in regions of the Atlantic coastline facing significant urbanization or energy development can provide insight into which breeding populations may be adversely affected by stopover habitat loss or collision mortality.

Stable hydrogen isotope analysis has emerged as an important tool for investigating migratory connectivity and documenting the catchment areas of stopover
sites (Hobson et al. 2014). The ratio of stable hydrogen isotope (deuterium; δ2 H) in rainfall varies predictably across the North American continent in a latitudinal and altitudinal gradient because heavy isotopes are distilled from air masses as they move to cooler higher latitudes, or over orographic barriers (Bowen et al. 2005). Stable hydrogen isotopes in precipitation are transferred up trophic levels into metabolically inert feathers that retain a constant isotope signature and therefore reflect the geographic origin of feather growth (Mazerolle and Hobson 2005). The δ2 H signature of feathers can thus be used to characterize the summer provenance of migratory songbirds. Stable hydrogen isotopes have been successfully used to identify the natal and breeding origin of many migratory bird species (Wassenaar and Hobson 2001, Wilgenburg and Hobson 2011).

The δ2 H signature of feathers has also been used to study geographic patterns in migration phenology, offering valuable insights into avian migration and ecology (Kelly et al. 2002, Clegg et al. 2003, Dunn et al. 2006, Kelly 2006).

One of the major limitations with using δ2 H to elucidate spatial and temporal patterns of migration is that individuals from the far western portions of North America have similar δ2 H signatures to those originating in the southern boreal forests of Canada. This reduces the assignment resolution for species with broad geographic breeding ranges, and limits the utility of using δ2 H signatures to investigate whether the timing of migration is geographically structured within a species. However, some morphological traits in songbirds, such as wing length or body size can also show predictable geographical variation (Conklin et al. 2011, Rushing et al. 2014). Thus, morphometric
measures can also provide information about the temporal and spatial geographical structuring of migrants at stopover sites.

We used stable hydrogen isotope markers to identify geographic provenance of Blackpoll Warblers (Setophaga striata: hereafter blackpolls) and Red-eyed Vireos (Vireo olivaceus: hereafter vireos) passing through a coastal stopover area in the Gulf of Maine on fall migration. The Gulf of Maine hosts migrant songbirds from both the eastern Canadian provinces as well as boreal breeders as far west as Alaska (Leppold and Mulvihill 2011, Leppold 2016) making this an apt region for identifying catchment populations. Our second goal was to test whether there was geographic structure to the timing of migration for blackpolls and vireos using δ2 H signatures and wing length data as indices of distance travelled to the capture site. We expected blackpoll wing length could serve as proxy for migration distance because geographic size variation has been documented for this species (Pyle 1997, DeLuca et al. 2013, Morris et al. 2015). We used continental-scale wing length data measured on breeding blackpolls and vireos as part of the Monitoring Avian Productivity and Survivorship (MAPS) program (DeSante and Kaschube 2009) to validate that wing length varies predictably across latitude and longitude for blackpolls, and to assess whether it varied predictably enough across latitude and/or longitude for vireos to serve as a proxy for migration distance.

1.2 Methods

1.2.1 Data collection
Vireos and blackpoll warblers were captured in the fall of 2013 and 2014 at the 888 ha Petit Manan Point section of the Maine Coastal Islands National Wildlife Refuge (Fig. 1) in Steuben Maine, United States (44.40846° N, -67.90502° W). We captured birds between September 6 and October 13 using passive mist-nets located in mixed forest and shrubland habitats. We outfitted all vireos and blackpolls captured with a USGS aluminum band, and recorded age, un-flattened wing chord and tarsus length (0.1mm), subcutaneous fat score (0-5), mass (0.1g), and the time of capture. We only sampled feathers from hatch year vireos, as they constitute ~98% of the demographic in coastal areas, but sampled from both hatch year and after hatch year blackpolls. Both focal species both undergo a first prebasic molt on the breeding grounds that includes the body feathers (Pyle 1997), so feathers accurately reflect the natal/breeding origin. We sampled the third retrix (R3) on the right for vireos, as this is less prone to loss and subsequent regrowth than outer rectrices. Following Leppold (2016), we sampled upper back feathers between the scapulars from blackpoll warblers, to avoid interference with flight capability.

1.2.2 Stable isotope analysis

Feathers were prepared and analyzed for δ²H at the Cornell University Stable Isotope Laboratory (COIL), Ithaca New York. Feathers were held at the lab for a week before preparation, washed in 2:1 chloroform: methanol solution overnight, and dried for several days in a fume hood. Subsamples were cut from the distal vane, and weighed (0.35± 0.02mg) into silver capsules without grinding. The samples were analyzed for stable hydrogen isotope content on a Thermo Delta V isotope ratio mass spectrometer.
(IRMS) interfaced to a Temperature Conversion Elemental Analyzer (TC/EA). The samples were analyzed under the comparative equilibrium method of Wassenaar and Hobson (2003) with three calibrated keratin $\delta^2$H references run every 10 samples: CBS, KHS and an internal COIL keratin standard. Isotope corrections were performed using the two established CBS and KHS standards of Wassenaar and Hobson (2003). Across all the sample runs the standard deviation for the internal keratin, CBC and KHS standard was 2.6‰, 2.1‰ and 2.4‰ respectively in 2013 and 3.3‰, 2.7‰ and 2.6‰ respectively in 2014. We reported all results for nonexchangeable $\delta^2$H in delta notation of units per mil (‰), normalized to the Vienna Standard Mean Ocean Water (VSMOW) standard scale, where $\delta = (R_{\text{sample}} - R_{\text{standard}})/R_{\text{standard}}$, and $R$ is the abundance ratio of the heavy and light hydrogen isotopes (Bowen 2010).

1.2.3 Assignment of molt origins

We estimated geographic origins based on spatially-explicit likelihood-based assignment methods (e.g. Hobson et al. 2012, 2014). Bowen et al. (2005) developed a GIS model of expected $\delta^2$H in precipitation ($\delta^2 H_p$) over the growing season. We converted this GIS model to a digital map of expected $\delta^2$H feather values ($\delta^2 H_f$) using the rescaling equation presented in Hobson et al. (2012) for non-ground foraging Neotropical migrants:

$$\delta^2 H_f = -17.75 + 0.95 \times \delta^2 H_p$$  \hspace{1cm} \text{Eq. 1}
Hobson et al. (2012) derived Eq.1 by relating δ²Hᵣ to δ²Hᵣ for a ‘calibration’ set of birds with known breeding origins. We used digital range maps from Bird Life International (Ridgely et al. 2011) to restrict the resulting feather isoscape to each species’ respective breeding range, and thus limit the geographic range of assignments. We applied a likelihood-based density model to construct assignment models for each species (e.g. Hobson et al. 2012, 2014). Previous studies have incorporated abundance data from the Breeding Bird Atlas Surveys (BBS) as Bayesian priors under this approach to improve estimates; however, we did not use this method as it is not recommended for species that breed north of the region covered by BBS routes (Hobson et al. 2014). We calculated the probability that each cell in the feather isoscape represented the origin for each bird using a normal probability density function:

\[ f(y' | \mu_c, \sigma_c) = \frac{1}{\sqrt{2\pi\sigma_c}} e^{-\frac{1}{2\sigma_c^2} (y' - \mu_c)^2} \quad \text{Eq. 2} \]

…where \( y' \) is the unknown origin of an individual bird, \( \mu_c \) is the expected δ²Hᵣ value of a given cell \( c \), and \( \sigma_c \) is the expected standard deviation of δ²H for birds growing their feathers at the same location. We used the \( \sigma_c \) value of 14.4 ‰ reported in Hobson et al (2012) for non-ground foraging Neotropical migrants in North America; the value was derived from the residuals of their best model relating δ²Hᵣ to δ²Hᵣ for birds with known origins.

We used Eq. 2 to generate a spatially-explicit map for each individual bird that represented the probability of origin in each cell of the feather isoscape based on
expected and observed $\delta^2$ Hf values. For each individual bird, we standardized each cell value in the isoscape by the total probability summed over all cells; we subsequently assigned each cell a value of 1 if the probability value in the cell was $\geq$ the 67% quantile of probability of origin values for that individual and a 0 if it was not (Hobson et al. 2014). This effectively assigned a cell as a possible origin based on a 2:1 odds ratio of being correct, and allowed multiple possible origins per individual (Hobson et al. 2014). The 2:1 odds ratio was chosen because previous studies demonstrated that this level of certainty resulted in classification rates that were better than that expected by chance alone (Chabot et al. 2012, Hobson et al. 2012). We summed the cell values for all individuals by species to generate a probability surface representing likely origins of individuals within our sample (Hobson et al. 2009, Van Wilgenburg and Hobson 2011). We conducted this analysis in the R statistical environment (R Core Team 2016) using the maps (Becker and Wilks 2015), maptools (Bivand and Lewin-Koh 2015), raster (Hijmans and Van Etten 2012), and shapefiles (Stabler 2013) packages.

1.2.4 Migration Timing

We used un-flattened wing chord data collected across North America during the breeding season from 1989 to 2015 by the Monitoring Avian Productivity and Survivorship (MAPS) program (DeSante and Kaschube 2009) to test if wing length varied predictably across the continent for blackpolls and vireos. For each species, we removed birds with an un-flattened wing chord measurement $\geq$3 SD from the mean to account for errors, and included only birds measured in June and July. We only included data from banding stations located $> 44^\circ$ N to limit our analysis to plausible breeding
latitudes for our capture site, and excluded stations with < 5 wing measurements for a species. This resulted in a data set of 2480 vireos measured at 97 MAPS stations, and 556 blackpolls measured across 29 MAPS stations (Fig 1.2). Following (Rushing et al. 2014), we related mean un-flattened wing chord at each station latitude and longitude by species using general linear models.

We fit linear regression models relating $\delta^2$ H to capture date to test whether the timing of migration was geographically structured. We analyzed the two species separately because we expected they could exhibit different patterns. For each species, we scaled capture date and $\delta^2$ H values by their mean to account for any inter-annual differences in these values before pooling the two years of data. Although age-related differences in $\delta^2$ H enrichment have been found in previous studies (Haché et al. 2012, Holberton et al. 2015, Leppold 2016), we found no differences in $\delta^2$ H enrichment between ages for blackpolls ($t = -0.65$, $p = 0.051$), so we pooled the data for adult and hatch year birds. We used general linear models to test the hypotheses that 1) $\delta^2$ H values were related to capture date, and 2) wing length was related to capture date. We considered covariates as highly significant predictors if 95% confidence intervals for the parameter estimate excluded zero, and as moderately significant predictors if 90% confidence intervals excluded zero.

1.3 Results

We collected feathers from 23 blackpoll warblers and 58 vireos in 2013, and 70 blackpolls and 82 vireos in 2014. Both the blackpolls and vireos we sampled at the capture site covered a broad isotopic range with blackpoll $\delta^2$ H values ranging from
−73.8‰ to −177.7‰, and vireo $\delta^2 H$ values from −56.2‰ to −119.9‰ (Table 1.1). We captured migrant blackpolls with putative origins from as close as the Adirondacks, New Brunswick, and northwestern Maine, and potentially as far as Alaska. We captured vireos with putative origins from as close as Maine and Nova Scotia, and potentially as far as British Columbia and Alberta. Sixty nine percent of our blackpoll sample had $\delta^2 H$ values consistent with origins north and west of Manitoba (i.e., $\delta^2 H < -120$ ‰; Fig. 1.3), and 71% of our vireo sample had $\delta^2 H_f$ values consistent with origins well north and west of Lake Superior (i.e., $\delta^2 H < -85$ ‰). The likelihood-based assignment indicated that the vireos we captured were primarily from the central portion of their breeding range, with most individuals assigned to central Quebec, central and western Ontario, southeastern Manitoba, northwestern Minnesota, North and South Dakota, Wyoming, Washington state and southern British Columbia (Fig 1.4). However, we can likely exclude Wyoming and South Dakota as origins for our vireo sample, as these sites are south of the study area. Based on the likelihood-based model we captured blackpolls from throughout their breeding range, but largely from the northwestern portion (Fig 1.4). Most individuals were assigned to northwestern British Columbia, northern Alberta, the southern reaches of the Northwest Territories, and eastern Alaska.

Vireos measured at MAPS stations from more eastern longitudes (general linear model; $\beta = 0.01$; $P = 0.03$), and southern latitudes (general linear model; $\beta = -0.06$; $P = 0.002$) had significantly longer wings than birds from more western longitudes and southern latitudes (Fig 1.5). Despite this continental-scale variation in wing length, we did not find a significant relationship between wing length and $\delta^2 H$ values for our sample
of migratory vireos (general linear model; $\beta = 0.02; P = 0.37$). Blackpoll wing length varied significantly across the continent, but showed the opposite pattern to that of vireos. Blackpolls measured at MAPS stations from more western longitudes (general linear model; $\beta = -0.03; P<0.001$), and northern latitudes (general linear model; $\beta = 0.10; P = 0.001$) had longer wings than birds from more eastern longitudes and southern latitudes (Fig 1.5). Reflecting this, blackpolls with more negative $\delta^2$H values (i.e. from more western breeding latitudes) had significantly longer wings than birds with larger $\delta^2$H values (general linear model; $\beta = -2.2; P = 0.02$).

Blackpoll capture date and $\delta^2$H values were not significantly related (general linear model; $\beta = -0.06; p = 0.87$). However, we found a significant relationship between blackpoll wing length and capture date indicating that birds with longer wings— and thus likely from more western and northern breeding regions— passed through the capture site earlier in the season than more local breeders (general linear model; $\beta = -2.2; P = 0.02$). In contrast, we found moderate evidence of a significant relationship between capture date and $\delta^2$H for vireos (general linear model; $\beta = -0.19; p = 0.07$) indicating that vireos from more distant breeding latitudes passed through the capture site later in the season. Vireo wing length and capture date were not however significantly related (general linear model; $\beta = -0.02; p = 0.51$).

1.4 Discussion

1.4.1 Breeding and natal origins of migrants
This is the first study to the best of our knowledge to identify putative breeding-season origins for migrant Red-eyed Vireos in the Gulf of Maine. Despite the coarse precision of the likelihood assignment, our results demonstrate that the Gulf of Maine is very likely a catchment area for both eastern and western populations of this species during fall migration. Roughly 95% of the vireos we captured (N = 133) had an $\delta^2$H signature that indicated a putative origin west or north of the capture location (i.e. $> -75 \delta^2$H‰), suggesting that migration monitoring in the Gulf of Maine can sample vireos from a broad continental range, not just local breeders. Furthermore, at least 120 individuals from our sample were assigned origins in the northern reaches of Newfoundland and central Quebec where BBS routes are not well represented (Environment Canada 2012). Thus, the Gulf of Maine, and nearby coastal stations could serve as an important migration monitoring area for these more remote Red-eyed Vireo breeding populations.

Reflecting this, Manomet Bird Observatory on the east coast of Massachusetts observed a significant 40% decline in fall and spring capture rates of Red-eyed Vireos from the 1970-1985 and 1986-2001 migration monitoring periods despite increases or non-significant decreases across the local physiographic strata (Lloyd-Evans and Atwood 2004), and an overall range-wide increases of 0.75% for the species between 1966 and 2015 across BBS routes (Sauer et al. 2017). Our results suggest that it is possible that Manomet trends could reflect declines at northern breeding areas poorly represented by BBS routes; indeed, despite general overall population increases, western breeding populations of Red-eyed Vireos decreased by 2% annually from 1980-1994, with
particularly large declines of 2.4% in British Columbia and 2.6% in the central Rockies from 1966-1994 (Cimprich et al. 2000). Thus, characterizing δ² H signatures for Red-eyed Vireos at a range of coastal sites in the Northeastern US with well-established migration monitoring programs may be valuable for understanding trends for this species, particularly given the low recapture rates between breeding and migration for vireos (<0.003%; USGS unpublished data).

Although it is well known that blackpolls have a significant eastern component to their fall migratory movements, there is limited information on where different populations reach the Atlantic shoreline (Warnock 2010). Our results demonstrate that mid-coast Maine is a catchment area for blackpolls from across their breeding range, but that most migrants originated from the central/northwest portion of the breeding range, and eastern Alaska. These findings are congruent with those of Leppold (2016) who sampled blackpolls at a site ~100km southwest of our study site during 2009-2011, and indicate that the Gulf of Maine can serve as an excellent location for blackpoll migration monitoring, since much of this species’ boreal breeding range is poorly represented in BBS routes (Dunn et al. 2006). In contrast to our results, migration monitoring just north and east of our study site, at the Atlantic Bird Observatory in southern Nova Scotia found that blackpolls were predominantly from breeding grounds east of Hudson Bay and the Great Lakes (Dunn et al. 2006). Holberton et al. (2015) found that blackpolls captured west of the Gulf of Maine, in the Great Lakes region and Pennsylvania were from Canadian breeding sites further northwest than those primarily represented in our sample, and that individuals collected southwest of our study site in Boston and Manomet Bird
Observatory were primarily from Canadian breeding ranges to the southwest or our study site, but further west in Alaska. Collectively, these results suggest that there may be reasonably strong connectivity between breeding populations and stopover regions for blackpolls, however replicated sampling at more geographic areas would be necessary to test this fully.

Our results also indicate that habitat loss and energy development in this region could pose threats to blackpoll breeding populations that are already facing the most dramatic declines. Although blackpoll warblers have exhibited one of the highest sustained rates of population decline of any Neotropical migrant in the last few decades (Rosenberg et al. 2016, Sauer et al. 2017), trends appear to be highly variable across breeding populations. In specific, the western boreal and Alaskan populations of blackpolls that are most commonly represented in our sample are facing the most severe declines with 71 and 95% regional population declines respectively from 1970 to 2014 (Rosenberg et al. 2016). As noted by Holberton et al. (2015), the breeding regions that are strongly represented in our blackpoll migrant sample from the Gulf of Maine have experienced some of the greatest rates of forest decline in North America in the last decade or so, (Hansen et al. 2013) and these losses may be responsible for the 70% decline in blackpolls numbers observed during fall migration at Manomet Bird Observatory on the Massachusetts coast since the 1970s (Lloyd-Evans and Atwood 2004). Given that this region serves as an important staging resource for blackpolls to refuel before epic transoceanic migratory flights (DeLuca et al. 2015, Smetzer and King
in review; Chapter 2), conservation of these regional stopover resources is likely an important priority for blackpolls.

1.4.2 Temporal migration patterns

Using a combination of intrinsic markers, we successfully identified geographic structure to the timing of migration for both species, despite overlap in the δ2 H signatures for blackpolls originating from southern boreal forests and western portions of North America. The results of our stable isotope regression coincide with numerous previous studies that found no significant relationship between δ2 H signatures and capture date for blackpolls (Dunn et al. 2006, Kirchman et al. 2011, Holberton et al. 2015, Leppold 2016). However, by validating that blackpoll wing length varied geographically across North America, and using this morphological feature as an additional index for distance to breeding locale, we provide indirect evidence that blackpolls from more distant breeding areas reached the Gulf of Maine before their more southern and eastern conspecifics. This migration pattern could be a result of the earlier changes in temperature and food resources at northern latitudes, such that a strategy of leaving ‘early’, in anticipation of impending snow is more important and particularly adaptive for individuals breeding at higher latitudes (Rappole 2013). Indeed, seasonal declines in ecological productivity across North America are strong predictors of migratory departure, particularly for omnivorous or insectivorous species (La Sorte et al. 2015). In further support of this hypothesis, similar migratory patterns have been seen for Yellow Warblers (∙ petechia) and Wilson’s Warblers (∙ Cardellina pusilla), which both
also have breeding ranges that extend to the far northern and northwestern limits of North America (Kelly et al. 2002, Kelly 2006).

Vireos exhibited the opposite pattern of blackpolls with individuals from northern latitudes passing through the study site later in the fall migration period than more southern conspecifics. This pattern has also been observed for Yellow-rumped Warbler, Northern Waterthrush (Dunn et al. 2006), Orange-crowned Warblers (*Vermivora celata*), and Common Yellowthroats (*Geothlypis trichas*; Kelly et al. 2002). It is possible that we observed this geographic structure to migration simply because breeders from more southern latitudes reached the coast sooner than conspecifics that had further to travel. One hypothesis that is commonly offered for southern breeders migrating earlier than northern breeders is that southern populations forgo the opportunity for double brooding in favor of the benefits that may be gained from earlier arrival on the breeding grounds (Rappole 2013). Though our sample was entirely hatch year birds, if adults in northern latitudes tended to double brood more frequently than more southern conspecifics, the breeding season, and thus the departure of juveniles could be delayed in more northwestern breeding regions.

It is also possible that Red-eyed Vireos exhibit Type I leapfrog migration, in which southern breeding populations migrate earlier than northern conspecifics, and occupy the more northern portions of the species wintering range (Smith et al. 2003). In Type I leapfrog migration, it is often the larger individuals that occupy the more southern breeding areas, and the more northern wintering latitudes, and smaller individuals that tend to inhabit northern breeding latitudes and more southern wintering areas, possibly as
an evolutionary repercussion of smaller individuals being forced out of the closer (i.e. more northern) wintering sites through competition (Pienkowski et al. 1985). In support of this hypothesis, we found that vireos from southern latitudes and eastern longitudes had longer wings, and migrated earlier than their northern/western conspecifics. Further study of where different breeding populations of Red-eyed Vireos winter could help test whether vireos do in fact exhibit this Type I leapfrog pattern, like other species with similar geographic variation in body size.

1.4.3 Conclusion

Migration monitoring indicates that many songbirds are exhibiting significant long-term declines (Lloyd-Evans and Atwood 2004, Dunn et al. 2006). Effectively conserving these species requires a ‘full life cycle’ understanding of what factors are limiting populations, and information about where specific breeding populations face anthropogenic threats throughout the annual cycle (Marra et al. 1998, Runge and Marra 2005). Although migration is a time of exceptional energy demand and mortality for songbirds, more research on connectivity has focused on breeding and winter ground connectivity than migratory stopover sites. While our work demonstrates that mid-coast Maine serves as a catchment area for both Blackpoll Warblers, and Red-eyed Vireos, and provides some evidence that connectivity between breeding areas and stopover sites may be strong for blackpolls, additional study linking breeding and stopover sites across the migratory range of both species is necessary to understand more fully how strong connectivity is between breeding and stopover areas for these species. Additional study linking stopover
sites to wintering locations will also ultimately be needed to fully model threats across the annual cycle for these species.
Table 1.1. Summary statistics for stable hydrogen isotope samples from Blackpoll Warbler (*Setophaga striata*) and Red-eyed Vireo (*Vireo olivaceous*) feathers. Data are from fall migration sampling at Petit Manan Point in Steuben Maine, in 2013 and 2014.

<table>
<thead>
<tr>
<th>Species</th>
<th>Year</th>
<th>Date</th>
<th>N</th>
<th>HY</th>
<th>AHY</th>
<th>U</th>
<th>Mean $\delta^2$H$_f$‰</th>
<th>Range $\delta^2$H$_f$‰</th>
</tr>
</thead>
<tbody>
<tr>
<td>BLPW</td>
<td>2013</td>
<td>09/17</td>
<td>23</td>
<td>19</td>
<td>4</td>
<td>0</td>
<td>-122.4</td>
<td>-157.7 to -73.8</td>
</tr>
<tr>
<td>BLPW</td>
<td>2014</td>
<td>09/23</td>
<td>70</td>
<td>55</td>
<td>13</td>
<td>1</td>
<td>-131.9</td>
<td>-177.7 to -76.1</td>
</tr>
<tr>
<td>REVI</td>
<td>2013</td>
<td>09/24</td>
<td>58</td>
<td>58</td>
<td>0</td>
<td>0</td>
<td>-86.6</td>
<td>-109.3 to -56.2</td>
</tr>
<tr>
<td>REVI</td>
<td>2014</td>
<td>09/26</td>
<td>82</td>
<td>82</td>
<td>0</td>
<td>0</td>
<td>-95.3</td>
<td>-119.9 to -57.2</td>
</tr>
</tbody>
</table>

NOTE. — Date = median date of capture, N = feather sample size for feathers, HY = number of hatch year samples, AHY = number of after hatch year samples, U = number of birds with unknown age
Figure 1.1. Location of the Petit Manan Point study site where migrants were captured in the fall of 2013 and 2014.
Figure 1.2. Monitoring Avian Productivity and Survivorship (MAPS) stations used to compare Blackpoll Warbler (*Setophaga striata*) and Red-eyed Vireo (*Vireo olivaceous*) wing lengths across latitude and longitude. The breeding range of each species is shown in white.
Figure 1.3. Stable hydrogen isotope values of migrant red-eyed vireos and blackpoll warblers captured during fall migration at Petit Manan Point in Steuben ME. Isotope maps are clipped to the range of each species. Histograms demonstrate the number of individuals within each isotope color band for each species.
Figure 1.4. Likelihood-based assignment of putative breeding/natal origin for red-eyed vireos and blackpoll warblers captured during fall migration at Petit Manan Point in Steuben Maine in 2013 and 2014, based on stable hydrogen isotope analysis of migrant feathers. The scale on the legend indicates the number of individuals that were consistent with the isotope value in a given cell of the isotope map, under 2:1 odds of correct assignment. The breeding range of each species is outlined in black.
Figure 1.5 Relationship between Blackpoll Warbler (*Setophaga striata*) and Red-eyed Vireo (*Vireo olivaceous*) wing lengths across latitude and longitude.
CHAPTER 2

FALL MIGRATORY DEPARTURE DECISIONS AND ROUTES OF BLACKPOLL WARBLERS (SETOPHAGA STRIATA) AND RED-EYED VIREOS (VIREO OLIVACEUS) AT A COASTAL BARRIER IN THE GULF OF MAINE

2.1 Introduction

Each fall, millions of migrant songbirds concentrate in coastal areas of the eastern US where natural and anthropogenic factors amplify the demands of migration (Buler and Moore 2011). Many songbirds face especially high energy demands and low fuel stores when they reach the eastern coast of the US (Moore et al. 1990, Petit 2000) where they encounter unfamiliar habitats with high competition and predation pressure (Richardson 1978, Åkesson 1993, Ydenberg et al. 2007). Since stopover habitat can influence energetic condition (Moore et al. 1995), the ability to evade predators (McCabe and Olsen 2015a), migration rate (Wikelski et al. 2003, Åkesson et al. 2012), and fitness in subsequent life stages (Runge and Marra 2005, Smith and Moore 2005, Newton 2006, Norris and Taylor 2006), the habitat choices that migrants make in coastal environments may have important fitness consequences.

After landfall, migrant songbirds make landscape-scale stopover flights that are thought to represent short ‘within stopover’ relocations, rather than a continuation of migration (Mills et al. 2011, Taylor et al. 2011). In coastal regions, many songbirds specifically re-orient inland after landing – a behavior thought to be an adaptive strategy
for finding better stopover habitats (Richardson 1978, Lindström and Alerstam 1986, Åkesson et al. 1996, Åkesson 1999). In support of this hypothesis, inland stopover flights in coastal areas are more common for lean individuals (Deutschlander and Muheim 2009, Smolinsky et al. 2013) and in regions with high predation pressure (Woodworth et al. 2014). They also appear to be unrelated to weather conditions (Woodworth et al. 2015).

If stopover flights at the coast are indeed an important adaptive strategy for finding better habitats, the propensity for this behavior may be expected to differ predictably across individuals facing very different selective pressures. For instance, inland flights may be more common in species with exceptional energetic demands during migration, particularly later in the season when resources are limited. In addition, since diet and habitat structure both influence stopover habitat use (Suomala et al. 2010, Wolfe et al. 2014), species with markedly different diets and habitat preferences may differ in their propensity to move inland at the coast. Similarly, since females and juveniles are known to be sub-dominant and can be excluded from habitats (Parrish and Sherry 1994, Komar et al. 2005, Rappole 2013, Akresh et al. 2015), inland movements may be more frequent for these sex and age classes.

In addition to their habitat choices along coastlines, the manner in which migrants negotiate ecological barriers posed by open water can influence the duration, energy expenditure, and risks of migration (Alerstam 2001). Overwater travel limits feeding and resting opportunities, and can be fatal if poor weather arises, but can be a safe and time-minimizing option if birds have adequate fat stores and favorable weather (Covino and Holberton 2011, Schmaljohann and Naef-Daenzer 2011, Schmaljohann et al. 2011,
Detouring around a barrier minimizes the danger of navigational errors, and effects of poor weather or low fuel stores (Butler 2000, Newton 2007) but increases the length of the migratory journey, and as such, overall energy expenditure and exposure to predators and disease (Cimprich et al. 2005, Ydenberg et al. 2007, Hahn et al. 2014).

Given the acute stressors that songbirds face in coastal landscapes, even small differences in experience, skill, social status, or selection pressures could cause marked differences between individuals in the choice of migratory route. How individuals balance risk, energy expenditure, and speed at a barrier may differ by sex and capture date, since stopover behavior, fuel deposition rates, and time constraints can vary markedly between sexes and throughout the season (Morris et al. 1994, Rappole 2013, Seewagen et al. 2013, La Sorte et al. 2015). There is also some evidence that route choice can differ by age presumably because of differences in experience and risk management (Crysl er et al. 2016). Finally, differences in breeding origin may influence route choice at an ecological barrier due to migratory divides (Delmore et al. 2012) or more compensation for wind drift by individuals from more western populations (Fitzgerald and Taylor 2008). While the effects of weather and fat stores on route choice at an ecological barrier have been well studied (Covino and Holberton 2011, Schmaljohann and Naef-Daenzer 2011, Schmaljohann et al. 2011, Smolinsky et al. 2013, Deppe et al. 2015, Woodworth et al. 2015), the role that age, breeding origin, sex, and capture date play has received less attention. However, interspecific variation in route choice at ecological barriers has important implications for population dynamics because it can
lead to systematic differences in exposure to risk and mortality (Cristol et al. 1999, Mehlman et al. 2005, Longcore and Smith 2013).

We used regional-scale automated VHF radio telemetry to study inland stopover flights and migratory departure flights of Blackpoll Warblers (Setophaga striata; hereafter blackpolls) and Red-eyed Vireos (Vireo olivaceus; hereafter vireos) from a coastal stopover site in the Gulf of Maine. Our first objective was to characterize the orientation of stopover flights from the coast to determine if they were mainly inland movements. We also tested hypotheses that the probability of stopover flight from the capture site differed by sex, age, capture date or species. We expected vireos to undertake stopover flights less frequently than blackpolls that double their body mass in preparation for an extreme trans-oceanic migratory route (DeLuca et al. 2015). Our second objective was to characterize migratory routes within the study area to determine whether individuals that initially retreat inland from a coastal barrier subsequently continue migration by inland, coastal, or offshore routes.

Decades of data indicate that some songbirds circumnavigate the Gulf of Maine, while many others traverse this barrier in large overwater flights (Mcclintock et al. 1978, Richardson 1978, Leppold 2016). Our final objective was to investigate the interspecific factors that influence this decision. We tested a number of hypotheses that overwater orientation of migratory flight was more likely for 1) later migrants facing increased time constraints and more supportive tailwinds (Smith and McWilliams 2014, La Sorte et al. 2015), 2) males that may benefit more from early arrival on the wintering grounds (Parrish and Sherry 1994), 3) adults that have more experience navigating and assessing
if conditions are favorable for overwater passage (Ralph 1978, Moore 1984, McKinnon et al. 2014), and 4) individuals from eastern populations that may compensate for wind drift less than their more westerly conspecifics (Fitzgerald and Taylor 2008).

2.2 Methods

2.2.1 Data collection

We captured blackpolls and vireos at the Petit Manan Point section of the Maine Coastal Islands National Wildlife Refuge (Fig. 2.1) situated on a coastal peninsula in Steuben Maine, United States (44.40846 ° N, -67.90502° W). The 888 ha refuge is 90% mixed deciduous forest (McCabe and Olsen 2015b) composed of mountain ash *Sorbus Americana*, red maple *Acer rubrum*, red *Picea rubens*, black *P. mariana* and white spruce *P. glauca* interspersed with dense fruit-bearing shrubs (McCabe and Olsen 2015a) including alder *Alnus* spp. wild raisin *Viburnum cassinoides*, raspberry *Rubus* spp., bayberry *Myrica* spp., and blueberry barrens *Vaccinium* spp. We captured birds between September 6 and October 13, 2014 using mist-nets located primarily in mixed-forest and shrub habitats. We placed a USGS aluminum band on all individuals, and recorded age, wing and tarsus length, mass, and subcutaneous fat score (0 = none; 0.5= trace; 1 = lining furculum; 2= filling furculum; 3 = mounded in furculum and beginning to cover abdomen; 4 = mounded on breast and sides of abdomen). We collected blood from a clipped toenail for all radio-tagged individuals for DNA sexing.

We collected feather samples for stable hydrogen isotope (δ² H) analysis to serve as a rough proxy for breeding origin. Both species undertake a prebasic molt on the
breeding grounds that includes body feathers (Pyle 1997), so during fall migration the $\delta^2$H ratio of feathers can indicate the relative breeding origin (Wassenaar and Hobson 2001). Following Leppold (2016), we sampled the third retrix on the right for vireos, and upper back feathers between the scapulars from blackpolls to avoid flight interference. Feathers were cleaned and weighed at the Cornell University Stable Isotope Laboratory, and analyzed for $\delta^2$H on a Thermo Delta V isotope ratio mass spectrometer. The samples were analyzed under a comparative equilibrium method with three calibrated keratin $\delta^2$H references (CBS, and KHS; Wassenaar and Hobson 2003), and an internal standard run every 10 samples. Isotope corrections were performed using the CBS and KHS standards. We reported all results for nonexchangeable $\delta^2$H in delta notation of units per mil ($\permil$), normalized to the Vienna Standard Mean Ocean Water standard scale (Bowen 2010).

We outfitted 49 blackpolls and 47 vireos with coded VHF radio transmitters (Avian NanoTag NTQB—2, Lotek Wireless Inc., Newmarket, ON; 40 d expected tag life). Transmitters and figure-eight leg-loop harness attachments (Rappole et al. 1991) were 0.29 g and < 3% of body mass for all individuals. Each radio transmitter emitted a uniquely coded signal at 166.38 MHz every 11-15 s. We tracked birds at the capture site with two automated telemetry stations, each with 3 nine-element Yagi antennas mounted atop an 8-m tower, and a sensorgnome receiver (www.sensorgnome.org) that logged a GPS-synchronized time and signal strength for each tag detection. We tracked subsequent movements with an array of coastal and island telemetry stations deployed from Nova Scotia to Maryland within the Motus Wildlife Tracking System (Taylor et al. in review;
Previous calibration studies with similar equipment recorded a maximum detection range of 12 km for birds aloft (Mills et al. 2011, Taylor et al. 2011); simultaneous detections on towers situated 24 km apart indicated we achieved a similar range. To eliminate false positives, we only included detection events that contained ≥ 3 bursts of an ID that occurred at multiples of the burst interval for the corresponding tag (Woodworth et al. 2015).

2.2.2 Deriving movement tracks

We used graphs of signal strength over time at the two capture-site telemetry stations (hereafter ‘banding array’) to pinpoint final departure time from the capture site (Mills et al. 2011, Taylor et al. 2011; Fig. 2). We assigned departure time from the capture site as the time at which the maximum signal strength was recorded during a final departure flight (Mills et al. 2011). If a clear departure flight was not evident, but a bird was redetected outside the banding array we used the last detection at the banding array as the departure time from the capture site. If an individual did not exhibit a clear departure flight and was not redetected outside the banding array, we excluded it from all subsequent analysis and considered its fate as unknown.

We followed the general procedure of Mitchell et al. (2015) to estimate the spatial midpoint of detections at each tower outside of the capture location because triangulation methods for automated telemetry are not well developed. Birds on the ground can only be detected within 0.5 – 2 km of a receiver (Taylor et al. 2011), so detections beyond the banding array were predominantly birds in flight. Thus, for all stations outside the banding array we assigned individuals a single location 6 km (half the detection range of
a bird in flight) along the bearing of the antenna that recorded the greatest signal strength value. We used the antenna that recorded the strongest signal to determine position relative to a station because power received from a transmitting antenna is maximized along the beam of a receiving directional antenna (Friis 1946, Shaw 2013). The detection power of the antennas we used also drops by 50% within 22.5° of the beams’ main axis (PLC1669; http://www.arcantenna.com), and is greatly limited behind the antenna by a high (20 dB) front/back ratio, so the method can reasonably summarize multiple detections at a receiver as a single estimate of mean position. Furthermore, there was no reason localization error would be systematically different between the species, sexes, age groups, or dates across which we compared movement metrics.

Beyond the banding array, we used the duration of detections at each telemetry station to determine if birds were detected during a single sustained ‘flyby’ or were detected in flight during arrival and subsequent departure from a nearby stopover site. There was a clear gap in the data such that the time between the first and last detection at any site was either < 100 min (n= 326; median = 11.9 min; mean = 7.3 ± 13.0 min) or > 180 min (n= 24; median = 44.7 h; mean = 116.3 ± 178.7 h). We thus identified any series of detections at a station < 100 min as a flyby, and assumed a bird stopped near a station if the span between first and last detections was > 180 min. Though 100 min is a lengthy duration given our likely detection range, this interval could occur in strong headwinds, or if a bird flew past a receiver in a highly indirect route during re-orientation, or abandoned migratory flights. Following Mitchell et al. (2015), we used the time of the maximum signal strength recorded at a station to estimate the time of flybys. We used the
first and last detections at a site to mark the arrival and departure for series of detections classified as a stopover.

We calculated the movement rate for every segment of every bird’s movement track to classify behavior between telemetry stations as a ‘sustained migratory flight’ or ‘slow movement’. Since error in our localization routine can lead to inexact movement rates, particularly where towers were adjacent, we used thresholds in the movement rates to classify behavior, rather than absolute values. There was a clear threshold at 1 m/s, indicating a behavioral difference above and below this value. All track segments < 1 m/s were > 177 min in duration, and 97% were > 5 h, indicating that the slow rates calculated for these segments of the movement track were not a function of localization error. Birds likely halted flight at some point during slow track segments; however, since we could not specifically identify the location or duration of stopovers, we classified these segments as ‘slow movements’. We categorized track segments with movement rate ≥ 1 m/s as a ‘sustained migratory flight’, except for a few segments (n = 15; 0.04%) that spanned multiple nights of flight. This classification produced logical results: all segments > 5 m/s (n = 239) were classified as sustained migratory flights, and this is the lower end of groundspeeds for long-distance migrants (Nilsson et al. 2014).

2.2.3 Classifying departure flights

We classified final departure flights from the capture site as ‘migratory flights’, ‘stopover flights’, or ‘ambiguous’. We only classified departure flights from the capture site. Previous studies have used the timing of flights, the timing and location of subsequent redetections, and flight orientation to differentiate between migratory and
stopover flight from a stopover site (Taylor et al. 2011; Woodworth et al. 2014, 2015).

Because we had an extensive tracking array with high redetection rates and were specifically interested in comparing the orientation of stopover and migratory flights, whenever possible we only classified ‘migratory flights’ and ‘stopover flights’ based on their timing and the movement rates directly following the flights.

We catalogued a departure from the capture site as a migratory flight if a) it occurred between twilight and dawn, b) the track segment immediately following the departure was a sustained migratory flight, and c) the bird did not make a stopover within 50 km of the capture site. We used this last criterion to ensure that any movement rates > 1 m/s between the capture site and adjacent telemetry stations that may have been inflated due to localization error and/or short flight durations did not result in a migratory flight classification if a bird halted movement near the capture site. We recorded a departure as a stopover flight if we recorded a) a stop within 50 km of the capture site, b) slow movement (i.e. < 1m/s) in the track segment immediately after departure, or c) a brief nocturnal redetection at the banding array > 24 h later during a presumed departure from a nearby location. We classified a departure as ambiguous if we did not redetect an individual in the external array and did not have adequate detections to clearly distinguish a departure flight. Six vireos and three blackpolls met these criteria and were excluded from all subsequent analyses.

We used graphs of signal strength over time to classify departure flights (e.g. Mills et al. 2011, Taylor et al. 2011; Fig. 2) for six vireos and four blackpolls not redetected beyond the banding array. We recorded flights between twilight and dawn
that indicated departure from the capture site with a vanishing signal on the 299, 215, 173 or 120° (northwest to southeast) antennas as migratory flights, and flights any time of day on the 357 or 25° antennas as stopover flights (e.g. Taylor et al. 2011, Woodworth et al. 2015).

We calculated orientation of migratory flights from the capture site as the great-circle bearing between banding array station that recorded final departure and an individual’s first position estimate beyond the banding array. Four birds departed the capture site by migratory flight but were not detected in the external array, so we used graphs of signal strength over time to determine which single antenna best represented their vanishing bearing. We used these graphs to similarly classify flight orientation for birds that departed the capture site on stopover flights because 95% of re-detections after stopover flights occurred > 12 h after departure and were not necessarily representative of departure orientation from the capture site. Since our estimates of flight orientation were coarse, we categorized migratory and stopover flights from the capture site into meaningful behavioral categories of inland (271 - 90°), coastal (235 -270°) or overwater (91-234°) orientation.

2.2.4 Statistical analyses

Each bird was included only once in each model (Table 2.1) as the data included one final departure from the capture site per bird. We did not explicitly estimate breeding origin from δ2 H but instead used δ2 H values to represent a rough index of relative origin/migration distance in models as lower values indicate a more northern/western breeding area (Wassenaar and Hobson 2001; Fig 2.2). Although fat stores can influence
departure and orientation decisions for songbirds (Deutschlander and Muheim 2009, Ktitorov et al. 2010, Covino and Holberton 2011, Schmaljohann and Naef-Daenzer 2011, Deppe et al. 2015), most individuals were quite lean (75% birds < 2 fat score).

Furthermore, > 70% of birds remained at the capture site for > 1 d, so fat levels at capture were not necessarily representative of fuel stores at departure. Preliminary analyses indicated that fat did not significantly influence response variables, or differ between species, sexes, or age groups, so we excluded it from analyses.

We used logistic regression (Binomial generalized linear models-glm) to relate species, sex, age, and capture date to the probability of departing the capture site by a stopover or migratory flight. The orientation of migratory and stopover flights were non-normal, so we used Watson-Wheeler tests for homogeneity (Watson 1962, Zar 2010) to examine whether the orientation of stopover and migratory flights from the capture site differed. We only used individuals that were detected in the external array in this comparison (n = 77), as their departure flight classification was not dependent on flight orientation. We used ordered logistic regression (cumulative link models with a logit link) to relate the probability of inland, coastal, or offshore migratory flight orientation from the capture site to sex, δ²H values, and capture date.

We used Akaike’s information criterion corrected for small sample size (AICc; Burnham and Anderson 2002) to rank the candidate logistic and ordered logistic regression models. We reported AICc, Δ AICc, Akaike weight (ωi), and the parameter estimates ± SE for covariates for all models (Supplementary material Appendix 1). We considered a variable as important if the 90% confidence intervals for its parameter
estimate did not contain zero across any of the candidate models in which it was considered, and strongly supported if 95% or 99% confidence intervals did not contain zero. To assess model uncertainty, we considered whether the effect of predictor variables (positive or negative) was consistent across candidate models for a given response variable (Cade 2015). We did not model average parameter estimates because our intent was not prediction, and this practice can produce unreliable results since regression coefficients can have different units and interpretations across models that contain different sets of covariates (Cade 2015). We conducted all analyses in the R statistical environment version 3.3.1 (R Core Team 2016) using the ‘maptools’ (Bivand and Lewin-Koh 2015), ‘oce’ (Kelley and Richards 2015), ‘sp’ (Bivand et al. 2013) ‘rgdal’ (Bivand et al. 2015), ‘geosphere’ (Hijmans 2015) ‘circular’ (Agostinelli and Lund 2013), and ‘ordinal’ packages (Christensen 2015).

2.3 Results

We classified the final departure from the capture site as a migratory flight (n = 29) or stopover flight (n = 58) for 46 blackpolls and 41 vireos; the remaining birds with ambiguous departures were not included in analyses. Sixty-three percent of blackpolls and 48% of vireos were female. All vireos and 74% of blackpolls were juveniles. The wide range of stable isotope values for blackpolls (-177.71 to -76.06‰) and vireos (-111.97 to -57.24‰) indicated that we captured birds from a broad geographic breeding area extending from the Canadian Maritimes and New England for both species, to as far away as northwestern North America for blackpolls, and central Quebec, western
Ontario, and southeastern Manitoba for vireos (Fig 2.2). Blackpolls remained at the capture site for an average of 3.5 ± 3.6 d after capture and vireos for 3.8 ±2.9 d.

Blackpolls exhibited a significantly greater probability of stopover flight from the capture site (40/46; 87.0%) than vireos (18/41; 43.9%; Binomial glm; Table 2.2). However, we found no evidence that capture date, age, or sex predicted the probability of stopover flight from the capture site for either species (Binomial glm; Table 2.3, Table 2.4).

We classified 86% of migratory flights (25/29) and 81% of stopover flights (47/58) from the capture site based on departure time and subsequent behavior (i.e. without considering flight orientation). Based on this sample, migratory and stopover flights from the capture site differed significantly in orientation with migratory flights oriented southwest (n = 25; 220 ± 1.4°) and stopover flights to the north (n = 47; 357 ± 1.2°; Watson Wheeler test of homogeneity; W = 21.14; p < 0.0001). We pooled the two species for this comparison because Fisher’s exact tests (Agresti 1990), indicated that the proportion of stopover flights oriented for inland, coastal, or offshore flight did not differ between the species (p = 0.32; Table 2.5), nor did the proportion of migratory flights in each directional category (p = 0.35). A small percentage of stopover flights from the capture site were notably oriented offshore for blackpolls (10%; 4/40) and vireos (22%; 4/18). These movements were all nocturnal, and may represent abandoned migratory flights that resulted in relocation.

Both species departed on migratory flights with coastal or offshore trajectories more frequently than inland trajectories, and vireos captured later in the season oriented
offshore more than earlier conspecifics. We determined orientation for all 29 migratory flights from the capture site and for 91% of the stopover flights (53/58; Table 2.5). Mean orientation of migratory flights was southwest for blackpolls (n = 6; 235± 0.97°) and south for vireos (n = 23; 189 ± 1.78°). Eighty three percent of blackpoll migratory flights from the capture site were oriented for coastal (33%; 2/6) or overwater flight (50%; 3/6). Seventy percent of vireo migratory flights were oriented for coastal (9%; 2/23) or offshore travel (61%; 14/23). We did not have an adequate sample size of blackpoll migratory flights from the capture site to test if orientation varied by sex, age, or capture date. The orientation of vireo migratory flights from the capture site exhibited a significant shift from inland to offshore as the season progressed (Ordered logistic regression; Table 2.6). We found no evidence that breeding origin or sex influenced the orientation of vireo migratory flights from the capture site.

Both species primarily exhibited a coastal or overwater route through the study area, regardless of how they initially departed the capture site (Fig. 2.3). Nine percent of blackpolls (4/46) and 7% of vireos (3/41) departed inland from the capture site and were never redetected. We last detected 30% of blackpolls (n = 14) at coastal or offshore sites in the central or southern Gulf of Maine, 37% (n = 17) in the Cape Cod/ Long Island region where the eastern US coastline protrudes into the Atlantic Ocean, and only 2% (n = 1) south of Long Island, suggesting that many individuals moved overwater to and/or from the Long Island area (Fig. 2.3). Three vireos (7%) were last detected making a migratory flight from the capture site in an overwater orientation, 37% were last detected in south or central Gulf of Maine, 17% in the Cape Cod/Long Island region, and 15%
south of Long Island. Eighty four percent of blackpolls and 83% of vireos that departed the capture site by inland stopover flight were subsequently redetected at coastal or island receivers, indicating that initial inland movement from the coast did not necessarily dictate an inland flight route.

Five individuals of each species traveled in an unexpected migratory direction to Nova Scotia, New Brunswick, or Ontario. Three blackpolls were last detected departing south, and overwater from southeastern Nova Scotia. Three vireos made overwater movements from the capture site to Nova Scotia, and back, while a fourth was last detected departing south, overwater from the New Brunswick coast. The detections were too sparse to determine final flight orientation for the other individuals that travelled to Canada.

2.4 Discussion

Though coastal stopover flights are assumed to represent an adaptive behavior for finding alternative stopover habitats inland (Richardson 1978, Lindström and Alerstam 1986, Åkesson et al. 1996, Åkesson 1999), direct study of this behavior has only recently been possible (e.g. Woodworth et al. 2014, 2015). By using a regional-scale telemetry array to classify behavior and movement rates after departure, we characterized most final departures from the capture site as stopover or migratory flights independent of their orientation, and thus could successfully compare the direction of stopover and migratory flights. Birds seldom made stopover flights from the capture site that were oriented for coastal or offshore flight, even though the Schoodic peninsula < 20 km to the southwest of the capture site is an easily visible target for landscape-scale stopover movements in a
seasonally appropriate direction. That stopover flights were primarily oriented inland, and migratory flights for coastal or offshore travel lends further support to the hypothesis that stopover flights at a coastal barrier represent birds seeking alternate habitats inland.

Blackpolls made more inland stopover flights than vireos, supporting our hypothesis that this behavior may be advantageous for species with high energetic demands. Most blackpolls depart for wintering sites from the northeastern coast of North America on multi-day trans-Atlantic flights (DeLuca et al. 2015) that require extensive fat deposition (Nisbet et al. 1963). In contrast, vireos are regularly sighted along the eastern US coastline during migration (Sullivan et al. 2016), and often circumnavigate rather than cross the Gulf of Mexico (Deppe et al. 2015), suggesting a less energy-demanding migratory strategy compared to blackpolls. Thus, the selection pressure and fitness consequences of finding prime stopover habitat for refueling and evading predators may be more important for blackpolls.

It is possible that differences in diet and habitat preference also contributed to the behavioral differences that we observed between blackpolls and vireos. As we saw for vireos, some species occupy small geographic areas during stopover (Paxton et al. 2008, Ktitorov et al. 2010). In contrast, others may make large stopover movements (Chernetsov 2006, Taylor et al. 2011), or move fairly continuously throughout stopover (Aborn and Moore 1997, Chernetsov 2005). Food availability and habitat structure both influence stopover habitat use (Buler et al. 2007, Mudrzynski and Norment 2013, McCabe and Olsen 2015a, b), and thus the degree to which migrants relocate during stopover to fine-tune habitat selection (Chernetsov 2006). Fruit availability plays a
principal role for highly frugivorous species, and vegetation structure for more omnivorous migrants (Wolfe et al. 2014). During migration, vireos are highly frugivorous (Parrish 1997, Smith and McWilliams 2010), and strongly associated with deciduous and mixed-deciduous forests, dense hardwood understory (Moore and Simons 1992, Suomala et al. 2010), and abundant fruits (McCabe and Olsen 2015a). The capture site contained all these habitat attributes, and likely provided excellent stopover resources for vireos. In contrast, blackpolls are more omnivorous than vireos during migration (Parrish 1997) and are associated with montane or spruce-fir forests habitats (Rimmer and McFarland 2000, DeLuca et al. 2013) that were not plentiful at the capture site. By departing inland, where coniferous forests are more abundant (McWilliams et al. 2005), blackpolls were likely able to find more suitable stopover habitats.

Predation pressure is also thought to play a strong role in motivating inland stopover flights because predators are highly concentrated along coastlines (Richardson 1978, Åkesson 1993, Ydenberg et al. 2007, Woodworth et al. 2014). Though re-detection rates indicate that mortality was relatively high at the capture site (< 14% for blackpolls, < 19% for vireos) we do not know the extent to which predation influenced inland movement in our study.

In contrast to our hypothesis, migratory flight orientation was not related to $\delta^2$H, and most individuals oriented for coastal or offshore flight regardless of breeding origin, suggesting that the blackpolls and vireos we sampled were actively selecting coastal and offshore routes. Many migrants are assumed to occupy coastal and offshore areas mainly due to navigational errors or wind displacement (Drury and Keith 1962, Ralph 1978).
Consequently, individuals from western breeding areas may re-orient inland to regain their intended migratory route (Fitzgerald and Taylor 2008). In contrast to this expectation, < 10% of blackpolls disappeared inland, despite arriving from as far away as western North America. Furthermore, we found no relationship between stable isotope value and departure orientation for vireos, though our sample contained individuals from as far as western and central Canada.

That vireos were more likely to orient offshore during migratory departure as the season progressed provides support for our hypothesis that an overwater route may be more strategic later in the fall. Seasonal changes in food resources and raptor abundance along the coast (Ydenberg et al. 2007, Smith and McWilliams 2014) may make a longer coastal route less favorable later in the season, while increased time constraints may cause the time-saving benefits of overwater travel to outweigh the risk of navigational errors and unexpected storms. The favorable tailwinds that appear to support overwater flight at an ecological barrier (Shamoun-Baranes et al. 2010, Deppe et al. 2015) also tend to increase throughout the fall (La Sorte et al. 2015). The offshore flight orientation we observed for later vireos may therefore be an adaptive advantage for time minimization that is supported by seasonal changes in wind condition.

2.4.1 Conservation Implications

The tendency for vireos and blackpolls to follow coastal and offshore routes is of conservation interest because these behaviors can increase exposure to hazards like wind turbines or communication towers that cause sporadic mass mortality events (Crawford and Engstrom 2001, Manville 2009, Longcore et al. 2012, Loss et al. 2013, Ronconi et al.)
Man-made structures are of particular concern in coastal and offshore areas where turbines are typically larger (Loss et al. 2013), flight altitudes are significantly lower (Drewitt and Langston 2006a, Hüppop et al. 2006, Petterson 2011, Hill et al. 2014), and songbirds are attracted to lights more frequently during poor weather (Hüppop et al. 2006, Manville 2009). The flights that both species made to Canada may also increase exposure to collision hazards because ‘reverse migrations’ involve traversing landscapes repeatedly (Hüppop et al. 2006), often at lower flight altitudes (Bruderer and Liechti 1998, Komenda-Zehnder et al. 2002, Nilsson and Sjöberg 2015).

Collision hazards are a conservation concern because migration mortality may limit populations for some species (Butler 2000, Dionne et al. 2008, Faaborg et al. 2010). Mortality accrued in coastal landscapes may have a particularly large impact on songbird population dynamics due to the sheer density of migrants (Newton 2006, 2008), particularly juveniles (Ralph 1981, Morris et al. 1996) for which high mortality rates can have a pronounced impact on population dynamics (Clark and Martin 2007).

Furthermore, our results suggest that later migrating vireos tend to choose more hazardous routes in the Gulf of Maine region, and so may be exposed to collision hazards and poor weather more frequently than other portions of the populations. As coastal landscapes face increasing pressure from development, continued research that can identify flight altitudes, and important stopover hotspots will likely be critical in improving the fitness and survival of songbirds during the migratory period.

2.4.2 Conclusions
Our work highlights the importance of studying migration, and conserving stopover resources at a large spatial scale. Without the use of a large regional array, we may not have been able to compare the orientation of stopover and migratory flights from the capture site, determine that most individuals took coastal or offshore routes despite making an initial inland departure, or detect birds making large-scale movements to the north and east after their initial departure from the capture site. Similarly, only by studying migration at a large spatial scale, could we confirm that most vireos remained at the capture site until migratory departure, and demonstrate that the dense coastal scrub and deciduous forests at the capture site likely provided valuable stopover resources for this species. These findings reinforce the importance of maintaining stopover habitats with mature fruiting shrubs for more frugivorous migrants (Smith and McWilliams 2010, Mudrzynski and Norment 2013), particularly in the Gulf of Maine where frugivorous species from across the boreal region concentrate in the fall (Leppold and Mulvihill 2011, Leppold 2016). The regional array also revealed that most blackpoll departures were inland stopover flights, not true migratory departures. This underscores the importance of conserving stopover habitats at a broad spatial scale, and implicates inland habitats as more favorable for blackpoll fat deposition. Though we were unable to specifically measure the scale of inland movements or habitat choices of blackpolls that relocated inland, our results suggest that a dense array of receivers just inland from the coast may help to elucidate the stopover needs of this rapidly declining species (Rosenberg et al. 2016).
Table 2.1. Candidate models considered in analyses relating sex, capture date, stable hydrogen isotope values, age, and species to movement metrics of Blackpoll Warbler (*Setophaga striata*) and Red-eyed Vireo (*Vireo olivaceus*) radio-tracked in the Gulf of Maine in fall 2014.

<table>
<thead>
<tr>
<th>Response variables</th>
<th>Stopover vs. migratory flight (intraspecific)</th>
<th>Stopover vs. migratory flight (interspecific)</th>
<th>Migratory flight orientation (inland/coastal/offshore) **</th>
</tr>
</thead>
<tbody>
<tr>
<td>Candidate models</td>
<td>sex</td>
<td>species</td>
<td>sex</td>
</tr>
<tr>
<td></td>
<td>day ***</td>
<td>species + sex</td>
<td>day</td>
</tr>
<tr>
<td></td>
<td>age ***</td>
<td></td>
<td>Δ²H</td>
</tr>
<tr>
<td></td>
<td>sex + day</td>
<td></td>
<td>sex + Δ²H</td>
</tr>
<tr>
<td></td>
<td>sex + age ***</td>
<td></td>
<td>sex + Δ²H</td>
</tr>
<tr>
<td></td>
<td>day + age ***</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>day + sex + age ***</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

NOTE. — Day = capture date; Δ²H = stable hydrogen isotope values (used as a proxy for breeding origin).

* The species differed significantly in mean capture date and Δ²H value, so we did not include these variables in interspecific models.

** We only had an adequate sample size of migratory departures to run models for Red-eyed Vireos. Capture date was correlated with Δ²H for Red-eyed Vireos, so we did not combine these variables in models.

*** Only Blackpoll Warblers, as all Red-eyed Vireos were juveniles.
Table 2.2. Candidate Binomial generalized linear models comparing Blackpoll Warbler (*Setophaga striata*) and Red-eyed Vireo (*Vireo olivaceus*) probability of stopover flight versus migratory departure from a coastal stopover site.

<table>
<thead>
<tr>
<th>Models</th>
<th>sex (M)</th>
<th>Species (REVI)</th>
<th>AIC&lt;sub&gt;c&lt;/sub&gt;</th>
<th>Δ AIC&lt;sub&gt;c&lt;/sub&gt;</th>
<th>ω&lt;sub&gt;i&lt;/sub&gt;</th>
</tr>
</thead>
<tbody>
<tr>
<td>species + sex</td>
<td>-0.80 ± 0.52</td>
<td>-2.09 ± 0.51</td>
<td>95.75</td>
<td>0.00</td>
<td>0.53</td>
</tr>
<tr>
<td>species</td>
<td>-2.14 ± 0.54</td>
<td>96.0</td>
<td>0.47</td>
<td>0.47</td>
<td></td>
</tr>
</tbody>
</table>

NOTE. — Beta estimates ± 1 standard error are shown and represent males relative to females, and Red-eyed Vireos relative to Blackpoll Warblers. AIC<sub>c</sub> = Akaike’s information criterion corrected for small sample sizes, Δ AIC<sub>c</sub> = the difference between the AIC<sub>c</sub> of the top-ranked model and the corresponding model, and ω<sub>i</sub> = Akaike Weight. The species differed significantly in mean capture date and δ<sup>2</sup>H values, so we did not include these variables in models. Data are from automated telemetry conducted in the Gulf of Maine in fall, 2014.

* Parameter estimates have 99% confidence intervals that do not include zero.
Table 2.3. Candidate Binomial generalized linear models relating Blackpoll Warbler (*Setophaga striata*) probability of stopover flight versus migratory departure from a coastal stopover site to sex, capture date (day), and age.

<table>
<thead>
<tr>
<th>Models</th>
<th>sex (M)</th>
<th>day</th>
<th>age (HY)</th>
<th>AIC&lt;sub&gt;c&lt;/sub&gt;</th>
<th>Δ AIC&lt;sub&gt;c&lt;/sub&gt;</th>
<th>ω&lt;sub&gt;i&lt;/sub&gt;</th>
</tr>
</thead>
<tbody>
<tr>
<td>sex</td>
<td>-1.02 ± 0.97</td>
<td></td>
<td></td>
<td>34.25</td>
<td>0.00</td>
<td>0.26</td>
</tr>
<tr>
<td>day</td>
<td></td>
<td>0.14 ± 0.13</td>
<td></td>
<td>34.63</td>
<td>0.09</td>
<td>0.24</td>
</tr>
<tr>
<td>age</td>
<td></td>
<td></td>
<td>0.83 ± 0.99</td>
<td>35.01</td>
<td>0.47</td>
<td>0.20</td>
</tr>
<tr>
<td>age + sex</td>
<td>1.05 ± 1.04</td>
<td></td>
<td></td>
<td>35.86</td>
<td>1.32</td>
<td>0.13</td>
</tr>
<tr>
<td>age + day</td>
<td>0.79 ± 1.00</td>
<td>0.13 ± 0.13</td>
<td></td>
<td>36.33</td>
<td>1.79</td>
<td>0.10</td>
</tr>
<tr>
<td>age + day + sex</td>
<td>-1.16 ± 1.04</td>
<td>0.14 ± 0.15</td>
<td>0.94 ± 1.05</td>
<td>37.40</td>
<td>2.86</td>
<td>0.06</td>
</tr>
</tbody>
</table>

**NOTE.** — Beta estimates ± 1 standard error are shown and represent males relative to females, and juveniles relative to adults. AIC<sub>c</sub> = Akaike’s information criterion corrected for small sample sizes, Δ AIC<sub>c</sub> = the difference between the AIC<sub>c</sub> of the top-ranked model and the corresponding model, and ω<sub>i</sub> = Akaike Weight. Data are from automated telemetry conducted in the Gulf of Maine in fall, 2014.

* Parameter estimates have 90% confidence intervals that do not include zero.

** Parameter estimates have 95% confidence intervals that do not contain zero.
Table 2.4. Candidate Binomial generalized linear models relating Red-eyed Vireo (*Vireo olivaceus*) probability of stopover flight versus migratory departure from a coastal stopover site to sex and capture date (day).

<table>
<thead>
<tr>
<th>Models</th>
<th>sex (M)</th>
<th>day</th>
<th>AIC&lt;sub&gt;c&lt;/sub&gt;</th>
<th>Δ AIC&lt;sub&gt;c&lt;/sub&gt;</th>
<th>ω&lt;sub&gt;i&lt;/sub&gt;</th>
</tr>
</thead>
<tbody>
<tr>
<td>sex</td>
<td>-0.89 ± 0.65</td>
<td></td>
<td>58.57</td>
<td>0.00</td>
<td>0.46</td>
</tr>
<tr>
<td>day</td>
<td>-0.06 ± 0.06</td>
<td></td>
<td>59.33</td>
<td>1.60</td>
<td>0.31</td>
</tr>
<tr>
<td>sex + day</td>
<td>-0.85 ± 0.65</td>
<td>-0.06 ± 0.06</td>
<td>59.92</td>
<td>5.74</td>
<td>0.23</td>
</tr>
</tbody>
</table>

NOTE. — Beta estimates ± 1 standard error are shown and represent males relative to females. AIC<sub>c</sub> = Akaike’s information criterion corrected for small sample sizes, Δ AIC<sub>c</sub> = the difference between the AIC<sub>c</sub> of the top-ranked model and the corresponding model, and ω<sub>i</sub> = Akaike Weight. Data are from automated telemetry conducted in the Gulf of Maine in fall, 2014.
Table 2.5. Stopover flights and migratory departures by orientation for radio-tagged Blackpoll Warblers (*Setophaga striata*) and Red-eyed Vireos (*Vireo olivaceus*) departing a coastal stopover site in the Gulf of Maine in fall 2014.

<table>
<thead>
<tr>
<th>Orientation</th>
<th>Blackpoll Warblers</th>
<th>Red-eyed Vireos</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Stopover flights</td>
<td>Migratory flights</td>
</tr>
<tr>
<td>Inland (91 – 269°)</td>
<td>31</td>
<td>1</td>
</tr>
<tr>
<td>Coastal (235 - 270°)</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>Offshore (90 – 234°)</td>
<td>4</td>
<td>3</td>
</tr>
<tr>
<td>Unknown</td>
<td>4</td>
<td>0</td>
</tr>
<tr>
<td>Total</td>
<td>40</td>
<td>6</td>
</tr>
</tbody>
</table>

NOTE. — Unknown represents departures for which we could not determine flight orientation.
Table 2.6. Candidate ordered logistic regression models relating sex, capture date (day), and stable isotope value ($\delta^2$H; as a proxy for breeding latitude) to the probability of inland, coastal, or offshore orientation for Red-eyed Vireo *olivaceus* during migratory departure from a coastal stopover site.

<table>
<thead>
<tr>
<th>Models</th>
<th>sex (M)</th>
<th>day</th>
<th>$\delta^2$ H</th>
<th>$\text{AIC}_c$</th>
<th>$\Delta \text{AIC}_c$</th>
<th>$\omega_i$</th>
</tr>
</thead>
<tbody>
<tr>
<td>day</td>
<td>0.19 ± 0.09 *</td>
<td>41.54</td>
<td></td>
<td></td>
<td></td>
<td>0.67</td>
</tr>
<tr>
<td>day + sex</td>
<td>0.83 ± 0.96</td>
<td>0.20 ± 0.10 *</td>
<td>43.73</td>
<td>2.19</td>
<td>0.22</td>
<td></td>
</tr>
<tr>
<td>sex</td>
<td>0.80 ± 0.85</td>
<td></td>
<td></td>
<td>46.68</td>
<td>2.90</td>
<td>0.05</td>
</tr>
<tr>
<td>$\delta^2$ H</td>
<td></td>
<td>-0.02 ± 0.03</td>
<td>47.23</td>
<td>0.56</td>
<td>0.04</td>
<td></td>
</tr>
<tr>
<td>sex + $\delta^2$ H</td>
<td>0.76 ± 0.85</td>
<td>-0.02 ± 0.03</td>
<td>49.39</td>
<td>2.17</td>
<td>0.01</td>
<td></td>
</tr>
</tbody>
</table>

**NOTE.** — Beta estimates ± 1 standard error are shown and represent males relative to females. $\text{AIC}_c$ = Akaike’s information criterion corrected for small sample sizes, $\Delta \text{AIC}_c$ = the difference between the $\text{AIC}_c$ of the top-ranked model and the corresponding model, and $\omega_i$ = Akaike Weight. Capture date was correlated with $\delta^2$H values, so we did not combine these variables in models. Data are from automated telemetry conducted in the Gulf of Maine in fall, 2014. * Parameter estimates have 95% confidence intervals that do not contain zero.
Figure 2.1. (a) Map of regional automated telemetry stations used to track radio-tagged Blackpoll Warbler (*Setophaga striata*) and Red-eyed Vireo (*Vireo olivaceus*) in fall 2014. Points represent receiver sites. (b) Automated telemetry receivers surrounding the capture site, shown in red. Solid black lines show the orientation and 12 km approximate detection range for telemetry receivers and their antenna.
Figure 2.2. Isotopic regions of North America based on calibration of the stable isotope precipitation map ($\delta^2$ Hp) of Bowen et al. (2005) using the algorithm presented in Hobson et al. (2012) for translating $\delta^2$ Hp into $\delta^2$ H feather values for non-ground-foraging, long-distance migrants.
Figure 2.3. Map of (a) Blackpoll Warbler (*Setophaga striata*) and (b) Red-eyed Vireo (*Vireo olivaceus*) migratory routes observed by automated telemetry, in fall 2014 for the northern portion of the study area in which the majority of detections occurred. Direct flights are shown with solid lines, and likely represent actual flight paths. Slower movements are shown with dashed lines and may not represent actual routes. Estimated locations at receiver stations are shown in red and locations of observed stopovers at a telemetry station are blue.
CHAPTER 3

PROLONGED STOPOVER AND CONSEQUENCES OF MIGRATORY STRATEGY ON LOCAL-SCALE MOVEMENTS WITHIN A REGIONAL SONGBIRD STAGING AREA

3.1 Introduction

During fall migration, songbirds must balance tradeoffs between energetic needs, survival, and progress to the wintering grounds. Optimal migration theory predicts that birds balance the costs and benefits of different migratory decisions to minimize total time spent on migration, energy expenditure, predation risk, or some combination of these factors (Alerstam and Lindström 1990, Åkesson and Hedenström 2000). Many songbirds minimize time by seeking out optimal stopover habitats and accumulating large departure fuel stores rapidly in order to fuel long-distance flights (Hedenström 2008), while others minimize risk or energy expenditure by carrying smaller fuel loads, stopping more frequently, and making shorter flights (Bolshakov et al. 2003, Åkesson et al. 2012, Tøttrup et al. 2012). The shorebird literature dubs these tactics respectively as ‘skip’ and ‘hop’ strategies, and outlines an additional strategy in which individuals accumulate extreme fat stores during lengthy staging events to fuel subsequent ‘jump’ flights >1000 km (Piersma 1987, Warnock 2010). Such a ‘jump’ strategy is congruent with a program of time minimization since birds quickly depart from low-quality areas to seek highly productive sites where they make prolonged stopovers (Gudmundsson et al. 1991, Warnock 2010).
Though staging activity is typically attributed to shorebirds and waterfowl (Dunne et al. 1982; Newton 2008) geolocator studies have recently reported passerines making stops ranging from 8 to 29 d (Heckscher et al. 2011, Stutchbury et al. 2011, Åkesson et al. 2012, Delmore et al. 2012, Tøttrup et al. 2012, Callo et al. 2013, Fraser et al. 2013, Jahn et al. 2013, Kristensen et al. 2013, Renfrew et al. 2013, Wolfe and Johnson 2015) that are analogous in length to staging events. Stops >7 d surpass the amount of time theoretically expected for migratory refueling under optimality models (Alerstam 1991), and have been classified as ‘prolonged stopover’- a behavior distinct from typical songbird stopover (reviewed in Mckinnon et al. 2013). Though it is still unclear why songbirds exhibit this behavior, these extended stops may be an adaptive strategy for accumulating large fat stores at food-rich sites to fuel lengthy migratory flights (Tøttrup et al. 2012, Callo et al. 2013), especially just before or after a barrier (Bayly et al. 2012, Delmore et al. 2012, Fraser et al. 2013). This behavior highlights that songbirds may be using resources differently across geographic regions. For songbirds that exhibit prolonged stopover, effective conservation may require identifying staging areas, and understanding behavioral patterns at these sites, because localized loss of staging habitats can pose a significant ecological bottleneck (Myers 1983, Buehler and Piersma 2008).

Although geolocators have revealed prolonged stops for multiple songbird species, understanding of stopover and movement behavior in these staging areas is still limited, since the coarse latitudinal precision of geolocators (~300-km) precludes study of fine-scale behavior (McKinnon et al. 2014, Deppe et al. 2015). Geolocator sample size restrictions have also limited study of how prolonged stopover differs between
individuals. However, inter and intra-specific differences in migratory strategy are probable given the well-documented variability in stopover behavior, migratory routes, and migratory timing between sexes, age groups (Morris et al. 1994, Rappole 2013, Seewagen et al. 2013, McKinnon et al. 2014, Woodworth et al. 2015, Crysler et al. 2016), and conspecifics from different breeding latitudes (Delmore et al. 2012, Fraser et al. 2013, La Sorte et al. 2015).

We used automated VHF radio telemetry along the eastern coast of North America to study the stopover and regional-scale movements of two songbird species that differ markedly in migratory strategy, route, and diet during fall migration. Red-eyed vireo (Vireo olivaceus; hereafter vireos) are regularly sited along most of the eastern U.S. coastline throughout the migratory period (Sullivan et al. 2009) and thus represent a skip or short jump migrant. In contrast, most blackpoll warblers (Setophaga striata; hereafter blackpolls) exhibit a jump strategy, concentrating in coastal areas of the northeastern US before making a 2500 km nonstop trans-Atlantic flight to South-American wintering grounds (DeLuca et al. 2015). Prolonged stopovers have been recorded for both species in the spring (Callo et al. 2013, DeLuca et al. 2015) but not in the fall. Though blackpolls are presumed to make lengthy stops in the northeastern U.S. to accrue fuel stores for their long trans-Atlantic flights, the duration of these stops remains unknown (Warnock 2010). We documented whether these species exhibited prolonged stopover (i.e. >7d; McKinnon et al. 2013) in the Gulf of Maine, and tested whether multiple aspects of migratory strategy - including fat stores at capture, number of stopover bouts, total time spent in
stopover, mean flight duration per stopover bout, and migration rate - differed by species, age groups, sex, capture date, or breeding latitude.

3.2 Methods

3.2.1 Data Collection

We captured blackpolls and vireos at the 888 ha Petit Manan Point unit of the Maine Coastal Islands National Wildlife Refuge (Fig. 3.1), located on a peninsula in Steuben Maine, United States (44.40846° N, 67.90502° W). The refuge unit is composed of mixed-deciduous forests containing mountain ash (*Sorbus Americana*), red maple (*Acer rubrum*), white (*Picea glauca*), red (*Picea rubens*) and black spruce (*P. mariana*), and an extensive shrub component including raspberry (*Rubus* spp.), alder (*Alnus* spp.), wild raisin (*Viburnum cassinoides*), bayberry (*Myrica* spp.), and blueberry (*Vaccinium* spp.).

We captured birds with passive mist-nets between September 6 and October 13, 2014. All birds were fitted with a USGS aluminum band, and measured for fat stores (0 = none; 0.5= trace; 1 = lining furculum; 2= filling furculum; 3 = mounded in furculum and beginning to cover abdomen; 4 = mounded on breast and sides of abdomen). We collected blood samples for DNA sexing, and feather samples for stable hydrogen isotope analysis (Wassenaar and Hobson 2001). The stable hydrogen isotope ratio (δ2H) of feathers collected during fall migration can be used as a proxy for breeding-latitude for blackpolls and vireos because both undertake a first prebasic molt on the breeding grounds that includes body feathers (Pyle 1997). Feathers were cleaned, weighed and
analyzed for $\delta^2$H at the Cornell University Stable Isotope Laboratory (COIL), Ithaca New York following the methods of (Wassenaar and Hobson 2003). We reported all nonexchangeable $\delta^2$H results for in the standard delta notation of units per mil ($\text{‰}$), normalized to the Vienna Standard Mean Ocean Water standard scale (VSMOW; Bowen 2010).

We attached coded VHF radio transmitters (Avian Nano Tag NTQB—2, Lotek Wireless, Newmarket, Canada; 40 d mean battery life) to 49 blackpolls and 47 Vireos with leg loop harnesses (Rappole et al. 1991). The total mass of the transmitters, including attachment materials (0.29 g) was <3% of body mass for all individuals. The transmitters emitted a signal at 166.38 MHz every 11-15 seconds, allowing us to identify and track all individuals at once. We tracked the birds using an array of receiver stations within the Motus Wildlife Tracking System that were deployed in coastal or island locations from Maryland to northern Nova Scotia (Taylor et al. 2017). Receiver stations consisted of 1-6 elevated Yagi antennas, and a datalogger (either Lotek; www.lotek.com, or a hand-made sensorgnome; www.sensorgnome.org) that recorded signal strength and GPS-synchronized time for each tag pulse detected by the antennas. Consistent with previous calibration studies (Mills et al. 2011, Taylor et al. 2011) we achieved a 12-km detection range for birds in flight.

3.2.2 Interpreting Telemetry Data

Movement tracks and behavioral classifications were previously derived for these data (Smetzer et al. in review; Chapter 2). Briefly, we used graphs of signal strength over
time to determine the time of final departure from the capture site for each bird (e.g. figure 2 Mills et al. 2011, Taylor et al. 2011). Since detection range is limited to 0.5 – 2 km for birds on the ground (Taylor et al. 2011), we assumed birds detected beyond the two capture site towers (i.e. in the ‘external array’) were in flight unless they exhibited a sustained signal at a telemetry station for >3 hr. Indeed, birds were detected at stations in the external array for either relatively brief (<100 min; n = 326; mean = 7.3 ± 13.0 min) or lengthy (>180 min; n = 24; mean = 116.3 ± 178.7 hr) durations. We thus used the duration of detections to determine whether individuals were detected at stations in the external array during a sustained ‘flyby’ or during arrival and departure flight from a nearly stopover site. For all flyby events, we summarized arrival time at the station as the time stamp of the maximum signal strength recorded at the station (Mitchell et al. 2015). We used the first and last detections at a telemetry station as the arrival and departure time if a bird was deemed to stop at or near the station. Finally, we summarized the spatial midpoint of each bird’s detections at an external array station as a single point 6 km from the station along the bearing of the antenna that recorded the greatest signal strength value (Mitchell et al. 2015). We chose 6 km because it is half the detection range for a bird aloft, and used the bearing of the antenna with the greatest signal strength because the power received by our directional Yagi antennas is maximized along the beam (Friis 1946, Shaw 2013).

We calculated the groundspeed for every segment of every bird’s movement track. We classified segments that were ≥1 m/s, and less than the duration of a single night of flight (<525 min) as a ‘sustained migratory flight’. There were clear thresholds in
the data that supported this classification (Smetzer et al. in review). We labeled the remaining track segments as ‘slow movements’ as birds likely halted movement at some point during these track segments. The result was a time-referenced movement track for each bird with a behavioral estimate for each segment of the route.

We used the movement tracks to generate the stopover and movement metrics we considered in statistical analyses (Table 3.1). We calculated the total number of stopover bouts for each bird by summing the number of distinct stopovers (including stopover at the capture site and periods of >3 hr of detection at any other telemetry station) and track segments that were slow movements. We quantified the total time spent in stopover throughout the entire study area by individual by summing the duration that an individual was detected at the capture site and the duration of all slow movement track segments. We also calculated total stopover duration specifically within the Gulf of Maine to assess whether individuals exhibited prolonged stopover (i.e. >7 d; McKinnon et al. 2013). All stopover values are minimum estimates because we do not know how long birds were at the capture site before we outfitted them with radio transmitters.

For each bird detected beyond the capture site (40 blackpolls and 37 vireos), we calculated the distance of each sustained migratory flight recorded between telemetry stations. To derive a metric that represents the ratio of flight to stopover, we also calculated the mean distance travelled per stopover bout (i.e. total distance over which we tracked a bird divided by the total number of estimated stops). We determined overall regional movement rates using the great-circle distance between the banding site and the last location estimate for the individual and the duration between capture and last
detection. This metric can be indicative of regional prolonged stopover activity, since individuals engaging in prolonged stopovers can exhibit markedly slow movement rates in some portions of their migratory routes, and rapid movement in other regions (Callo et al. 2013, Fraser et al. 2013).

3.2.3 Statistical Analyses

We used principle components analysis on a suite of migration strategy metrics, including fat stores at capture, total number of stopovers, mean duration of individual stopover bouts, maximum duration of individual stopover bouts, total time spent in stopover, flight distance per stopover, and movement rate to extract the dominant gradients of variation in migration strategy across individuals. We transformed metrics as needed to improve normality, scaled all data to a mean of 0 and SD of 1, and reported only principle components with loadings >0.4.

We established a small set of candidate models for each response variable (Table 3.1). We included age, capture date, sex, and δ² H value (as a proxy for breeding latitude and migration distance) in interspecific models and incorporated quadratic terms when model diagnostics indicated they were appropriate. We ran separate models to test whether the response variables differed between the species. We used ordered logistic regression (cumulative link models) to test whether fat stores at the time of capture (0 - 4) were influenced by the covariates. Most birds remained at the capture site for >2 d, and some were tracked for as many as 38 days. We thus did not include fat as a covariate for other response variables because fat at capture did not necessarily represent body condition at departure. We related covariates to number of stopover bouts using
generalized linear models (glm) with a Poisson error distributions and to total stopover duration using general linear models. We transformed total stopover duration in intraspecific models to improve the normality of residuals, and used generalized least squared models with a variance term for species in interspecific models. We employed generalized linear models with Gamma errors to model flight distance per stop and movement rate as these metrics were greater than zero and right-skewed.

We used Akaike’s information criterion corrected for small sample size to rank the candidate models in each modeling exercise (AICc; Burnham and Anderson 2002). We considered a variable as strongly supported if 95% or 99% confidence intervals did not overlap with zero, and important if 90% confidence intervals excluded zero. We reported the parameter estimates ± 1 SE for each model within 2 AICc of the top model, as well as the AICc, Δ AICc, Akaike weight (ωi), with factors stated as vireos relative to blackpolls, and adults relative to juveniles. We reported all results as mean ± SE unless otherwise noted. All analyses were completed in the R statistical environment version 3.3.1 (R Core Team 2016), and multivariate analyses were conducted using the ‘vegan’ package (Oksanen et al. 2016).

3.3 Results

Three out of 49 blackpolls and 6 out of 47 vireos were not detected beyond the capture site, and did not exhibit a clear departure flight. These individuals were likely depredated, or lost their tag and were excluded from all analyses. All vireos and 74% of blackpolls were juveniles. Blackpoll δ² H values ranged from -177.71 to -76.06‰ and vireo from -111.97 to -57.24 ‰, with lower δ² H values indicating a more northern/
western breeding area. These δ²H values indicate likely breeding origins ranging from the eastern Maritime provinces for both species to as far away as northwestern Canada and possibly Alaska for blackpolls, and as far west as central Quebec, western Ontario, and southeastern Manitoba for vireos (Fig. 3.2). We were unable to calculate movement rate or mean flight distance per stopover for 6 blackpolls and 4 vireos that were not re-detected beyond the capture site.

A Monte Carlo permutation test indicated that the correlation structure of the first two retained principle components was statistically significant ($P < 0.001$). The first principal component (PC1; eigenvalue = 3.1) explained 44% of the variance and was positively related to movement rate (0.49) and negatively correlated with number or stops (-0.59), total time spent in stopover (-0.97), mean duration of stopover bouts (-0.82), and maximum duration of stopover bout (-0.95). The second principle component (PC2; eigenvalue = 1.6) explained 23% of the variance and was negatively correlated with movement rate (-0.74), and flight distance per stopover (-0.93). Thus, PC1 largely represented stopover behavior, and PC2 movement behavior. Blackpolls varied more across PC1 (stopover behavior) whereas vireos varied more across PC2 (flight behavior; Fig. 3.3).

The fat stores at the time of capture did not differ between species, but varied significantly by capture date for blackpolls, and moderately by breeding origin for vireos. The mean fat score at capture did not differ significantly between blackpolls ($1.27 \pm 0.91$; range 0.5-4) and vireos ($1.26 \pm 0.70$; range 0-3; ordered logistic regression; $\beta = 0.28 \pm 0.41; P = 0.50$; Table 3.3). Blackpolls captured later in the season carried significantly
more fat stores than earlier conspecifics (ordered logistic regression; $\beta = 0.32 \pm 0.10; P < 0.001$; Table 3.2). Vireos from closer breeding origins exhibited significantly greater fat stores than more distant conspecifics (ordered logistic regression; $\beta = 0.06 \pm 0.03; P = 0.05$; Table 3.3); however, the null was within 1.17 AICc of this model indicating model uncertainty.

The number of stopover bouts and total time spent on stopover differed significantly between the species, and by breeding origin for blackpolls. We recorded at least one stopover bout after departure from the capture site for 83% of blackpolls and 56% of vireos. Individual stopover bouts ranged from less than a single day to 25 d for blackpolls ($5.3 \pm 6.3$ d), and from less than a single day to 14 d for vireos ($4.1 \pm 3.4$ d).

Individual blackpolls made $2.84 \pm 1.21$ stopover bouts (range 1-6), and spent $15.1 \pm 10.6$ d on stopover throughout the study area (range $0.5 – 37.9$). Individual vireos made $2.0 \pm 1.1$ stopover bouts (range 1-5), and spent $8.2 \pm 5.5$ d in stopover (range $0.3 – 20.1$).

Blackpolls made significantly more stopover bouts (Poisson glm; $\beta = -0.37 \pm 0.14; P = 0.01$; Supplemental Material Table S3), and spent significantly more total time in stopover than vireos (generalized least squares model; $\beta = -2.74 \pm 0.74; P < 0.001$; Table 3.4). The latter model was >10 AICc of the null indicating high confidence in this result. Blackpolls from more southern breeding origins made significantly more stopover bouts (Poisson glm; $\beta = 0.01 \pm 0.003; P = 0.05$; Supplemental Material Table S1), and spent significantly more total time in stopover than their northern conspecifics; however, the null was within 1.40 AICc of the top model for number of stopover bouts, indicating model uncertainty (general linear model; $\beta = 0.01 \pm 0.01; P = 0.04$; Table 3.2). We found
no compelling evidence that number of stopover bouts or total stopover duration was related to sex, breeding origin, or capture date for vireos as the null was the most strongly supported model for both response variables (Table 3.3).

Both species exhibited prolonged stopovers in the Gulf of Maine. The average total stopover duration in the region (i.e. excluding stopovers Cape Cod or south) was 14.4 ± 10.5 d for blackpolls and 7.6 ± 4.9 d for vireos. Fifty nine percent of blackpolls and 35% of vireos made at least one individual stopover in the Gulf of Maine that exceeded 7 d. Furthermore, regional movement rate was 0.69 ± 0.63 km/day for blackpolls (n = 40) and 2.09 ± 2.72 km/day for vireos (n = 37), much lower than is typically reported for overall migration rates of passerines.

Movement rates differed significantly between the two species and by capture date for vireos. Blackpoll movement rates were significantly slower than those of vireos (Gamma glm; β = 1.10 ± 0.25, P < 0.001). The model comparing migration rates between species was > 10 AICc from the null, indicating high confidence in this result. To understand these results better, we also made a post-hoc comparison of the geographic distance and time span over which we tracked each species using Wilcoxon rank sum tests. The distance over which we tracked blackpolls (261.6 ± 222.5 km; range 0 - 806.4) and vireos (312.9 ± 316.4 km; range 0 – 1060) was similar (Wilcox test; W = 682.5, P = 0.59). However, we detected blackpolls in the study region for nearly twice as much time (16.3 ± 10.6 days; range 0.5 - 38.3) as vireos (8.0 ± 5.7 days; range 0.4 - 20.8; Wilcox test; W = 1330; P < 0.001). We found no compelling evidence that movement rate was related to age, sex, breeding origin or capture date for blackpolls, as the null model was
the most strongly supported (Table 3.2). In contrast, vireos captured later in the season exhibited significantly more rapid movement rates than earlier conspecifics (Gamma glm; \( \beta = -0.05 \pm 0.01, P < 0.001 \)).

Individuals of both species traversed the study area in multiple short flights rather than in a single sustained migratory movement; however, this behavior was more common in blackpolls than in vireos and in earlier vireo migrants relative to later conspecifics. The median distance of the recorded sustained migratory flights was 42.73 km (maximum 275.9) for blackpolls \((n = 40)\) and 147.4 km (maximum 761.2) for vireos \((n = 37)\). The ratio of flight distance per stopover bout was greater for vireos \((153.67 \pm 150.49 \text{ km/stop})\) than blackpolls \((85.07 \pm 72.11 \text{ km/stop}; \text{Gamma glm}; \beta = 0.51 \pm 0.21; P = 0.02; \text{Supplemental Material Table S3})\). We found no compelling evidence that flight distance per stopover bout was related to capture date, age, sex, or breeding origin for blackpolls, as the null model was the most strongly supported (Table 3.2). Vireos captured later in the migratory period exhibited significantly higher ratios of flight distances per stopover bout than earlier conspecifics (Gamma glm; \( \beta = 5.49 \pm 2.12; P = 0.01; \text{Table 3.3})\). The top model also included a negative quadratic term for capture date indicating that the ratio of flight distance per stop increased more rapidly as the season progressed (Gamma glm; \( \beta = -0.01 \pm 0.004; P = 0.01 \)).

3.4 Discussion

Using a regional array of automated radio telemetry receiving stations that extended from northern Nova Scotia to Maryland, we confirmed decade-long predictions
(Nisbet et al. 1963, 1995; Nisbet 1970) that blackpolls commonly exhibit prolonged stopover in the Gulf of Maine during fall migration, and provide the first evidence of this behavior for Red-eyed Vireos in the fall. The stopover durations we observed were consistent with geolocator studies documenting prolonged stopover for Purple Martins (*Progne subis*) in the fall (16 ± 9 d; Fraser et al. 2013), Red-eyed Vireos in the spring (19 ± 5 d; Callo et al. 2013), and Swainson’s Thrushes (*Catharus ustulatus*) in the spring (8-29 d) and fall (11-29 d; Delmore et al. 2012). Blackpolls and vireos both also exhibited movement rates that were markedly lower than those typically reported for long-distance migrants from banding (60 km/d; Ellegren 1993) or geolocator studies (68-473 km/day; Fraser et al. 2013) suggesting both species predominantly engaged in stopover in the tracking region. Although prolonged stopover may be analogous to the well-studied staging behavior of shorebirds and waterfowl, it is still is poorly understood for songbirds. By studying prolonged stopover at a finer scale than previously possible, our work provides a first glimpse of the regional-scale stopover ecology of songbirds within the Gulf of Maine staging area.

Our comparison of regional-scale movements of blackpolls and vireos provides clear evidence that prolonged stopover is significantly more common and pronounced in an extreme jump strategist. Blackpolls spent nearly twice as much time in the tracking region and in actual stopover than vireos, and nearly twice as many blackpolls exhibited stops >7 d in the Gulf of Maine. Blackpolls likely exhibited prolonged stopover more frequently and for longer durations than vireos because their subsequent migratory movements are typically much longer than those of vireos. Blackpolls deposit more fat
than congeners in the fall (Nisbet et al. 1963), often nearly doubling their mass, primarily with fat deposits. Furthermore, many long-distance migrants increase their digestive capacity to facilitate fat deposition, but subsequently re-absorb digestive organs and non-essential flight muscles and increase pectoral and heart muscle before flight, making longer but less frequent stopovers advantageous (Piersma and Gill 1998, Karasov and Pinshow 2000). Prolonged stopovers can thus lower the overall physiological cost of endurance flights (Schwilch et al. 2002), an advantage that is presumably more beneficial to blackpolls than vireos. Though prolonged stopover has also been linked to molt-migration in some species (Barry et al. 2009, Jahn et al. 2013) this is unlikely in our study as both species complete molt on the breeding grounds (Pyle 1997).

Dietary differences may also drive some of the migratory differences we observed between blackpolls and vireos. Vireos are highly frugivorous during the fall migratory period, whereas blackpolls appear to be more omnivorous (Parrish 1997, Smith and McWilliams 2010). Highly frugivorous species tend to exhibit greater fuel-deposition rates those with a more strictly insectivorous or omnivorous diet (Bairlein and Gwinner 1994, Smith et al. 2007, Smith and McWilliams 2010). Thus, a greater capacity for rapid fat mobilization may have partially facilitated vireos making shorter less frequent stopovers, and longer flight bouts between stopover events. The distribution and predictability of food resources can also greatly influence migration strategy and how birds structure their periods of stopover and flight (Schaub and Jenni 2000). Though we did not measure of food resources in the study area, it is conceivable that blackpolls and
vireos experience differences in the distribution and predictability of food, since insects typically decline earlier in the fall than fruits (La Sorte et al. 2015).

By studying prolonged stopover at a finer scale than has been previously possible, this study is the first to demonstrate that this behavior can include a single protracted stopover event or multiple relocations within an extensive geographic area. Though we tracked blackpolls in a region where they were largely engaged in prolonged stopover, this activity was often characterized by frequent short flights, and multiple stopover events. Long-distance migrants are thought to actively seek out stopover sites that offer high refueling opportunities with limited tradeoffs of predator vigilance (McCabe and Olsen 2015a), particularly for extended stopovers (Warnock 2010). However, finding high-quality sites can involve fine-tuning habitat choices through repeated movements (Aborn and Moore 1997; Chernetsov 2005, 2006; Taylor et al. 2011). Making short and frequent movements in search of prime stopover habitat could represent an optimal short-term strategy to avoid risk and minimize energy expenditure during extended stopover, especially in coastal landscapes where migrants and their aerial predators are heavily concentrated (Richardson 1978, Åkesson 1993, Ydenberg et al. 2007). This behavior is analogous to a hop strategy that minimizes energy expenditure during flight (Alerstam and Lindström 1990, Hedenström and Alerstam 1992) and reduces risk by allowing greater vigilance during foraging (McCabe and Olsen 2015a) and easier predator evasion (Hedenström and Alerstam 1992, Kullberg et al. 1996). The physiological changes required for hyperphagia and extreme fat storage also take significant time and energy (Newton 2008, Rappole 2013), so seeking optimal habitats for fuel accumulation may
ultimately also save time and energy. Migration strategy may thus be scale dependent: within an overall jump program of time minimization, blackpolls may exhibit a short-term hop strategy of energy minimization while seeking optimal stopover habitats.

Our results also suggest that the tendency for energy and risk minimization during prolonged staging events may be more pronounced for southeastern populations of blackpolls, compared to more northwestern populations. Blackpolls from more distant breeding areas exhibited fewer total stopovers, which may indicate they made less exploratory movements. These more distant breeders may be willing to accept or ‘settle’ for riskier foraging situations, as has been seen previously for migrants that travel greater distances and have higher energetic demands (Metcalf and Furness 2006, Pomeroy et al. 2008, McCabe and Olsen 2015a). Similarly, that blackpolls from more distant breeding grounds spent less total time on stopover could reflect lower predator vigilance, which has been seen in energetically stressed individuals (Lima 1998, Cimprich and Moore 2006). These patterns are all consistent with the expectation that birds from more distant breeding areas are under greater selection for time minimization (La Sorte et al. 2015).

Later blackpolls also exhibited a tendency toward time minimization in that they carried greater fat stores than earlier conspecifics. This finding is in line with previous studies (Nisbet et al. 1963, Morris et al. 2015). Although rapidly accruing and carrying large fuel stores can be energetically costly (Alerstam and Lindström 1990, Hedenström and Alerstam 1997) and risky in terms of predation (Hedenström and Alerstam 1992, Kullberg et al. 1996, Metcalfe and Furness 2006), it may be an optimal choice for later
migrants facing declining food stores, temperatures, and day lengths (Schaub and Jenni 2000, La Sorte et al. 2015). A seasonal increase in fat stores may be due to seasonal intensification of fuel deposition rates (Lindström et al. 1994, Schaub and Jenni 2000, Dänhardt and Lindström 2001, Leppold 2016), and more supportive tailwinds later in the fall (Koch et al. 2006, Archer and Caldeira 2008, Pena-Ortiz et al. 2013). We found no indication that later blackpolls made longer flights per stopover, so it is unlikely that they carried larger fuel stores simply because they arrived by shorter flights (and burned less fuel). However, vireos did notably show a seasonal decrease in fat stores and a seasonal increase in flight distance per stopover, indicating that later vireos may simply have had lower fat stores at capture because they drained more fuel stores making longer flights to reach the capture site.

Later vireos also exhibited traits of time minimization, including greater migration rates and flight distances per stopover throughout the season. A seasonal increase in migration rate has been seen in several other long-distance migrants, and is thought to represent selection for time minimization (Ellegren 1993, Fransson 1995). A seasonal increase in the ratio of flight distance to stopover may be related to a corresponding seasonal increase in 1) flight speeds, 2) the availability and/or increased selection of supportive tailwinds, 3) decision to engage in flight for a greater portion of the night, or 4) a combination of these factors (Alerstam and Lindström 1990, Ellegren 1993). Later conspecifics of this same sample of vireos also departed from the capture site in an over-water trajectory more frequently than earlier individuals, indicating a time-minimizing tendency for more direct, and rapid travel (Smetzer et al. 2017; Chapter 2).
3.4.1 Conservation Implications

Our evidence that the Gulf of Maine serves as a staging resource has important conservation implications, particularly for blackpolls. Stopover resources can influence migratory pace (Wikelski et al. 2003, Åkesson et al. 2012), energetic condition (Moore et al. 1995), and condition in subsequent life stages (Runge and Marra 2005, Smith and Moore 2005, Newton 2006, Norris and Taylor 2006). Staging areas that support large concentrations of birds in making flights over ecological barriers are particularly important and represent ecological bottlenecks where localized habitat loss can have population-level consequences (Myers 1983, Warnock 2010). Blackpolls may therefore be particularly vulnerable to localized habitat loss since falling short on energetic reserves during overwater flight can have dire consequences and population-level effects (Butler 2000). Furthermore, as our isotope results show, localized habitat losses could affect much of the breeding population. Blackpoll warblers have already experienced a global population decline of 92% in the last 40 years, and populations are projected to drop by another 50% within the next 16 years if current trends continue (Rosenberg et al. 2016). Protecting Gulf of Maine staging areas may therefore be an important conservation priority for this species.

That some individuals made short, frequent movements in the region, and even during prolonged stopover also has important conservation implications because flight behavior can have a large influence on the degree to which birds are exposed to collision hazards like communication towers and wind turbines (Drewitt and Langston 2006a, Minerals Management Service 2009, Langston 2013). These structures can pose a
significant threat to migrant songbirds (Crawford and Engstrom 2001, Hüppop et al. 2006, Manville 2009, Longcore et al. 2012, Loss et al. 2013), particularly during takeoffs, landings, and short flights (Drewitt and Langston 2006a). In turn, predictable differences in behavior – as was observed in this study – can lead to systematic differences in exposure to risk and possible implications for population dynamics (Cristol et al. 1999, Mehlman et al. 2005, Longcore and Smith 2013).

Finally, our study provides further evidence that migrants that depart later, or travel from more distant breeding areas via longer migratory routes are more strongly adapted for time minimization than earlier/closer conspecifics. This in turn, suggests that some of the individuals reliant on this regional stopover resource may be more seriously affected by anthropogenic stressors in the region than other conspecifics. Birds with significant time and energy constraints have smaller ‘margins of safety’ to safeguard against the risks of poor weather, or low food supplies and may need to sacrifice safety to try to ‘catch up’. (Faaborg et al. 2010a). These individuals may therefore be more affected by habitat loss, and shifts in polar-front jet stream patterns and plant and insect phenology that are accompanying climate change (Cramer et al. 2001, Archer and Caldeira 2008, Miller-Rushing et al. 2008, Francis and Vavrus 2012, Pena-Ortiz et al. 2013). Exacerbating this, migrants from more distant breeding areas may also have a lower capacity to adapt to rapid climatic change due to lower behavioral plasticity, genetic variability, or both (Cox 2010). Experimental study of phenotypic plasticity in the Gulf of Maine may be an important conservation priority, especially for blackpolls that are facing rapid and extreme populations declines.
Table 3.1. Candidate models considered in analyses relating age, capture date (day), sex, δ² H values, fat stores, and species to movement metrics.

<table>
<thead>
<tr>
<th>Response variables</th>
<th>Fat stores</th>
<th>Number of stopover bouts</th>
<th>Total duration of stopovers</th>
<th>Flight distance per stopover</th>
<th>Migration rate</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intraspecific</td>
<td>age*</td>
<td>age*</td>
<td>age*</td>
<td>age*</td>
<td>age*</td>
</tr>
<tr>
<td>models</td>
<td>sex</td>
<td>sex</td>
<td>sex</td>
<td>sex</td>
<td>sex</td>
</tr>
<tr>
<td></td>
<td>δ³ H</td>
<td>δ² H</td>
<td>δ² H</td>
<td>δ² H</td>
<td>δ² H</td>
</tr>
<tr>
<td></td>
<td>day</td>
<td>day</td>
<td>day</td>
<td>day x day² **</td>
<td>day</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Interspecific</td>
<td>species</td>
<td>species</td>
<td>species</td>
<td>species</td>
<td>species</td>
</tr>
<tr>
<td>models</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

NOTE. —
* Only Blackpolls, as all Vireos were hatch-year individuals.
** Quadratic term improved model residuals and was only included for Vireos.
Table 3.2. Models relating migratory response variables to age (juveniles relative to adults) capture date (Day), stable isotope values ($\delta^2$H) and sex (males relative to females) of Blackpoll Warblers (*Setophaga striata*).

<table>
<thead>
<tr>
<th>Response Variable</th>
<th>Models</th>
<th>Age (HY)</th>
<th>Day</th>
<th>$\delta^2$ H</th>
<th>Sex (M)</th>
<th>$\Delta$ AIC$_c$</th>
<th>$\omega_i$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fat at capture</td>
<td>day</td>
<td></td>
<td>0.32 ±0.10 **</td>
<td></td>
<td></td>
<td>0.00</td>
<td>0.99</td>
</tr>
<tr>
<td>Number of stopovers</td>
<td>$\delta^2$ H</td>
<td></td>
<td>0.01 ± 0.003 **</td>
<td></td>
<td></td>
<td>0.00</td>
<td>0.50</td>
</tr>
<tr>
<td></td>
<td>null</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>1.40</td>
<td>0.25</td>
</tr>
<tr>
<td>Total stopover Duration</td>
<td>$\delta^2$ H</td>
<td></td>
<td>0.01 ± 0.01 **</td>
<td></td>
<td></td>
<td>0.00</td>
<td>0.60</td>
</tr>
<tr>
<td>Flight distance per stopover</td>
<td>null</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.00</td>
<td>0.33</td>
</tr>
<tr>
<td></td>
<td>sex</td>
<td></td>
<td></td>
<td>0.37 ± 0.28</td>
<td></td>
<td>0.82</td>
<td>0.22</td>
</tr>
<tr>
<td></td>
<td>day</td>
<td></td>
<td></td>
<td>-0.04 ± 0.04</td>
<td></td>
<td>1.54</td>
<td>0.15</td>
</tr>
<tr>
<td></td>
<td>$\delta^2$ H</td>
<td></td>
<td></td>
<td>-0.01 ± 0.01</td>
<td></td>
<td>1.58</td>
<td>0.15</td>
</tr>
<tr>
<td></td>
<td>age</td>
<td></td>
<td></td>
<td>-0.25 ± 0.32</td>
<td></td>
<td>1.80</td>
<td>0.14</td>
</tr>
<tr>
<td>Regional movement rate</td>
<td>null</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.00</td>
<td>0.35</td>
</tr>
<tr>
<td></td>
<td>sex</td>
<td></td>
<td></td>
<td>0.29 ± 0.30</td>
<td></td>
<td>1.33</td>
<td>0.18</td>
</tr>
<tr>
<td></td>
<td>$\delta^2$ H</td>
<td></td>
<td></td>
<td>-0.01 ± 0.01</td>
<td></td>
<td>1.53</td>
<td>0.16</td>
</tr>
</tbody>
</table>

NOTE. — Only candidate models with $\Delta$ AIC$_c$ ≤ 2 are shown. Beta estimates ± 1 standard error are shown and represent males relative to females, and juveniles relative to adults. AIC$_c$ = Akaike’s information criterion corrected for small sample sizes, $\Delta$ AIC$_c$ = the difference between the AIC$_c$ of the top-ranked model and the corresponding model, and $\omega_i$ = Akaike Weight. Data are from automated telemetry conducted in the Gulf of Maine in fall, 2014.

** Parameter estimates have 95% confidence intervals that do not include zero.

*** Parameter estimates have 99% confidence intervals that do not contain zero.
Table 3.3. Models relating migratory response variables to capture date (Day) stable isotope values (δ²H) and sex of Red-eyed Vireo (Vireo olivaceus).

<table>
<thead>
<tr>
<th>Response Variable</th>
<th>Models</th>
<th>Day</th>
<th>Day²</th>
<th>δ²H</th>
<th>Sex (M)</th>
<th>Δ AICc</th>
<th>ωᵢ</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fat at capture</td>
<td>δ²H</td>
<td></td>
<td></td>
<td>0.06 ± 0.03 **</td>
<td>0.00</td>
<td>1.17</td>
<td>0.51</td>
</tr>
<tr>
<td></td>
<td>null</td>
<td></td>
<td></td>
<td></td>
<td>0.00</td>
<td>0.28</td>
<td></td>
</tr>
<tr>
<td>Number of stopovers</td>
<td>null</td>
<td></td>
<td></td>
<td>0.00</td>
<td>0.00</td>
<td>0.21</td>
<td>0.37</td>
</tr>
<tr>
<td></td>
<td>day</td>
<td></td>
<td></td>
<td>-0.03 ± 0.02</td>
<td>0.21</td>
<td>0.34</td>
<td></td>
</tr>
<tr>
<td></td>
<td>sex</td>
<td></td>
<td></td>
<td>0.17 ± 0.23</td>
<td>1.60</td>
<td>0.17</td>
<td></td>
</tr>
<tr>
<td>Total stopover duration</td>
<td>null</td>
<td></td>
<td></td>
<td>0.00</td>
<td>0.00</td>
<td>0.41</td>
<td></td>
</tr>
<tr>
<td></td>
<td>sex</td>
<td></td>
<td></td>
<td>0.71 ± 0.69</td>
<td>1.23</td>
<td>0.22</td>
<td></td>
</tr>
<tr>
<td></td>
<td>day</td>
<td></td>
<td></td>
<td>-0.05 ± 0.06</td>
<td>1.31</td>
<td>0.21</td>
<td></td>
</tr>
<tr>
<td></td>
<td>δ²H</td>
<td></td>
<td></td>
<td>-0.02 ± 0.03</td>
<td>1.88</td>
<td>0.16</td>
<td></td>
</tr>
<tr>
<td>Flight distance per stopover</td>
<td>day +</td>
<td></td>
<td></td>
<td>5.49 ± 2.13 **</td>
<td>0.00</td>
<td>0.86</td>
<td></td>
</tr>
<tr>
<td></td>
<td>day²</td>
<td></td>
<td></td>
<td>-0.01 ± 0.004 **</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Regional movement rate</td>
<td>day</td>
<td></td>
<td></td>
<td>-0.05 ± 0.01 ***</td>
<td>0.00</td>
<td>0.97</td>
<td></td>
</tr>
</tbody>
</table>

NOTE. — Only candidate models with Δ AICc ≤ 2 are shown. Beta estimates ± 1 standard error are shown, and represent males relative to females. AICc = Akaike’s information criterion corrected for small sample sizes, Δ AICc = the difference between the AICc of the top-ranked model and the corresponding model, and ωᵢ = Akaike Weight. Data are from automated telemetry conducted in the Gulf of Maine in fall, 2014.

** Parameter estimates have 95% confidence intervals that do not include zero.

*** Parameter estimates have 99% confidence intervals that do not contain zero.
Table 3.4. Results of models comparing migration metrics between Blackpoll Warblers (*Setophaga striata*) and Red-eyed Vireos (*Vireo olivaceus*).

<table>
<thead>
<tr>
<th>Response Variable</th>
<th>Models</th>
<th>Species (REVI)</th>
<th>Δ AIC&lt;sub&gt;c&lt;/sub&gt;</th>
<th>ω&lt;sub&gt;i&lt;/sub&gt;</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fat at capture</td>
<td>null</td>
<td></td>
<td>0.00</td>
<td>0.72</td>
</tr>
<tr>
<td></td>
<td>species</td>
<td>0.28 ± 0.41</td>
<td>1.85</td>
<td>0.28</td>
</tr>
<tr>
<td>Number of stopovers</td>
<td>species</td>
<td>-0.37 ± 0.14 **</td>
<td>0.00</td>
<td>0.92</td>
</tr>
<tr>
<td>Total stopover duration</td>
<td>species</td>
<td>-2.74 ± 0.74 ***</td>
<td>0.00</td>
<td>1.00</td>
</tr>
<tr>
<td>Flight distance per stopover</td>
<td>species</td>
<td>0.51 ± 0.21 **</td>
<td>0.00</td>
<td>0.86</td>
</tr>
<tr>
<td>Migration rate</td>
<td>species</td>
<td>1.10 ± 0.25 ***</td>
<td>0.00</td>
<td>1.00</td>
</tr>
</tbody>
</table>

NOTE. — Only candidate models with Δ AIC<sub>c</sub> ≤ 2 are shown. Beta estimates ± 1 standard error are shown, and represent vireos relative to blackpolls. AIC<sub>c</sub> = Akaike’s information criterion corrected for small sample sizes, Δ AIC<sub>c</sub> = the difference between the AIC<sub>c</sub> of the top-ranked model and the corresponding model, and ω<sub>i</sub> = Akaike Weight. Data are from automated telemetry conducted in the Gulf of Maine in fall, 2014.

** Parameter estimates have 95% confidence intervals that do not include zero.

*** Parameter estimates have 99% confidence intervals that do not contain zero.
Figure 3.1. (A) Map of automated telemetry stations used to track radio-tagged Blackpoll Warbler *Setophaga striata* and Red-eyed Vireo *Vireo olivaceus* in fall 2014. Points show receiver sites. (B) Inset map of the automated telemetry receivers at and near the capture site (red). Solid black lines show the orientation and approximate detection range (12 km) of telemetry receivers. Adapted from Smetzer et al. (2017; Chapter 2).
Figure 3.2. Map of breeding-season feather isotope content in North America for non-ground foraging, long-distance migrants (from Smetzer et al. 2017; Chapter 2). The figure was generated by translating the precipitation map (δ^2H_p) of Bowen et al. (2005) from δ^2H_p into δ^2H feather values using the algorithm from Hobson et al. (2012).
Figure 3.3. Principle components analysis of migration metrics derived from automated VHF radio telemetry conducted on Blackpoll Warblers (*Setophaga striata*) and Red-eyed Vireos (*Vireo olivaceus*) during fall 2014 in the Gulf of Maine. Migration metrics include number of stopovers (num stops), total time spent in stopover (total stop time), mean duration of individual stopover bouts (mean stop time), maximum duration of individual stopover bouts (shown with a green dot), fat score at capture, migration rate (mig rate), and flight distance per stopover (flight dist).
CHAPTER 4

COLONY ATTENDANCE PATTERNS OF COMMON (STERNA HIRUNDO) AND ARCTIC TERNs (STERNA PARADISAEA) IN THE GULF OF MAINE AND IMPLICATIONS FOR OFFSHORE WIND ENERGY DEVELOPMENT

4.1 Introduction

Offshore wind energy development (OWED) is a critical component of renewable energy growth; however, environmental concerns pose a key barrier to implementation in the US (Firestone and Kempton 2007). Birds are thought to be one of the taxa most severely impacted by OWED (Garthe and Hüppop 2004). Wind farms can adversely affect birds directly through collision mortality and indirectly via diversion of flight paths (i.e. ‘barrier effects’), displacement from breeding and foraging habitats, and alteration of foraging habits and prey (Exo et al. 2003, Garthe and Hüppop 2004, Drewitt and Langston 2006b, Masden et al. 2010, Furness et al. 2013). Marine birds are thought to be particularly vulnerable to population-level effects from collision mortality or indirect adverse effects of OWED because they are long-lived, have relatively delayed sexual maturity, and often exhibit low reproductive success (Sæther and Bakke 2000, Desholm 2009). Predicting the adverse effects of OWED on seabirds is therefore an important priority in the sustainable and timely expansion of renewable energy (Goodale and Milman 2016).

Unfortunately, estimating the degree to which marine birds are exposed to OWED collision hazards remains a significant challenge because basic flight behavior
information is lacking for many species (Furness et al. 2013). Several aspects of flight behavior can increase exposure to OWED hazards, but are difficult to quantify for small marine birds (Drewitt and Langston 2006b). For instance, daily amount of time spent in flight can influence collision exposure; yet, collision vulnerability assessments have historically been limited to qualitative scoring for flight activity for many species (Garthe and Hüppop 2004, Furness et al. 2013). Nocturnal activity also increases collision vulnerability, since detection and avoidance of structures is more difficult in darkness or twilight (Drewitt and Langston 2006b, 2008). However, degree of nocturnal activity is often unknown for small marine birds because they are difficult to track or monitor at night (Bluso-Demers et al. 2010).

Understanding how OWED may adversely affect seabirds through displacement or barrier effects is also challenging, and requires species-specific data on energetic and time constraints in foraging, especially during the breeding season (Scott et al. 2014). OWED can increase daily energy expenditure if birds must regularly detour around wind farms, particularly for species that make several foraging trips per day and spend significant time in flight (Fox et al. 2006, Masden et al. 2010, Langston 2013, Scott et al. 2014). In turn, increases in energy expenditure and commuting distance can result in poor adult body condition (Becker and Fink 1985, Wendeln 1997), longer intervals between chick provisioning, selection of lower quality prey (Frank 1992), and reduced growth rate and survival of chicks (Dänhardt and Becker 2011).

As OWED progresses in US waters, developers and wildlife agencies will need to evaluate the degree to which it may affect protected seabird populations. The Gulf of
Maine has been identified as an outstanding location for offshore wind development by the U.S. Department of Energy, based on its excellent wind resource (Schwartz et al. 2010). However, this region hosts protected seabird species, including Arctic Terns (*Sterna paradisaea*) that are listed as threatened in Maine and Common Terns (*S. hirundo*), a species of Special Concern in Maine. Despite active predator control and vegetation management in Maine, (and considerable recovery since the 19th century), adults have been unable to adequately provision chicks in recent years, and both species have experienced 40-50% declines in productivity (US Fish and Wildlife Service 2012). The number of nesting Arctic Terns has also decreased significantly in the last five years (US Fish and Wildlife Service 2006, US Fish and Wildlife Service 2008), with Gulf of Maine populations showing a 44% decrease in the last decade (USFWS unpublished data). Arctic Terns in the Gulf of Maine are also particularly susceptible to habitat displacement from OWED as they have a high reliance on specific foraging grounds, and over 95% of individuals currently breed on only four islands. These trends highlight an urgent need to identify the limiting factors in for these species in the region, and to understand the degree to which OWED may exacerbate existing challenges.

OWED in the Atlantic is expected to pose a risk to tern species during the breeding, staging and migratory periods (Burger et al. 2011). Terns have displayed little avoidance of wind turbines (Everaert and Stienen 2007, Langston 2013), and have increased activity at some facilities post-construction (Boesen and Andersen 2005). Though terns are agile flyers, and typically forage near the water surface below the rotor zone (ca. 20-150 m ASL), they focus their attention downward while hunting, which may
increase collision risk (Langston 2013). Terns must feed their chicks nearly once every hour (Limmer and Becker 2009), and thus spend a large amount of time in flight compared to other marine birds (Garthe and Hüpppop 2004, Furness et al. 2013). Terns are surface-feeding central-place foragers, and thus have limited habitat flexibility (Suddaby and Ratcliffe 1997, Rock et al. 2007). This in turn, can increase vulnerability to habitat displacement from OWED (Gill et al. 2001, Drewitt and Langston 2006b, Fox et al. 2006). In addition, reduced prey availability, which is sometimes associated with OWED (e.g. Perrow et al. 2006) can dramatically impact terns through reductions in clutch size and growth rate of chicks, and high rates of nest abandonment and chick starvation (Becker and Fink 1985, Wendeln 1997, Dänhardt and Becker 2011). Common and Arctic Terns nesting on Petit Manan Island have faced all these issues in response to declining forage fish (USFWS unpublished data), indicating that barrier effects, displacement, or habitat decline from OWED may further reduce tern productivity.

Despite decades of management and monitoring at Common and Arctic Tern breeding colonies, some vital foraging metrics such as daily time spent in flight, number of foraging trips per day, and degree of nocturnal activity remain unknown. To help address these gaps, we used automated VHF radio telemetry to quantify colony attendance patterns and daily foraging metrics for Common and Arctic Terns in the Gulf of Maine. We compared foraging metrics between incubation and chick rearing, since shifts in flight activity throughout the breeding period can equate to differences in exposure to OWED hazards. Since piscivorous birds face heightened energetic demands during chick rearing (Drent and Daan 1980, Anderson et al. 2005), we hypothesized that
daily time spent foraging would increase during this period through increases in number of foraging flights per day, flight durations, or both. We also expected the orientation of flight departures to shift between incubation and chick rearing due to selection of specific prey species for chick provisioning (Dänhardt et al. 2011) and/or seasonal changes in prey in availability (Anderson et al. 2005). Further, we anticipated that foraging metrics could also differ between species, because Arctic Terns tend to deliver less diverse (Hall et al. 2000), and smaller prey items more frequently to chicks (Robertson et al. 2016), and forage in more pelagic, deeper waters than Common Terns (Rock et al. 2007).

4.2 Methods

4.2.1 Data Collection

Common and Arctic Terns were captured in 2013 on Petit Manan Island (PMI) in Steuben Maine, United States (44.3676° N, 67.8644° W). This 8-ha island is located roughly 2.5 km from the coast and is actively managed by the US Fish and Wildlife Service Maine Coastal Islands National Wildlife Refuge (MCINWR). PMI has historically been one of the most important colonial seabird nesting islands in the Gulf of Maine; in 2013, this colony supported 817 pairs of Common Tern and 616 pairs of Arctic Tern (US Fish and Wildlife Service 2013a). Seasonal technicians reside on the island for 12 weeks each summer monitoring the seabird colony and controlling predators.

We captured and radio-tagged adult terns on the nest during incubation (June 13-21) using walk-in treadle traps and bow nets (Burger et al. 1995). Trapping occurred when vegetation was dry, temperature was > 50 °F, and winds were < 15 mph. We
banded each captured tern with a USGS band, and back-mounted Lotek Nano Tag coded VHF radio transmitters with two dissolvable sutures (NTQB—2, Lotek Wireless Inc., Newmarket, ON; 1.4 g; 163 d expected tag life). The tags comprised < 2% of the body mass for all individuals. Previous has work demonstrated that tags do not influence productivity of terns (Loring 2016). Each radio transmitter emitted a uniquely coded signal at 166.380 MHz over a unique burst interval of 4-5 sec, allowing us to track all individuals simultaneously. We used an array of automated telemetry receivers deployed at the colony site on a 41-m light house, and at surrounding islands to track the terns (Fig. 4.1). Each automated telemetry station had 2-4 nine-element Yagi antennas mounted atop a 10-m tower or other existing structure, and a sensorgnome receiver (www.sensorgnome.org) that logged a signal strength and GPS-synchronized time stamp for each tag detection. The colony receiver was fully functional for all but 3 d throughout the 42-d study period. We screened for false positives by only including detection events that contained 3 sequential bursts of an ID and occurred at multiples of the tag’s burst interval (Woodworth et al. 2015).

We monitored the nests of all tagged birds daily before eggs hatched, and every other day once all eggs in the nest hatched. During each visit, we recorded date, clutch size, egg status, sign of predation, chick weight, and noted any dead chicks. Chicks were banded within 24-48 h of hatching.

4.2.1 Statistical analyses

We assumed that lack of detection indicated absence from the colony. However, since signals can be more difficult to detect if birds are on the ground in topographical
depressions, we only included tagged individuals in the analysis if they exhibited consistent detections while on the nest. We assessed the consistency of detections by inspecting plots of signal strength over time (e.g. Taylor et al. 2011) at night when terns generally spend longer contiguous periods on the nest (Bluso-Demers et al. 2010). We analyzed foraging metrics and colony attendance patterns during the breeding season only (i.e., detections before July 25), thereby excluding post-breeding colony dispersal.

We defined a foraging trip as a lack of detections at the colony for > 15 min and < 7 h. The 15-min cutoff allowed us to capture the bulk of foraging trips without confounding true departures and false negatives (e.g., lack of detection due to body position or topography). Although the 15-min cutoff may have excluded some short foraging trips, it likely allowed us to capture most foraging events; provisioning rates at this colony were 0.8 feedings/h for Common Terns, and 0.59 feedings/h for Arctic Terns (USFWS unpublished data), while maximum observed provisioning rates in Gulf of Maine colonies was ~ 2 feedings/h (Rosell et al. 2000). We excluded the 5% of absences that were ≥7 h from the analyses to remove anomalous behaviors; these absences may not represent foraging activities.

For each bird (n = 7 individuals of each species consistently detected on the nest), we calculated the duration of each foraging trip (i.e. each absence), the daily number of daytime and nocturnal foraging trips, daily total time spent in flight, daily duration of nocturnal flights, and percent of daylight hours spent in flight. We assumed that birds were primarily in flight during absence from the colony, as there are no other islands south of the PMI colony, and terns travelling towards the mainland are rarely observed
loafing (L. Welch, personal communication). The directional antennas could detect birds up to approximately 4.5 km from the colony, limiting our ability to distinguish between very localized foraging and nest attendance; therefore, forage trip estimates were all minimum values. We classified foraging trips as nocturnal if both the time at which the event was initiated and ended (i.e. a return to the colony, or re-detection on a different receiver away from the colony) occurred between civil dusk and dawn. We used this conservative approach to avoid misclassifying any long flights initiated just before dawn as nocturnal. We classified a flight as diurnal if any portion of the flight occurred between dawn and dusk. We categorized each foraging trip as occurring during incubation or chick rearing based on the time at which the event was initiated and the nest status of the corresponding bird on that day. Any dates for which a chick was not observed at a nest, but was detected on previous and following dates were classified as chick-rearing days. We only included movements that occurred on a day that nest status was known (n = 1653) in analyses. Finally, we identified the last antenna on which birds were detected during each foraging flight departure from the colony as a coarse measure of directionality of foraging.

We used mixed-effects generalized linear models (Poisson errors with a log link) to test if number of flights per day differed between species and nest status (incubation vs. chick rearing). We used mixed-effects weighted least squares models (Gaussian errors) to test if daily time spent foraging and flight duration (log-transformed) differed between species and nest status. To account for unequal variances, we incorporated a variance term in the models of total time spent foraging (for individual birds) and flight
duration (for species). Species, nest status, and their interaction were treated as fixed effects and, individual bird as a random effect. We used generalized mixed effects models (Poisson errors with a log link) to test whether the number of nocturnal flights related to lunar phase, since an increase in flight activity on nights with more illumination can provide indirect evidence that birds are foraging during absences. We coded the lunar phase as a value between 0-1, to reflect the proportion of the moon that was illuminated on a given night, and included a random effect for individual. Finally, we used Chi-square tests of independence to determine if the proportion of foraging flights that that were oriented in each of the four antenna directions differed either (1) between the two species or (2) by incubation and chick rearing, within species. We did not model the effect of species and nest status on percent of daylight hours in flight as this metric is somewhat redundant to total daily time spent foraging.

We selected the most parsimonious model using a backwards stepwise approach with a criterion of $\alpha = 0.01$ for likelihood ratio tests. We reported the mean ± SE for all summary statistics, and the sample size, $\beta \pm SE$ and $P$ values for all covariates retained in the most parsimonious models. Parameter estimates represent covariate effects on Common Terns relative to Arctic Terns and incubation relative to chick rearing. We conducted all analyses in the R statistical environment (R Core Team 2016) using the ‘lubridate’ (Grolemund and Wickham 2011), ‘lme4’ (Bates et al. 2015), ‘nlme’ (Pinheiro et al. 2017), and ‘LMERConvenienceFunctions’ (Tremblay and Ransijn 2015) packages.

4.3 Results
We recorded a total of 1.4 million detections for the birds considered in the analysis, including records at both the colony and at nearby islands during foraging flights. We recorded 399 foraging trips for Arctic Terns during the incubation period and 533 during chick rearing. We recorded 185 foraging trips during incubation for Common Terns, and 536 during chick rearing. Extended periods of cold rain and fog, and gull predation limited productivity in the tern colony in 2013, and Common Terns produced an average of 0.53 chicks/nest and Arctic Terns 0.29 chicks/nest (USFWS unpublished data). The terns included in the analysis exhibited similar productivity rates: three of the Common Terns fledged chicks, three abandoned their nest, and the fate of the remaining nest was unknown. One of the Arctic Terns fledged chicks, three abandoned the chicks, and one nest was predated; we could not determine the fate of the two other nests.

Daily time spent foraging, daily number of foraging flights, and flight duration differed significantly between incubation and chick rearing for both Common and Arctic Terns; however, the two species only differed markedly in flight duration. During incubation, Common Terns spent 4.8 ± 3.3 h/d foraging (22.6 ± 15.8% of daylight hours), and Arctic Terns 8.3 ± 4.8 h/d (42.1 ± 25.9% of daylight hours; Table 4.1). Daily time spent foraging was significantly less for both species in incubation than in chick rearing (Fig. 4.2; Linear mixed effects model; n = 206; β = -4.2 ± 0.6; P < 0.0001), when Common Terns spent 11.1 ± 5.3 h/d foraging (61.6 ± 31.9% of daylight hours) and Arctic Terns spent 13.9 ± 5.4 h/d (68.8 ± 23.2% of daylight hours). During incubation, Common Terns made an average of 5.8 ± 3.6 foraging trips per day, and Arctic Terns 8.1 ± 4.5. The daily number of foraging trips was significantly lower in incubation than in chick
rearing for both species (Fig. 4.2; Mixed effects Poisson GLM; n = 206; β = -0.15 ± 0.06; P = 0.009); Common Terns made 7.1 ± 3.8 flights/d during chick rearing and Arctic Terns 10.9 ± 4.6 flights/d. Individual foraging flights were 50.2 ± 56.0 min during incubation for Common Terns and 61.1 ± 75.0 min for Arctic Terns. Flight duration was significantly longer during chick rearing for both species (Fig. 4.2; Linear mixed effects model; n = 1653; β = -0.25 ± 0.06; P < 0.0001), with Common Terns making flights 94.3 ± 87.2 min in duration and Arctic Terns 76.8 ± 80.7 min. Foraging flight duration was greater for Common Terns than Arctic Terns; β = 0.33 ± 0.10; P = 0.008). The top model for flight duration also contained a significant interaction between nest status and species (β = -0.31 ± 0.10; P = 0.003) because Common Terns increased their flight duration more markedly than Arctic Terns during chick rearing.

Both species made nocturnal flights, and this behavior increased with greater moon illumination. Common and Arctic Terns made a total of 693 nocturnal flights during the tracking period, 67% of which were made by Arctic Terns. Individual Arctic Terns went undetected at the colony 3.1 ± 1.9 times per night, for a total of 2.4 ± 2.0 h. Common Terns went undetected 2.9 ± 2.0 times per night, for a total of 2.4 ± 1.7 h. These absences were 63.3 ± 72.8 mins in duration for Arctic Terns and 53.2 ± 52.2 mins for Common Terns. As further evidence of nocturnal flights, we also detected birds moving between Jordan’s Delight and the colony site, and Nash Island and Jordan’s Delight during the night (Fig 1). The number of nocturnal movements in a night was positively related to lunar phase (Poisson glm; n = 227; df = 224; β = 0.55 ± 0.13; P < 0.0001), with
birds exhibiting more frequent movements on nights when the moon was more fully illuminated.

Orientation of foraging departure flights differed between the species, and between incubation and chick rearing. During incubation, both species departed most commonly to the SSW (i.e. open ocean), and secondarily to the NNE (Table 4.2). Both Common ($\chi^2 = 77.9; P < 0.001$) and Arctic Terns ($\chi^2 = 16.4; P < 0.001$) differed significantly in the proportion of the departures they made in each direction between incubation and chick rearing. During chick rearing, Common Terns shifted their departure orientation more towards the NNE, and SSE. In contrast, Artic Terns continued to depart predominantly to the SSW during chick rearing, and reduced the frequency of departures to the NNE. Common and Arctic Terns differed significantly in the proportion of departures that they made in each direction from the colony ($\chi^2 = 77.9; P < 0.001$), with this difference largely driven by departure orientations during chick rearing.

4.4 Discussion

The foraging metrics we estimated in this study can help inform future efforts to estimate the adverse effects of OWED on Common and Arctic Terns in the Gulf of Maine. Our work provides the first estimates of daily time spent in flight for Common and Arctic Terns based on 24-h, continuous tracking data. This information is critical for predicting the extent to which barrier effects are likely to affect terns, and for improving collision vulnerability assessments, which have historically been based on qualitative scores of daily flight duration for both species (Furness et al. 2013). The flight metrics we estimated can also be used to parameterize individual-based models (Schaub 2012),
Markov models (Cranmer et al. 2017), and stochastic dynamic programming bioenergetic models (Schwarz et al. 2016) designed to predict the adverse effects of OWED and other anthropogenic disturbances. Finally, our results highlight that it may be apt to account for nocturnal foraging flights in collision vulnerability assessments, and to model collision vulnerability differentially by nest status for these two species, given the marked behavioral differences we observed between incubation and chick rearing.

That both Common and Arctic Terns nesting on Petit Manan Island were absent from the colony for a large proportion of the day suggests that barrier effects from OWED could significantly exacerbate existing stressors for both species at this colony. Individual terns spent at least 60% of daylight hours foraging on average, and some individuals spent close to 95% of daylight hours foraging. During the chick rearing period Foraging time was particularly long, with (conservatively estimated) cumulative flight times of 11.1 ± 5.3 h/d for Common Terns and 13.9 ± 5.4 h/d for Arctic Terns. These flight metrics are notable because species that already spend much of the day in flight simply may not have the time or energy to make multiple detours around physical barriers like OWED. Repeatedly detouring around OWED during daily foraging trips can increase daily flight distance, energy expenditure, time away from the nest, and decrease chick-feeding rates (Scott et al. 2014). In turn, increased energy expenditure can lead to poor adult body condition, nest abandonment, and chick starvation if adults cannot energetically afford to adequately forage for chicks (Becker and Finck 1985, Wendeln 1997, Dänhardt and Becker 2011).
Despite this large time investment in foraging, only 50% of the tagged Common Terns with a known nest fate (3/6), and 20% of the Arctic Terns (1/5) fledged chicks. Productivity of tagged terns was consistent with the overall colony trend for 2013, in which tern productivity (chicks surviving to 15 d/nest) was the second lowest since 1999, and much lower than the 18-yr average for both Common (0.53; 18-yr mean = 0.94) and Arctic Terns (0.35; 18-yr mean = 0.68; Fig. 4.3; US Fish and Wildlife Service 2013b). The USFWS concluded that poor productivity in 2013 was due to prolonged periods of cold wet weather, nest predation by Great Black-backed Gulls (Larus marinus), and chick starvation (US Fish and Wildlife Service 2013b). Collectively, these results suggest that Common and Arctic Terns at this colony did not have enough time to find adequate prey for their chicks, despite foraging > 60% of daylight hours. If faced with flight barriers, these birds would not likely have had much ‘extra’ time in 2013 to increase the distance or duration of foraging flights, the number of daily trips, the amount of daily foraging effort, or the amount of time spent attending chicks at the nest.

In addition to improving our understanding of how the flight barriers posed by OWED may adversely affect Common and Arctic Terns, our findings can also help inform collision vulnerability assessments. Since terns are difficult to track at night, vulnerability assessments have historically assumed minimal nocturnal activity for Common and Arctic Terns (Garthe and Hüppop 2004, Furness et al. 2013). However, both species consistently made nocturnal flights at the Petit Manan Island colony. Since the directional antennas could detect birds aloft for a maximum of 4.5 km, and nocturnal absences were typically 1-5 hours for both species, it is likely that absences were
foraging flights, and not just short disturbances away from the nest caused by predators. Furthermore, we also detected birds making nocturnal flights between automated VHF telemetry sensors on surrounding islands. Our finding that both species made nocturnal flights most often when the moon was more fully illuminated also provides indirect evidence that they were likely foraging during nocturnal absences.

The marked differences we observed in the frequency, duration, and orientation of flights between incubation and chick-rearing periods highlights that exposure to collision hazards, and vulnerability to habitat disturbance/displacement may be greater during chick rearing than incubation, and should be modeled as such in formal assessments. For instance, the increase in total daily flight time may equate to greater exposure to collision hazards, since daily flight time is an important factor in collision exposure (Garthe and Hüppop 2004, Furness et al. 2013). Similarly, if terns increase the number of foraging trips per day and foraging trip length, and alter their foraging location in response to raising chicks – as our data suggests– exposure to OWED may increase during chick rearing. Exposure to collision hazards may also increase during chick rearing because terns show reduced avoidance of flight barriers during periods of high energy demand (Henderson et al. 1996, Everaert and Stienen 2007). Furthermore, if Common and Arctic Terns are under significantly greater energetic and time demands during chick rearing – as is indicated by our data – the fitness consequences of alteration of (or displacement from) foraging habitats could be of markedly more significance during the chick-rearing period. Illustrating this, productivity of Little Terns nesting near the Scroby Sands Wind
Farm in Norfolk, UK decreased following a localized post-construction decline in Herring (*Clupea harengus*; Perrow et al. 2006).

There are several plausible explanations for why both species spent more time foraging and shifted the departure orientation of foraging flights during chick rearing. First, Common and Arctic Terns at this colony may have altered their selection of prey, and thus foraging habitats to meet the demands of raising chicks. Since provisioning chicks is more energetically demanding than self-feeding, and terns are single-prey loaders (Barrett et al. 2007), they tend to disproportionately provision chicks with prey items of high energetic value, and self-feed at lower trophic levels on inferior prey (Dänhardt et al. 2011, Gatto and Yorio 2016). Thus, Common and Arctic Terns may have spent more time foraging during chick rearing, and shifted the orientation of foraging flight departures to seek out more nutritious prey for chicks. However, both species may have also made longer and more frequent trips during chick rearing in responses to seasonal changes in prey availability as has been observed for Common (Safina and Burger 1989) and Caspian Terns (*Hydroprogne caspia*; Anderson et al. 2005). In addition, some of the long absences we observed later in the season could have been birds with predated or abandoned nests, as seabirds with failed nests have been shown to travel significantly further from the colony during the breeding season than conspecifics with active nests (Perrow et al. 2006).

The interspecific differences in foraging metrics we observed between Common and Arctic Terns provide indirect evidence that these species exhibit spatial segregation and resource partitioning – particularly during chick rearing, and as such could be
differentially exposed to OWED threats in the region. Common Terns made longer flights than Arctic Terns, particularly during chick rearing, indicating possible travel to more distant feeding areas. In line with the findings of Rock et al. (2007), strong differences in the orientation of foraging flights suggests that the two species also showed segregation in foraging habitat selection. Resource partitioning can be particularly advantageous and pronounced during energetically stressful periods for seabirds (Barger et al. 2016). Reflecting this, Common and Arctic Terns showed an increase in spatial segregation during chick rearing: while Arctic Terns consistently departed SSW throughout the breeding season, towards their preferred pelagic open water habitats (Hatch, J 2002, Rock et al. 2007), Common Terns shifted away from these habitats during chick rearing, towards the mouth of the Narraguagus Bay, and their favored nearshore habitats (Nisbet 2002).

Although the results we present here are only for a single year – in which periods of abnormal weather, and low prey availability appeared to impact productivity – they do give some indication of how OWED may interact with and exacerbate conditions that Common and Arctic Terns will likely face more regularly in the Gulf of Maine under climate change. For instance, a primary concern with barrier effects is that chicks left longer at the nest can die of heat exposure or starvation (Becker et al. 1997, Dänhardt and Becker 2011) or of cold and rain exposure, as occurred in 2013 at the Petit Manan Island colony. Climate change may intensify this threat: by the end of this century, New England is expected to experience a 50-80% increase in the number of warm-season thunderstorms (Harrison and Colle 2016), and an increase in the intensity and frequency
of extreme weather events (Christensen et al. 2013). Possible shifts in prey composition resulting from OWED (Perrow et al. 2006, van Deurs et al. 2016) may also be compounded by climate change. For instance, Atlantic Herring – one of the primary prey species for Common (34.6%) and Arctic Tern (49.7%) chicks at our study site in 2013 (US Fish and Wildlife Service 2013b) – are responding to sea surface temperature increase in the North Atlantic (Nye et al. 2009, Lucey and Nye 2010). Climate change is already thought to play a significant role in the declines in seabird breeding numbers (Russell et al. 2015), highlighting the importance of prioritizing responsible development of OWED, while also considering how the adverse effects of OWED may interact with future stressors.
Table 4.1. Foraging metrics for Common (*Sterna hirundo*) and Arctic Tern (*S. paradisea*) during incubation and chick rearing over the study period (June 13 - July 25, 2013).

<table>
<thead>
<tr>
<th>Foraging metric</th>
<th>Common Terns</th>
<th>Arctic Terns</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Incubation</td>
<td>Chick rearing</td>
</tr>
<tr>
<td>Number of flights per day</td>
<td>5.8 ± 3.6</td>
<td>7.1 ± 3.8</td>
</tr>
<tr>
<td>Flight duration (mins)</td>
<td>50.2 ± 56.0</td>
<td>94.3 ± 87.2</td>
</tr>
<tr>
<td>Hours foraging per day</td>
<td>4.8 ± 3.3</td>
<td>11.1 ± 5.3</td>
</tr>
<tr>
<td>Number flights per night</td>
<td>4.2 ± 2.3</td>
<td>2.4 ± 1.7</td>
</tr>
<tr>
<td>Night flight duration (mins)</td>
<td>33.2 ± 12.0</td>
<td>74.3 ± 78.5</td>
</tr>
<tr>
<td>Hours foraging per night</td>
<td>2.4 ± 1.7</td>
<td>2.4 ± 1.8</td>
</tr>
<tr>
<td>Percent of daylight hours in flight</td>
<td>22.6 ± 15.8</td>
<td>61.6 ± 31.9</td>
</tr>
</tbody>
</table>

NOTE. — Mean values ± 1 SD are presented for each metric. Daily foraging metrics represent values over a full 24-h period, and nocturnal between civil dusk and dawn. Data are from automated VHF radio telemetry conducted at Petit Manan Island in Steuben Maine.
Table 4.2. Percent of foraging flight departures in each of four directions covered by antennas for Common (*Sterna hirundo*) and Arctic Tern (*S. paradisea*) during incubation and chick rearing.

<table>
<thead>
<tr>
<th>Antenna orientation</th>
<th>Direction</th>
<th>Incubation</th>
<th>Chick-rearing</th>
<th>Incubation</th>
<th>Chick-rearing</th>
</tr>
</thead>
<tbody>
<tr>
<td>23 °</td>
<td>NNE</td>
<td>0.27</td>
<td>0.37</td>
<td>0.22</td>
<td>0.16</td>
</tr>
<tr>
<td>98 °</td>
<td>E</td>
<td>0.06</td>
<td>0.10</td>
<td>0.05</td>
<td>0.03</td>
</tr>
<tr>
<td>162 °</td>
<td>SSE</td>
<td>0.05</td>
<td>0.25</td>
<td>0.09</td>
<td>0.17</td>
</tr>
<tr>
<td>193 °</td>
<td>SSW</td>
<td>0.62</td>
<td>0.28</td>
<td>0.63</td>
<td>0.64</td>
</tr>
</tbody>
</table>

NOTE. — Data are from automated VHF radio telemetry conducted at Petit Manan Island in Steuben Maine from June 13 - July 25, 2013.
Figure 4.1. Distribution of automated VHF telemetry receiving stations used to track radio-tagged Common and Arctic Terns during 2013 breeding season. The birds were tagged at the Petit Manan Island breeding colony (PMI) in Steuben Maine. Additional receivers were stationed at Petit Manan Point (PMP), Nash Island (Nash), and Jordan’s Delight (JD). Lines show the orientation of antenna and extend to an approximate maximum detection range of 4.5 km.
Figure 4.2. Total daily time spent in flight, number of daily foraging trips, and log-transformed duration of foraging trips for Common (\textit{Steerna hirundo}) and Arctic Terns (\textit{S. paradisaea}) during incubation and chick rearing. Data are from automated VHF radio telemetry conducted at Petit Manan Island in Steuben Maine from June 13 - July 25, 2013.
Figure 4.3. Yearly mean productivity from 1999-2016 for Common (*Sterna hirundo*) and Arctic Terns (*S. paradisaea*) at the Petit Manan Island Colony in Steuben Maine, where birds were radio-tagged in 2013. The mean productivity over the 18-yr period is shown for Common Terns (dashed line) and Arctic Terns (solid line), and the 2013 productivity values are circled.
APPENDIX

A MARKOV MODEL FOR PLANNING AND PERMITTING OFFSHORE WIND ENERGY: A CASE STUDY OF RADIO-TRACKED TERNS IN THE GULF OF MAINE, USA

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A.1 Introduction

Environmental concerns are one of the key barriers to public acceptance and permitting of offshore wind energy development (OWED) in the US (Firestone and Kempton 2007; Goodale and Milman 2016). The risk that wind farms can pose to birds is a main environmental issue (Drewitt and Langston 2006; Fox et al. 2006; Langston 2013; Schuster et al. 2015). Siting wind farms in a way that minimizes adverse effects to wildlife is imperative for developing and sustaining public approval and easing regulatory uncertainties (Firestone and Kempton 2007; Firestone et al. 2009; Goodale and Milman 2016), but remains an exceedingly challenging task. The difficulty of siting and permitting wind farms and understanding adverse environmental effects is heightened in offshore environments due to obstacles such as inadequate baseline data on wildlife, limited understanding of movement patterns and habitat use, and difficulty in collecting post-construction collision data (Goodale and Milman 2016; Masden et al. 2015).

Addressing the environmental uncertainties of OWED with empirical data and robust analytical tools is a critical step toward facilitating a sustainable and timely development of this technology (Langston 2013; Marques et al. 2014).

As OWED proceeds in US waters, there is a need for spatial planning tools that can quantitatively balance ecological, technical, and social factors (Langston 2013). Spatially-explicit optimization models are apt tools for modeling ecological, economic, and social tradeoffs of development scenarios, and have been used in terrestrial planning scenarios (Polasky et al. 2008; Eichorn and Dreschler 2010). However, these methods
require estimates of space use and spatially-explicit collision probabilities that can be difficult to acquire, especially for small marine birds.

A commonly used method for wind energy development is to develop an impact function - describing collision fatality as a function of the distance between a wind farm and a nesting site (Eichorn et al. 2012; Schaub 2012). Although impact functions are commonly included in wind farm risk assessments (Carrete et al. 2012), to date they have been developed using only theory and expert opinion rather than empirical data (Schaub 2012; Eichorn et al. 2012). In this paper, we develop a methodology for using automated telemetry data to produce empirically-based impact functions.

For cases in which a population of birds is homogeneous in location and behavior, a Markov model can be used to model the movements of representative individual(s). These models can be used to develop impact functions in circumstances where tracking data are too sparse for more data-demanding agent-based methods (Eichorn et al. 2012). Markov models are a particularly apt choice for modeling bird movements because they are highly flexible and can be based on a large variety of data sources; they therefore can serve as a consistent and versatile tool for modeling movement data derived from rapidly evolving tracking technologies (Patterson et al. 2008). Markov models can also be run at many different physical and temporal scales, and in continuous time (e.g. Baker 1989), giving great flexibility to modeling applications. Finally, Markov models can be easily extended to simulation exercises (e.g. Cowling et al. 1997), and therefore are a valuable tool for making predictions.
In this paper, we develop a new method for using automated VHF telemetry data to derive impact functions for central-place foraging marine birds, based on a simple Markov model. We apply the model to empirical data on the duration of foraging flights and colony attendance bouts of common terns (*Sterna hirundo*) and Arctic terns (*S. paradisaea*) in the Gulf of Maine. We demonstrate the model’s utility for the development of impact functions, for identifying defensible set-back distances, for quantifying the tradeoffs between ecological risk and wind capacity in planning scenarios, and for estimating mean number of fatalities. Since the data we use in this application is limited to a single year, the results in this paper are not intended to specifically inform management at the study site in Maine. Rather, we demonstrate the development of a new, flexible tool that can be adapted to specific management problems when adequate data are available. To this end, we present results under simple scenarios to demonstrate easily understandable and intuitive qualitative insights, and discuss important issues in data collection and model extension for applying this tool successfully in an actual planning or management application.

A.2 Material and methods

A.2.1 Focal species

Common and Arctic terns are migratory water birds that nest colonially on islands and shorelines, and plunge dive and surface dip for prey. Both species are of conservation concern in the eastern US and are under active management (U.S. Fish and Wildlife Service 2008; 2012a). Terns are expected to be at risk in the Atlantic Ocean during the
breeding, staging and migratory periods (Burger et al. 2011). The degree to which wind energy development will impact terns in the US is still uncertain. Both species decreased in abundance at offshore pilot projects in Denmark and the Netherlands (Vanermen et al. 2015), and experienced high collision fatality rates (6.7 terns per turbine per year) at windfarms located <1 km from colony sites (Everaert and Steinen 2007).

A.2.2 Field methods

In 2013 on Petit Manan Island in Steuben Maine, USA (44.3676° N, 67.8644° W), we captured adult terns on the nest using walk-in treadle traps and bow nets (Burger et al. 1995). We back-mounted 1.4 g Lotek Nano Tag coded VHF radio transmitters (Avian NanoTag NTQB-4-2, Lotek Wireless Inc., Newmarket, ON; 163 day expected tag life) with dissolvable sutures. The tags comprised <2 % of mean body mass for all birds. Each transmitter emitted a uniquely coded signal at 166.380 MHz every 4-5 seconds, allowing us to track all individuals simultaneously. We tracked the terns with an array of automated telemetry receivers deployed at the colony site on a 41-m lighthouse, and at surrounding islands (Fig. A.1). Each telemetry station had 2-4 nine-element Yagi antenna mounted atop a structure, and a sensorgnome receiver (www.sensorgnome.org) that continuously logged a GPS-synchronized time and signal strength for each tag burst. We excluded false positives by requiring at least three subsequent tag bursts of a given ID at multiples of the ID’s unique burst interval.

We used presence and absence data at the colony receiver to generate empirical distributions of flight and attendance bout duration (i.e. discrete visits to the colony), each
in 4 min time bins. We used data from 7 individuals of each species that exhibited consistent detections at night. We determined this by visually inspecting plots of signal strength over time during nocturnal hours when terns generally spend longer contiguous periods on the nest (Bluso-Demers et al. 2010). We only included detections before July 25 in the analysis to ensure we excluded dispersal activity at the end of the breeding season. We identified foraging trips by determining each instance in which a bird was not detected at the colony for >15 min and <11 h. This cutoff eliminated potential instances in which a bird could be at the colony but undetectable for a short period due to topography or body position, but very likely still captured most foraging events, based on maximum provisioning rates of roughly 2 feedings per hour in Gulf of Maine colonies (Rosell et al. 2000). We excluded absences >11 h from analyses as these events represented < 2% of the data and may signify phenomena other than foraging events. We recorded 1,519 foraging flights for Arctic terns and 994 for common terns. We summed the time span between subsequent tag bursts by individual during each discrete visit to the colony to quantify the duration of colony attendance bouts. We recorded 1,560 colony attendance bouts for Arctic terns and 1,070 for common terns. We constructed empirical distributions (in 4 min time bins) of flight duration and colony attendance bout duration by species, pooled over the breeding season and over individuals to represent the average behavior across the colony and breeding season. Finally, we calculated the percent of flight departures that occurred on each of the four colony antennas for common and Arctic terns by identifying the last antenna on which a bird was detected when initiating a foraging movement.
A.2.3 Markov model

We used a Markov model of bird movement around a colony to estimate the risk turbine(s) at varying distance from the colony posed to an individual tern. Markov models consist of an agent that represents the organisms in question, a set of states in which the agent can exist, and a set of transition probabilities between the states that is formulated as a matrix whose elements are the probabilities of transitioning between each pair of states (Ross, 2007; Kulkarni, 2010). These stochastic models represent systems whose future states depend only on the present state of the system (Ross 2007; Kulkarni 2010).

The Markov model we developed is a movement model (Joo et al. 2013), so the states represent physical space (Fig. A.2A). The colony (C) is at the center of the space described by the model, and the other states are rings of equal radial distance defined in size by the distance a bird could travel over a given time. The tern is assumed to begin at the colony state; in each subsequent time step, it can remain at the colony, embark on a foraging flight (outbound arrow Fig. A.2A), remain in flight, or return to the colony (inbound arrow Fig. A.2A). We represented each non-colony location as both an outbound \{1, 2, 3\ldots\}, and inbound \{1', 2', 3'\ldots\} state (Fig. A.2B), to allow different behavior on inbound and outbound flights. For instance, we assumed birds either made direct flights to known feeding areas during outbound flights, or occasionally made nonlinear flights while seeking prey, since the location of food sources is highly dynamic (Perrow et al. 2011). To account for this in the model we allowed birds engaged in
outbound flight to remain in a state with a given probability, but did not allow birds to move back toward the colony until they found prey. We assumed a bird with prey returned directly to the colony to feed chicks with a probability of one. A wind farm in the model (M) represents a location (state) where a bird could collide with a turbine and transition to the fatality state. The fatality state was an absorbing state, meaning a bird remains in that state if it is reached. The model assumes that there are no other sources of adult fatality since the data only includes live birds that returned to the colony. To incorporate flight direction in the model we divided the model space into a set of discrete departure cones $\theta$ (e.g. $70^\circ$ - $85^\circ$). We based the probability $p(\theta)$ of a flight departing within a discrete departure cone $\theta$ on empirical departure data from the study site.

The results of the Markov model depend on important input parameters that can vary according to the application of the model, the study species, and the limitations and form of the empirical data. For example, in this study the terns are detected on the colony antenna at a range of 4 km, so the colony state is made up of the area within the 4-km range. We set the duration $t$ of each time step at 4 min and assumed a flight speed of 32.5 kph, based on mean flight speeds of 25-40 kph observed in this and other studies (Hatch 2002; Nisbet 2002; JRS, unpublished data). The width of each ring (i.e. state) is approximately 1 km, the distance a tern can fly in 4 minutes and a reasonable spacing between 5 MW wind turbines. We considered a season of 32,400 time steps, or 90 days, to represent the time span that terns typically spend at breeding colonies (Hatch 2002; Nisbet 2002). We set the maximum number of rings (i.e. states) in the model based on the
longest absence we included for any individual (650 mins). Assuming linear flight, this equated to 162 inbound and outbound states.

The model operates based on a matrix of probabilities, $P(d, \theta_M)$, whose elements are $p_{ij}$, where $i$ is the state that the bird came from and $j$ is the state the bird went to, $d$ is distance of the wind turbine from the colony, and $\theta_M$ is the direction cone (i.e. 70°-85°) in which the wind turbine is located. We used the empirical distribution of colony attendance bout durations to parameterize the probability of remaining at the colony, $p_{CC}$ from one time step to the next. Once a bird initiated a flight we used the empirical distribution of flight duration to determine the probability of continuing a flight, transitioning from state $i$ to state $i+1$, during a foraging bout (see Appendix 1). To allow for non-linear outbound foraging flights (representing birds in search of prey), a bird could continue an outbound flight in a time step with probability $p_{i,i+1}$ or remain in its current state $i$ with a probability $p_{i,i}=q$. We did not have empirical data on spatial foraging behavior at this colony, so we estimated $q$ from a visual tracking study at two colonies in the United Kingdom that observed 60 breeding-season foraging trips of 25 common terns and 28 trips of 7 Arctic terns (Perrow et al. 2011). Based on the mean total flight distances and mean total displacement from the colony during foraging bouts in the Perrow et al. (2011) study, 69% of travel distance was indirect, non-linear flight for common terns, and 67% for Arctic terns. We used a base value of 70% for $q$, and did sensitivity analysis with values of 60 and 80%. Once a bird initiated a return flight to the
colony, we assigned the probability of moving from state $i'$ to state $(i-1)'$ as one, in order to represent direct return flights.

We used the observed frequency of departure on the four colony antennas to parameterize the probability of flights initiated in each direction by species (Table A.1). We credited each departure to only one antenna, and assigned each antenna a liberal 90° cone of horizontal detection centered on the antennas’ orientation, based on the beam pattern of the 9-element Yagi antennas used in the study. We assumed all departure directions within each antenna’s detection range were equally likely. For all instances in which the assumed detection range of two antennas overlapped, we added the probabilities within the range of overlap (Fig. A.3). This left us with eight discrete directions (Table A.2), though we excluded the eighth direction altogether since the antennas did not cover it. A simple assumption of equally likely transitions between directions does not change the probability of occupancy or the probability of fatality. Knowledge of the locations of prey could inform the probability of flying between different directions; however, this information is unknown. Therefore, we assumed that the direction of departure was the direction of travel for the entire flight.

The model we have outlined to this point represents bird movements. To explore fatalities under different development scenarios we placed 5 MW turbine(s) (Jonkman et al. 2009) in the landscape of the model. This turbine is comparable in size to those proposed for Cape Wind (7.5 m longer in blade length) for which Hatch and Brault (2007) previously developed collision probabilities for terns using the Band et al. (2007) model. This size turbine is also typically spaced at roughly 1 km intervals within a wind
farm (Musial et al. 2013), which is the size of each non-colony state in the model, given the flight speed and time step used. To estimate the adverse effects of wind turbines in this system, we specified a probability of fatality $p_{iM}(d, \theta_M)$, the probability of transitioning during a single time step to the fatality state from state $i$, as

$$p_{iM}(d, \theta_M) = m(d, i) \cdot p(\theta_M) \cdot p(\text{rotor area} | i, \theta_M) \cdot p(\text{collision} | \text{rotor area})$$  \hspace{1cm} (1)$$

where $d$ is the distance from the colony to a wind turbine; $\theta_M$ is the discrete direction cone (i.e. $70^\circ$-$85^\circ$) in which the turbine is located; $m(d, i)$ is an indicator variable that is one if $d$ falls within the state $i$ and zero otherwise; and $p(\theta_M)$ is the probability of a bird departing in direction cone $\theta_M$. If we don’t distinguish directions, we can define theta to be the entire cone between $355^\circ$ and $255^\circ$, and $p(\theta_M) = 1$. We assume that the birds do not move between the discrete directions on their flights. The term $p(\text{rotor area} | i, \theta_M)$, is the probability of being in the rotor area given that a bird is in state $i$ and direction cone $\theta_M$. This is equal to the area of the rotor divided by the area of the wedge in which the turbine is located, where the wedge is described by state $i$ and the size of the direction cone $\theta_M$. The area of the rotor is the rectangle defined by the rotor diameter and the sum of the maximum blade chord length and the body length of the bird (Band 2012). The probability of a fatality is thus driven by 1) whether a turbine is in state $i$, $m(d, i)$, 2) the probability that a bird flies in the direction in which the turbine is located, $p(\theta_M)$, 3) the probability that a bird will pass through the area of the rotor, $p(\text{rotor area} | i, \theta_M)$, and 4) the probability of collision given that a bird passes through the area of the rotor,
Further mathematical details are provided in Cranmer et al. 2017).

There are a wide variety of behavioral and environmental factors that can contribute to the probability of collision for a bird that approaches the rotor area (Barrios and Rodriguez 2004; Drewitt and Langston 2008; Langston 2013; Band et al. 2007; Band 2012; Eichorn et al. 2012; Furness et al. 2013). Rather than specifying and varying these underlying parameters across model runs, we ran the model under a range of collision probabilities. We used observed collision probability values of 0.030 and 0.007 (Everaert and Stienen 2007), and theoretical values of 0.240, 0.130, 0.046, and 0.004 based on the 0.027 no-avoidance collision probability calculated for the morphologically and behaviorally similar roseate tern (S. dougallii; Hatch and Brault 2007), and adjusted for avoidance using

\[
p(collision \mid rotor \ area) = 0.027 \times (1 - p(avoidance))
\]  

(2)

where \(p(collision \mid rotor \ area)\) is the theoretical probability of collision and \(p(avoidance)\) is probability of avoidance. We used empirically observed avoidance values of 91\% (Everaert and Stienen 2007), and theoretical values of 95, 98.3, and 99.85\% used in collision risk models (e.g. Band, Madders and Whitfield 2007; Hatch and Brault 2007). The range of collision probabilities used in the model (Table A.2) represents periods of high avoidance (Chamberlain et al. 2006), and ones of lower avoidance that are possible during chick rearing or food stress (Henderson et al. 1996; Everaert and Stienen 2007).
A.2.4 Impact function

In Matlab (The MathWorks, Inc. 2014), we developed the Markov model to derive an impact function, \( r(d, \theta, n) \) where \( d \) is the distance of a wind turbine from the colony, \( \theta \) is the direction cone in which the turbines are located, \( n \) is the number of time steps, and \( r(d, \theta, n) \) is the probability of fatality of a single tern from a wind turbine at a distance \( d \) and location \( \theta \) over \( n \) time steps. This can be extended to multiple wind turbines at an average distance \( d \). We developed the impact function by using the transition matrix to calculate the probability of fatality once turbine(s) were put into the system (see Appendix 1). Briefly, the probability of fatality over time is the complement of the cumulative probability of not reaching the fatality state; we calculated this with an adjusted matrix, \( B(d, \theta) \), created by removing the row and column of the fatality state from the transition matrix, \( P(d, \theta) \). The cumulative probability of not dying over \( n \) time periods is

\[
v(d, \theta, n) = B^n(d, \theta) \ast e \quad (3)
\]

where \( e \) is a column vector of ones matching the number of columns in the matrix \( B(d, \theta) \), \( v(d, \theta, n) \) is a vector of cumulative probabilities where each element is the probability of not reaching the fatality state given an initial state \( i \). Assuming a bird starts at the colony state \( C \), the probability of fatality is given by
\[ r(d,\theta,n) = 1 - v_c(d,\theta,n) \quad \text{(4)} \]

where \( v_c(d,\theta,n) \) corresponds to initial state C.

A.2.5 Model scenarios

We derived impact functions under an initial set of simplistic model scenarios in which we assumed equal probability of flight direction, and a 0.7 probability of remaining in each state during the outbound flight. We ran these models for each species separately, under the six collision probabilities, with a single turbine located \{4, 5, 6\ldots33 km\} from the center of the colony, and a block of 100 turbines arranged 10x10 at a mean distance of \{8, 9\ldots37 km\} from the center of the colony. We also ran an additional set of models with a single turbine located \{4,5, 6\ldots33 km\} from the center of the colony, with the probability of remaining in a state during outbound flight set to 0.6 and 0.8 to assess sensitivity to this parameter. For all the model runs described above, the derived impact functions applied to all directions, since we assumed uniform flight departure probability. If flight directions are highly variable from year to year, this simple model would represent the long-run probability of collision averaged over all directions. If, however, flight directions are relatively stable from season to season an assumption of equal flight probability could result in significant underestimates or overestimates of collision fatality, depending on the location of turbines relative to the most highly-traveled flight paths.
In a second set of simple scenarios, we demonstrated the model’s ability to quantify collision risk in each specific direction cone. We ran the model for each species with a single turbine located at \{4, 5, 6….33 km\}, and in each model run, we varied the turbine location to each of the seven directions for which we have data on the probability of flight departure. In this formulation, we changed the probability of fatality for a given heading from the colony by adjusting the probability of being in the rotor area when a bird was in flight (Table A.3). Finally, we ran the model using the empirical flight probabilities, but with no turbines in the system, to demonstrate how this tool can be used to develop estimates of space use for central-place foragers.

A.3. Results

Since we ran the model using only one year of data, we present model results here to demonstrate the model output, and the type of heuristic comparisons possible with limited data, rather than making specific recommendations for wind energy planning at this site. The probability of fatality diminished for both species as the distance from the colony increased (Fig.A.4). The shape of the impact function reflects the distribution of absence durations used to parameterize the model and indicates that moving a wind farm from 5 km away to 10 km away from the colony results in a larger reduction of risk than moving a wind farm from 15 km to 20 km. Collision fatality was greater for Arctic terns than for common terns when turbines were <9 km from the colony, but at distances >9 km this was reversed (Fig.A.4). Arctic terns made shorter flights on average than
common terns, and were therefore more likely than common terns to encounter a wind farm close to the colony.

Both species departed most commonly to the south-southwest, and least frequently to the east-southeast (Fig. A.5), but space use appeared to be more concentrated for Arctic terns than common terns. Reflecting this, the probability of fatality was greatest for both species with a turbine at a bearing of 165°-207° from the colony and lowest for a turbine oriented at 85°-117° (Fig. A.6).

The results indicate that the model output is sensitive to input parameters, especially at locations closest to the colony. For instance, an increase in collision probability resulted in a similar increase in probability of fatality (Fig A.4). Furthermore, when we increased the probability of nonlinear outbound flight used in the model (q), probability of fatality increased at distances < 8 km; beyond this distance from the colony, probability of collision was similar across q values (Fig. A.7).

A.4 Discussion

A.4.1 Application and utility of model results

We used empirical colony attendance data to demonstrate the utility of a novel Markov model in general terms, and ran the model under simple scenarios to demonstrate easily understandable and intuitive results. Since we developed the model with limited data the results are not intended to be used for specific management or planning purposes, but rather to demonstrate the model’s utility.
Applying the model successfully in a specific wind farm planning exercise will require multiple years of data as movement patterns, departure flight orientations, and important foraging areas can be highly variable from year to year in dynamic marine systems (Thaxter et al. 2015). Typically, 2-3 years of data are required to capture the temporal and spatial variability of seabirds (Kinlan et al., 2012). Thus, we recommend the use of this model following the standards for offshore wind energy impact assessments, employing data collected over a period of 2-4 years. The U.S. Fish and Wildlife Service’s land-based wind energy guidelines recommend a minimum of two years of site-specific avian baseline data be collected for permitting, and additional years of study if baseline data indicates a moderate to high risk to avian species (U.S Fish and Wildlife Service 2012b). In the United Kingdom, a bare minimum of two years of data are similarly required for avian monitoring (Langston 2013). Though the Bureau of Ocean and Energy Management made similar recommendations for renewable energy development in federal waters (Bureau of Ocean and Energy Management 2013), avian surveys occurred over four years for the proposed Cape Wind facility (Minerals Management Service 2009), and over three years for the Block Island Wind Farm (U.S. Army Corps of Engineers 2014). Thus, the required data for this model may be reasonably collected within the typical timeline of a wind energy project’s impact studies.

The results presented for this case study demonstrate a wide variety of model applications. For one, we derive an empirically-derived impact function (e.g. Fig. 3, 7) that can be used instead of opinion-based impact functions. These can be used during marine spatial planning exercises to determine setback distances and test different
development scenarios and locations under a maximum level of tolerable risk for the breeding populations exposed to the wind farms. For instance, under a (hypothetical) threshold for maximum annual probability of fatality per individual of $1.48 \times 10^{-4}$ for common terns and $1.9 \times 10^{-4}$ for Arctic terns at this colony site, a single turbine could be placed 4 km away from the colony. If stakeholders wanted to increase the development scenario to 25 MW (with equivalent turbines), they would need to be located at least 10 km away from the colony to remain under the risk thresholds. Similarly, 125, 245, and 500 MW wind farms would need to be an average of at least 13, 19, and 24 km away from the colony, respectively. Building a larger wind farm with the same risk threshold would require building further from the colony (and therefore from shore), increasing the capital cost of development. The results also highlight the model’s utility for balancing the needs of multiple species. For instance, in this example the risk posed to Arctic terns would dominate decision making for a wind farm that was planned <10 km from the colony whereas planning at locations >10 km may be driven more by the needs of common terns. In addition, the model revealed that the increase in probability of fatality differed by distance to the colony in a non-linear manner for both species; the ability to quantify this type of complex and non-linear relationship is critical for balancing development and conservation goals.

The impact function can also be developed under directional flight to plan across the landscape to meet risk and capacity goals if departure flight orientations and flight durations are consistent from year to year. For instance, a 125 MW wind farm located at a bearing of 85-117° from the Petit Manan Island colony at an average of 8 km would
have the same probability of fatality as turbines placed an average of 16 km from the colony, at a bearing of 165-207°. Similarly, a 500 MW farm placed 12 km from the colony at 85-117° or a 50 MW wind farm at 14 km in 165-207° would equate to the same level of mean collision probability per individual. Whatever the arrangement, holding risk constant, building at a bearing of 85-117° from the colony would be better than building at 165-207° because it would maximize power production and minimize development costs by allowing larger development scenarios closer to the coastline. Alternatively, if departure flight orientation is highly variable from year to year, an impact function using random flight orientations would be most apt for guiding development planning at a specific site. This again highlights that effectively using the model in an actual planning exercise requires multiple years of site-specific data.

The model output can also be used to generate expected fatality under different development scenarios by multiplying the probability of fatality for a species by the number of individuals at the colony. For instance, the colony sampled for this study supported 817 pairs of common terns and 616 pairs of Arctic terns in 2013 (U.S. Fish and Wildlife Service 2013). Under a collision probability of 0.24%, a single turbine placed 5 km from the colony at 70-85° predicted an average of 0.24 common tern deaths per year, whereas a single turbine 5 km from the colony at 160-165° predicted an average of 0.10. In this manner, the model can be used to quantitatively compare the ecological impacts of different development alternatives as required under the U.S. National Environmental Policy Act during permitting. Though our estimates are lower than the annual fatality estimates recorded at the Zeebrugge wind farm in Belgium (6.7 terns/turbine; Everaert
and Stienen 2007), where turbines were 100-800 m from a colony, we were limited to placing hypothetical turbines ≥ 4 km from the colony.

The case study results highlight additional input data that would be useful to collect to apply this model in a specific wind energy development scenario. Consistent with the U.S. Fish and Wildlife Service wind energy guidelines (U.S. Fish and Wildlife Service 2012b) and European experience in wind energy planning (Langston et al. 2013) at least 2-3 years of site-specific data should be collected to use the model confidently in wind energy planning. Since the probability of fatality was sensitive to collision risk, more in-depth study of collision risk or avoidance probability at existing wind farms would be beneficial. Sensitivity to the probability of non-linear flight, q, demonstrates that site-specific data on the degree to which a species exhibits non-linear flight based on visual tracking (e.g. Perrow et al. 2011) are also necessary for using the model effectively for wind energy planning. Furthermore, in this case study we were limited to constructing an impact function at distances ≥ 4km from the colony because birds could be detected up to this distance out on the colony antenna. As such, it is difficult to compare our collision fatality estimates to observed annual collision fatality values, such as the 6.7 terns/turbine observed at the Zeebrugge wind farm in Belgium where turbines were 100-800 m from a colony. As demonstrated by the high collision rates at the Zeebrugge facility for turbines located < 800m from the colony, it would be useful to construct impact functions in a 0- 10 km range, in cases where a wind farm is proposed at a site in that range. When collecting data for specific wind energy planning applications, use of multiple short-range omnidirectional antennas at a colony site would allow for an impact
function that covered distances from the immediate vicinity of the colony and outward. Finally, use of more directional antennas at a site that allowed for finer-scale resolution of departure orientation (e.g. Smolinsky et al. 2013) and coverage of the entire region around a colony would be most effective for planning across the full landscape.

A.4.2 Model extensions and opportunities

Though we developed a very simplistic model of bird behavior in this study, the Markov model can easily be used to model bird behavior in a more sophisticated manner. For instance, we assumed constant collision probability, which in many cases may be related to the configuration and distribution of turbines (De Lucas et al. 2008, Ferrer et al. 2012), and thus unequal across a wind farm (Masden and Cook 2016). The Markov model can address this complexity by varying the collision probability across the turbines in the landscape to generate more accurate fatality estimates; macro-avoidance can be similarly modeled, where data are available. Moreover, the model could allow birds to move between direction sectors if data on the probability of these transitions were available. Finally, although we generalized over the population and breeding season for each species by pooling data, the model could be used to construct impact functions and estimate collision fatality for different groups or time periods by parsing empirical distributions of flight duration and colony attendance duration by factors of interest, such as sex or nest status. This is important because movement patterns, colony attendance, and collision probability can vary significantly for some marine birds by sex, time of day,
time of year and even by target prey (Garthe and Hüppop 2004; Stienen et al. 2008; Bluso-Demers et al. 2010; Camphyusen 2011; Thaxter et al. 2015).

The model we presented is also a highly adaptable tool that can easily be extended to address more complex questions when data are available. For instance, the model can be parameterized with greater detail for specific planning applications when multiple years of site-specific data are collected. In such a case, the model can consider a range of alternative wind farm designs with multiple turbines spanning a range of distances and directions, to compare across non-linear and complex scenarios. In extension, collision probability results can be combined with assessments of cost and power production in an optimization framework to identify alternatives that minimize collision risks to multiple species and maximize power production and profits. Fatality estimates can also provide useful information for investigating population-level effects via demographic models, particularly if they are generated for different age and sex groups, and across different time periods.

One of the great strengths of this Markov model as a spatial planning tool is its flexibility. For instance, though we focused in this study on common and Arctic terns, the model could easily be applied to other central-place foragers, including the federally listed roseate tern if empirical data were collected. The model is also flexible enough to accommodate different wind turbine specifications, and can employ a variety of collision risk models in equation 1 (e.g. Masden and Cook 2016). In addition, although we parameterized the transition probabilities in this case study with duration of absences and colony attendance bouts, data on actual foraging locations could also be used to
parameterize the probability of moving from one state to another. This versatility means
the model can be extended (and likely improved) with telemetry or GPS data that
documents actual foraging locations, and will help the model to remain a useful tool in
wind energy planning and permitting as bird tracking technology expands.
Finally, the model is also flexible enough to incorporate stochasticity in a variety of
manners, and with greater complexity than demonstrated here. Incorporating error in
collision fatality estimates is a much-needed development (Masden and Cook 2016) that
could be flexibly met with our model, based on availability of data. We integrated
multiple sources of uncertainty by considering a range of collision probabilities.
However, for a specific planning application, the model could be adapted such that
factors that are likely to contribute to variability in collision probability such as wind
direction, avoidance rates, angle of approach, flight altitude, etc. can each be incorporated
as additional states, with transition probabilities for these states included in the modeling
exercises. Furthermore, in this study we present a range of individual point estimates for
collision probability under a range of input parameters to generate simple intuitive
results, and to explore how the input parameters influence model results. However, the
model can be run thousands of times over a large range of the various input parameters
drawn from error distributions in each model run, and the mean output values and their
95% quantiles can be presented to indicate confidence in the results.

A.5. Conclusions
Data on flight routes and foraging areas for small marine species is extremely useful in wind energy planning, but exceedingly difficult to collect (Bogdanova et al. 2014). We have developed a novel Markov model that can use easily-attainable VHF automated radio telemetry data to inform wind energy planning. Our results demonstrate that even sparse data can be used as a heuristic tool to qualitatively compare development scenarios. Given multi-year, site-specific data, the model can be used to derive an impact function, and determine defensible setback distances under a landscape-scale planning approach. Determining no-development exclusion zones and identifying priority areas for finer-scale siting studies and monitoring efforts is often the first step in marine spatial planning exercises. The model can also be of utility in the U.S. NEPA process to estimate and compare collision fatality under a range of alternative spatially-explicit industrial-scale development scenarios. Fatality estimates can also provide important information for demographic models designed to investigate population-level effects under a specific development plan. This Markov model can guide managers in balancing wind energy development and conservation goals by providing qualitative insights in cases of limited data, or serving as a quantitative tool when more extensive data are available.
Table A.1. Percent of departures occurring on each of the four antennas located at the Petit Manan Island breeding colony for common and Arctic terns. Data are from automated VHF radio telemetry conducted at Petit Manan Island in Steuben Maine from June 13 - July 25 2013.

<table>
<thead>
<tr>
<th>Species</th>
<th>ESE</th>
<th>NE</th>
<th>SSW</th>
<th>SSE</th>
</tr>
</thead>
<tbody>
<tr>
<td>Common Tern</td>
<td>8.5</td>
<td>33.1</td>
<td>40.1</td>
<td>18.3</td>
</tr>
<tr>
<td>Arctic Tern</td>
<td>4.2</td>
<td>18.1</td>
<td>64.7</td>
<td>13.1</td>
</tr>
</tbody>
</table>
Table A.2. Percentage of departure per degree in each degree range (below). Data are from automated telemetry conducted on Petit Manan Island, Maine in summer 2013

<table>
<thead>
<tr>
<th>Bin</th>
<th>Degree range (θ)</th>
<th>Departures per degree (%)</th>
<th>Probability of departure (%)</th>
<th>Departures per degree (%)</th>
<th>Probability of departure (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>207-255</td>
<td>0.446</td>
<td>21.4</td>
<td>0.719</td>
<td>34.5</td>
</tr>
<tr>
<td>2</td>
<td>165-207</td>
<td>0.649</td>
<td>27.3</td>
<td>0.864</td>
<td>36.3</td>
</tr>
<tr>
<td>3</td>
<td>160-165</td>
<td>0.203</td>
<td>1.0</td>
<td>0.145</td>
<td>0.7</td>
</tr>
<tr>
<td>4</td>
<td>117-160</td>
<td>0.298</td>
<td>12.8</td>
<td>0.191</td>
<td>8.2</td>
</tr>
<tr>
<td>5</td>
<td>85-117</td>
<td>0.094</td>
<td>3.0</td>
<td>0.046</td>
<td>1.5</td>
</tr>
<tr>
<td>6</td>
<td>70-85</td>
<td>0.462</td>
<td>6.9</td>
<td>0.247</td>
<td>3.7</td>
</tr>
<tr>
<td>7</td>
<td>355-70</td>
<td>0.368</td>
<td>27.6</td>
<td>0.201</td>
<td>15.1</td>
</tr>
<tr>
<td>8</td>
<td>255-355</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>
Table A.3. Collision probabilities used in Markov movement model, including empirically observed collision probabilities, and theoretical collision probabilities based on estimates of non-avoidance collision probability for terns, and commonly applied avoidance probabilities.

<table>
<thead>
<tr>
<th>Non-avoidance collision probability (%)</th>
<th>Avoidance (%)</th>
<th>Collision Probability (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>2.70*</td>
<td>91.00†</td>
<td>0.240‡</td>
</tr>
<tr>
<td>2.70</td>
<td>95.30*</td>
<td>0.130‡</td>
</tr>
<tr>
<td>2.70</td>
<td>98.30*</td>
<td>0.046‡</td>
</tr>
<tr>
<td>NA</td>
<td>NA</td>
<td>0.030†</td>
</tr>
<tr>
<td>NA</td>
<td>NA</td>
<td>0.007†</td>
</tr>
<tr>
<td>2.70</td>
<td>99.85‡</td>
<td>0.004‡</td>
</tr>
</tbody>
</table>

* Hatch and Brault (2007)
† Everaert and Stienen (2007)
‡ Band (2007)
¶ Theoretical collision probability based on 2.7% non-avoidance collision probability for roseate terns, and commonly applied avoidance probabilities.
Figure A.1. Distribution of automated VHF telemetry receiving stations used to track radio-tagged common terns and Arctic terns tagged at the Petit Manan Island colony in Steuben Maine, USA during the 2013 breeding season. Lines show the orientation of antennas and extend to an approximate maximum detection range of 4 km.
Figure A.2: Conceptual diagram of Markov model. (A) Physical representation of Markov model with colony state C, outbound states \{1, 2, 3 \ldots\}, inbound states \{1', 2', 3' \ldots\}, and fatality state M. (B) Transition diagram for avian movement model. Transitions between and within states, are shown with arrows. A hypothetical turbine is in state three.
Figure A.3. Antenna orientations are shown in A, with a 90° angle shown around one antenna in grey for demonstration. The eight directional cones are shown in B, with the antenna in grey dashed lines.
Figure A.4. Impact function for Arctic terns (top) and common terns (bottom) at a range of collision probabilities for a single 5 MW turbine. Only distances ≤20 km are shown for ease of graphical interpretation. These results are based on a Markov model that assumed uniform departure flight orientation probability, a 70% probability of remaining in a state to forage during outbound flights, and excluded the landscape to the northwest of the colony (256-334°) not covered by the antennas.
Figure A.5. Probability of occupancy for common and Arctic terns in the landscape around the colony (point 0, 0), covered by the antenna array. These results are based on a Markov model with 70% probability of remaining in a state to forage during outbound flights. Probability of occupancy at the colony was 41.8 % for common terns and 37.6 % for Arctic terns.
Figure A.6. Probability of fatality for Arctic terns (top) and common terns (bottom) with a single turbine located a mean distance of 4-20 km from the center of the colony at different bearings, and under a scenario that assumed uniform flight orientation probabilities. These results are based on a Markov model that assumed a 0.24% collision probability, a 70% probability of remaining in a state to forage during outbound flights, and excluded the landscape to the northwest of the colony (256°-334°) not covered by the antennas.
Figure A.7. Sensitivity of model output to the probability of remaining in a state during outbound flight (i.e. to represent foraging behavior) for Arctic tern (top) and common tern (bottom). These results are based on a Markov model that assumed a 0.24% collision probability, uniform departure flight orientation probability, and excluded the landscape to the northwest of the colony (256°-334°) not covered by the antennas.
APPENDIX BIBLIOGRAPHY


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