Eastern Wild Turkey Population Ecology Across Land Use Gradients in Maine

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WILD TURKEY POPULATION ECOLOGY ACROSS LAND USE GRADIENTS IN MAINE

By

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A DISSERTATION
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Wild turkeys are a wide-ranging species with considerable cultural and economic significance. As they can exist across a variety of ecosystems, understanding how land use affects population vital rates can be a crucial component of informed population management. This is even more important for turkey populations in Maine, where harsh winters can have negative impacts on survival and reproduction.

I used a combination of banding and tracking data to better understand the relationship between turkey population ecology at their northern range limit and the diverse landscape gradient they occupy in Maine. I produced wildlife management district specific estimates of turkey abundance that accounted for spatial variation in harvest rate. I examined how turkeys moderated their movement behavior and resource selection according to weather factors during the winter. I expanded on traditional methods used to assess nesting habitat to produce a holistic estimate of turkey nesting habitat quality that accounted for multiple nesting stages and spatial scales. Finally, I simulated movement of turkeys during their seasonal movements between winter and spring to better understand how turkey populations were connected across the state.

Turkey populations in Maine appear to be largely stable over the past decade, with populations being most dense in the southern portion of Maine and becoming increasingly less dense.
farther north and inland. Turkeys during the winter adjust their movement behavior, which was associated with changes in resource selection, in response to increased snow depths and decreased wind chill. Such changes likely allow turkeys to shelter and reserve energy during periods of severe winter weather. During the spring, turkeys depart their winter ranges and establish nesting ranges according to large-scale landscape characteristics. Resource selection changed throughout the nesting period according to the specific behavioral phase a turkey was in, with turkeys interacting with their environment at increasingly finer scales as movement became more localized. Finally, we expect that a considerable number of turkeys move among wildlife management districts during seasonal movements between winter and spring ranges, which warrants consideration for management and monitoring efforts.
DEDICATION

To my mom,

Without your love, support, and guidance, I would not have made it here. Thank you.
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I would like to thank my advisor, Erik Blomberg, for providing a supportive space for me to explore my interests and find new ones. I am also thankful for his patience, calming nature, and sense of humor, because without this would have been a much worse experience. I would also like to thank Kelsey Sullivan, whose tireless work ethic and immense knowledge of turkeys and Maine allowed us to be as successful as we were. Thank you to Stephanie Shea and Pauline Kamath, for their contributions which were integral to this projects success. I am also very grateful for the remainder of my committee members – Alessio Mortelliti, Erin Simons-Legarrd, Joseph Zydlewski – specifically for their guidance and sharing of knowledge during my qualifying exams. Something that I was dreading immensely turned out to be a formative experience which made me trust my own knowledge and skills (although I am glad I never have to do it again).

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now without you. Mandi, you took a chance on me and moved across the country to live in a frozen forest. I know it hasn’t and will not always be easy, but I appreciate the sacrifices you’ve made for me to do what I love and I will never forget that.
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CHAPTER 1

INTRODUCTION

In contrast to wide-spread declines of avian species across North America (Nebel et al. 2010, Horns et al. 2018, Stanton et al. 2018), the restoration of wild turkeys is often viewed as one of the great successes in wildlife conservation (Eriksen et al. 2016). Eastern wild turkeys (*Meleagris gallopavo silvestris*, hereafter turkey), are a wide-ranging subspecies (Dickson 1992) with considerable cultural and economic significance (Watkins et al. 2018). Research already available for this species dates back over a century (Wright 1914) and fills books, journals, and symposia. Despite management successes, traditional research methods have been limited in their ability to provide a complete understanding of turkey ecology and management. Very high frequency (VHF) telemetry research has been the predominant method used for studying turkey ecology for over 50 years (Ellis and Lewis 1967) and is still being used today (Pollentier et al. 2017). While the information produced from these studies may be adequate for understanding certain aspects of turkey ecology such as survival (Niedzielski and Bowman 2015), the information provided to characterize movements and habitat selection is more limited (Collier and Chamberlain 2011). New technology in the form of GPS transmitters can provide locations of individuals at a quality and quantity not previously possible, and has already been used to provide insight into nest site selection, home range size, and movements during disturbance (Chamberlain et al. 2013, Byrne et al. 2014, Gross et al. 2015). Further exploring how this fine-scale movement data can inform management is a critical component of future turkey research.

Understanding why turkey restoration efforts were successful following significant declines in the 1930s (Blakey 1941) can inform management of current turkey populations and provide insight into conservation of other species declining or of concern. Effective wildlife management relies on an accurate understanding of the dynamics of populations, which in turn are influenced by rates of survival,
recruitment, immigration and emigration. As each of these vital rates vary according to landcover, understanding how animals interact with their environment is a crucial component of effectively management. Increased availability of food resources within rural and urban landscapes can lead to greater survival, especially during winter when resources are scarce (Brittingham and Temple 1988, Robb et al. 2008). However, these benefits can be offset by greater mortality risk caused by increased disease prevalence (Bradley and Altizer 2007) and predation rates (Evans 2004) associated with rural-urban land use gradients. Landcover also affects reproduction, causing decreases in productivity among species in landscapes experiencing fragmentation, loss of habitat, and altered forage availability due to human development (Paton 1994, Chamberlain et al. 2009). Landcover composition and configuration will also influence structural and functional connectivity, which can result in large scale impacts on immigration and emigration (Auffret et al. 2015, Crawford et al. 2016). Abundance estimation is also a critical component of successful conservation planning (Thogmartin et al. 2006), particularly for exploited species where managers set quotas or other regulations to restrict harvest based on population size (Nichols et al. 2007, Runge et al. 2009). Population monitoring that does not account for how species interact with their landscape can result in misleading conclusions about population trajectory and drivers of change (Robinson et al. 2014), especially for species in human-dominated landscapes where positive and negative forces vary in magnitude according to available landcover (Evans et al. 2015). Assessing the potential pressures and benefits associated with landcover provides important context for management decisions and helps to understand the status of a population as well as its trajectory going forward.

Landcover is not simply segregated on the landscape but rather exist as a spatially varying gradient of multiple habitat types which influences species persistence (Blair 1996). Where resources are more isolated, populations experience limited growth rates that lead to greater levels of local extirpation (Fahrig and Merriam 1985). The ability of a population to persist when resources are isolated
depends in part on the connectivity of the landscape, or the degree to which the landscape facilitates or impedes movement (Taylor et al. 1993). Loss of connectivity for species that exhibit seasonal movements to meet resource needs can lead to population collapse (Bolger et al. 2008). Alternatively, increased connectivity can have an adverse impact on populations by facilitating more rapid transmission of disease (Nobert et al. 2016). A full understanding of how resources are distributed, how movement is affected by landscape connectivity, and how these relate to population health, will also provide relevant insights for management.

Turkey population monitoring could also benefit from updated methodology. Current methods for monitoring trends in turkey populations include incidental roadside surveys and use of hunter harvest information (CDEEP, 2016; DNREC, 2020). While monitoring trends over time can be informative about population status, estimates of population size are more appropriate for management since management decisions may change depending on the size and demographic structure of a population (Lyons et al. 2008). The decision to use trend monitoring methods are often made to work within the financial limitations placed on state agencies, meaning any newly proposed method must be economical. One option is to integrate multiple available or more readily collected data types into a single model to estimate population size (Schaub and Abadi 2011, Chandler and Clark 2014, Wilson et al. 2016), which makes more efficient use of data, provides a means of estimating uncertainty that is propagated among all parameters, and has some capacity to make inferences about unmeasured aspects of turkey demographic rates. This detailed assessment of turkey populations, in combination with a better understanding of their relationship with the landscape they occupy, would provide a solid framework on which future management decisions can more confidently be made.

In the recent years, there has been a push for a more data-driven approach to turkey management (Leopold and Cummins 2016, Mason and Rudolph 2016) leading many states to reassess their current policies. For example, Maine, a state with a relatively young turkey population compared
to their core range (Bailey 1980, Eriksen et al. 2016), has explicitly stated this objective as a part of a large realignment of their turkey management policies (MDIFW, 2017). Historically, Maine’s turkeys were limited to southern counties (Forbush 1912) and along the eastern coast (Townsend 1881), until they were extirpated from the state due to over exploitation and habitat loss (Forbush 1912). Reintroduction attempts by private organizations began in 1942 but were not successful until the late 1970s when the Maine Department of Inland Fisheries and Wildlife (MDIFW) joined the effort and were able to successfully establish a population of turkeys in York County. These birds were then used to source reintroduction efforts across the remainder of Maine until 2012 when MDIFW felt they had met their management goals and shifted efforts from reintroduction to sustaining and growing their current turkey populations (MDIFW, 2017). Now, MDIFW seeks a better understanding of both current turkey population size and vital rates, from which they will assess future harvest regulations plans.

Maine encompasses a matrix of rural, forested, and suburban-urban land use types existing at the northern range limit of turkeys. The scarcity of food resources during the harsh winters typical in Maine likely have historically limited turkey populations to the southern part of the state and the coast (Austin and DeGraff 1975). The availability and configuration of resources have since changed with the expansion of rural and urban land use across the state, which has allowed turkey populations to establish in areas where they were probably historically absent. As turkey populations grow in these new areas, there is greater importance of understanding how movement, nesting, and densities of turkeys change in regions with fundamentally different land use types.

My dissertation examined current distribution of turkeys across the state, and how Maine’s land use gradients affect these current distributions. My objectives were to 1) provide statewide and management district specific estimates of turkey abundance (Chapter 2), 2) better understand how turkeys alter their movement and resource selection behavior in response to winter weather (Chapter 3), 3) produce a comprehensive assessment of turkey nesting habitat selection and associated outcomes.
(Chapter 4), and 4) quantify connectivity between Maine’s wildlife management districts to understand migration dynamics across the landscape during seasonal movements between winter and spring ranges (Chapter 5).
CHAPTER 2

INCLUDING A SPATIAL PREDICTIVE PROCESS IN BAND RECOVERY MODELS IMPROVES INFERENCE FOR LINCOLN ESTIMATES OF ANIMAL ABUNDANCE

1) Abundance estimation is a critical component of successful conservation planning, particularly for exploited species where managers often set quotas or other regulations to restrict harvest based on the current population size. An increasingly common approach for abundance estimation is through integrated population modeling (IPM), which uses multiple data sources in a joint likelihood to estimate abundance and additional demographic parameters. Lincoln estimators are one commonly used IPM component for harvested species which produces robust abundance estimates at large scales by combining information on the rate and total number of individuals harvested with an integrated band-recovery framework.

2) A major assumption of the Lincoln estimator is that banding and recoveries are representative of the whole population, which will be violated if major sources of heterogeneity in survival or harvest rates are not incorporated into the model. We developed an approach for incorporating spatial variation in harvest rates into an integrated population model for abundance using a spatial predictive process.

3) We simulated data sets under different configurations of spatial variation in harvest rate to assess potential model bias in parameter estimates, and applied the model to data collected from a field study of wild turkeys (Meleagris gallopavo) to estimate local and statewide abundance in Maine, USA.

4) We found that the spatial predictive process in the band recovery model consistently provided estimates of adult and juvenile abundance with low bias across a variety of spatial configurations of harvest and sampling intensities for simulated data. When applied to data collected on wild turkeys, a model that did not incorporate spatial heterogeneity in harvest underestimated harvest in some WMDs, which resulted in over-estimation of abundance in those districts, and statewide.
5) Our work demonstrates that a spatial predictive process is a viable mechanism to account for spatial variation in harvest rates to limit bias in abundance estimates from Lincoln estimators, and likely has more general relevance to estimation of population parameters in other ecological models as well.

2.1 Introduction

Abundance estimation is a critical component of successful conservation planning (Thogmartin et al. 2006), particularly for exploited species where managers often set quotas or other regulations to restrict harvest based on the current population size (Nichols et al. 2007, Runge et al. 2009). If abundance is overestimated, liberal regulations may lead to a larger portion of the population being removed than intended, which can have detrimental effects on long term stability (Johnson et al. 2012, Weinbaum et al. 2013). Alternatively, if population size is underestimated, then harvest regulations may be set more restrictively than is necessary, leading to inefficiencies in utilizing the resource in question and reducing opportunity to its consumers. In either instance, there is benefit in identifying and implementing tools that estimate abundance as accurately as possible.

An increasingly common approach for abundance estimation is through integrated population modeling (IPM; (Schaub and Abadi 2011, Chandler and Clark 2014, Wilson et al. 2016)), which uses multiple data sources in a joint likelihood to estimate abundance and additional demographic parameters. IPMs make efficient use of data, provide a means of estimating uncertainty that is propagated among all parameters, and have some capacity to infer latent parameters for which data are not available. IPMs are versatile in the types of data they can incorporate, including capture-mark-recapture, point counts, productivity surveys, dead recovery, and telemetry (Freeman and Crick 2003, Lee et al. 2015, Bled et al. 2017, Fay et al. 2019, Horne et al. 2019), with the key requirement that one or more parameters are shared among the components of the IPM (Zipkin and Saunders 2018).

Lincoln estimators are one commonly used method of abundance estimation for harvested species where band recovery and total harvest data are available (Lincoln, 1930), which produces robust
abundance estimates at large scales (Alisauskas et al. 2009) by combining information on the rate and total number of individuals harvested which can be generated using a band-recovery framework (Roberts et al. 2021). Temporal dynamics in abundance can then be represented in a state-space approach, and additional data sources may be included to inform demographic parameters estimated by the model (Tavecchia et al. 2009, Hostetler and Chandler 2015). While largely underutilized until recently, Lincoln estimators have been applied with great success in the management of a number of game species (Diefenbach et al., 2012; Hagen et al., 2014; Otis, 2006; Saunders et al., 2019), most notably to inform the harvest of waterfowl across North America (Alisauskas et al. 2013, Arnold et al. 2018).

Despite the advantages of IPMs, violating assumptions of component models can lead to inaccurate estimates, both for directly and indirectly estimated parameters (Riecke et al. 2019), making it important to both identify potential violations and implement reasonable solutions. A major assumption of the Lincoln estimator, shared by all band recovery models, is that banding and recoveries are representative of the whole population (Alisauskas et al. 2009). This assumption will be violated if major sources of heterogeneity in survival or harvest rates are not incorporated into the model (Pollock and Raveling 1982). Within a population, harvest rates may vary spatially according to variable harvest regulations, land access, weather, or land cover characteristics (Hansen et al. 1986, Norton et al. 2012, Burke et al. 2019). Similarly, survival may be linked to spatially varying factors like habitat, predation risk, or weather (Perkins et al. 1997, Fleskes et al. 2007, Tolon et al. 2009). Assumptions of constant harvest or survival may therefore be violated across large spatial scales, which will bias estimates at finer scales. When estimating parameters statewide and applying them to management objectives that are region-specific, it is often unrealistic to assume no heterogeneity exists among regions. Therefore, accounting for spatial heterogeneity is important to ensure accurate abundance estimates on which management will be based.
When incorporating spatial variation into models, accounting for multiple interacting factors can be difficult when each vary independently (Viana et al. 2013), and may be impractical to measure. As such, it may be simpler to ignore the specific causes of the spatial relationship, and instead take advantage of the underlying spatial correlations in the data to map the spatial structure in the parameter being estimated (Cressie 2015). Locations that are closer together in space are more likely to be similar than those farther apart (Burrough 1995), which can facilitate covariance functions to describe the spatially-dynamic nature of a parameter. One such approach, spatial predictive processes (SPP; Banerjee et al., 2008), projects the underlying correlation among sampling sites onto a set of evenly spaced spatial knots distributed across an area of interest. SPP was initially intended as a dimension reduction approach to reduce computation requirements in Kriging for larger datasets (Banerjee et al. 2008), but the underlying framework has advantages beyond computational efficiency. For one, the covariance function does not require additional information beyond the locations of data, meaning that identifying and measuring explanatory covariates is unnecessary to represent the underlying spatial heterogeneity in the process. Additionally, the even spacing of spatial knots uniformly covers the area of interest, which is sometimes impractical for observed data when sampling must take place where animals can be readily accessed. Thus, using parameter estimates at evenly spaced knots may be more representative than those from sampling sites. Use of SPP is sparse within the ecological literature – although see examples for applying such an approach to estimating spatial distribution of fisheries discards (Viana et al. 2013) or invasive plants (Latimer et al. 2009) - despite it’s broadly applicable approach for assessing spatial variation in vital rates, especially when the causes of the spatial relationship are unimportant or difficult to determine.

Here, we develop and present an SPP approach for incorporating spatial variation in harvest rates into an IPM to derive robust estimates of wild turkey (Meleagris gallopavo; hereafter turkey) abundance. We integrated band recovery, telemetry, and total harvest data to estimate region-specific
abundance of a two-aged (adult and juvenile), harvested population at the beginning of the hunting season (Figure 2.1). Band recoveries were used to estimate harvest and survival rates under a modified Brownie parameterization of the dead recovery model (Brownie 1985), in which we incorporated an SPP (Banerjee et al., 2008) to account for spatial variation in harvest risk between capture sites, and to allow estimation of harvest rates in areas where banding did not occur. To control for mortalities that occurred between banding and the beginning of the hunting season (Buderman et al. 2014), we linked survival in the band recovery model to a weekly survival rate estimated from telemetry data in a nest survival framework (Dinsmore et al. 2002). Using a state-space approach, final abundance estimates were generated using a Lincoln estimator (Lincoln 1930, Alisauskas et al. 2013). We simulated data sets under different configurations of spatial variation in harvest rate to assess bias in parameter estimates, and applied the model to data collected from a field study of wild turkeys to estimate abundance, and inform harvest decisions, across the state of Maine.

2.2 Materials and Methods

2.2.1 Integrated Population Model

2.2.1.1 Band Recovery Model. We used a modified version of the Brownie parameterization for dead recoveries (Brownie et al. 1985), where recovery rates, which we considered synonymous with reported harvest rate, were estimated as the combined probability that a bird was killed, retrieved, and reported by a hunter within a given hunting season. Harvest rates were estimated as a proportion of all mortalities (harvest plus non-harvest) that occurred between hunting seasons. One assumption of all band recovery models is that no mortalities occur between capture and the first hunting season, which is likely to be violated as time between the two events increases (Cooch et al. 2021). To better identify mortality that occurs between capture and the first hunting season, we separated the conventional band recovery encounter history into two distinct and alternating occasion types, capture and harvest.
The initial observation occurred during a capture occasion, and the terminal observation during a harvest occasion.

Figure 2.1. Band recovery, telemetry, and total harvest information in combination with a spatial predictive process can be used in a Lincoln Estimator to produce estimates of harvest rate, survival, and abundance. The flow of data and parameter estimates through the integrated population model is depicted here by a directed acyclic graph.
Survival was then differentiated according to three seasons that corresponded with the intervals between recovery occasions; the period from capture to the first day of harvest, the interval where harvest occurs (i.e. the hunting season), and the period from the last day of the harvest season to the following year’s capture. For a given interval within the model, a Bernoulli random variable ($\psi$) was used to determine the probable latent survival state ($z$) of individual $i$ at occasion $t$,

$$P(z_{i,t}) \sim \text{Bernoulli}(\psi) \quad \text{Eq. 1}$$

$$\psi = S_{i,t} \times w_{i,t-1} \quad \text{Eq. 2}$$

where $\psi$ was the probability of surviving all risks unrelated to reported harvests ($S_{i,t}$) given that the bird was alive at the end of the previous occasion ($w_{i,t-1} = 1$). We modeled the probability of observed data using a Bernoulli random variable ($\gamma$),

$$P(y_{i,t}) \sim \text{Bernoulli}(\gamma) \quad \text{Eq. 3}$$

$$\gamma = H_{i,t} \times z_{i,t} \quad \text{Eq. 4}$$

$$w_{i,t} = z_{i,t} - y_{i,t} \quad \text{Eq. 5}$$

where $y$ was the observed harvest of an individual and $H$ was the probability a bird was harvested and reported, given that it survived all other mortality risks since the previous occasion ($z_{i,t} = 1$). Here, we assumed 100% reporting of harvested birds, although incomplete reporting could be incorporated with additional information on reporting rate. Since harvests cannot occur during capture periods, we restricted $H = 0$ in capture occasions.

We modeled variation in harvest rate using a logit-linear model,

$$\text{logit}(H_{i,t}) = \beta_0 + \beta_1 \text{Age} + \beta_2 \text{Year} + \omega(c_i) + \epsilon_i \quad \text{Eq. 6}$$

where $\beta_{1,2}$ were categorical covariates that describe variation according to age of the individual (Juvenile or Adult) and year of harvest respectively. Covariates were given uninformative uniform priors.
\[ \beta \sim N(0, \sigma^2) \]  

\( \text{Eq. 7} \)

To account for spatial variation in harvest rates, we included a mean-zero SPP \( (\omega(c); \text{Viana et al. 2013; see section 2.1.2}) \) that was dependent on the harvest location for all individuals, \( c = \{c_1, c_2, \ldots, c_n\} \).

Remaining variation was modeled by a non-spatial error term \( (\varepsilon_i) \) where

\[ \varepsilon_i \sim N(0, \sigma^2). \]  

\( \text{Eq. 8} \)

2.2.1.2 Spatial Predictive Process. Following the methods of Viana et al. (2013), we accounted for spatial variation in harvest rate by incorporating a mean-zero SPP into the logit-linear regression. We defined a set of evenly distributed spatial knots, \( c^* = \{c_{*1}, c_{*2}, \ldots, c_{*m}\} \), across the study area on which we defined a Gaussian Process with exponential covariance,

\[ \tilde{\omega}(c^*) \sim \text{GP}(0, \sigma_s^2 \rho(c^*, c^* \mid \varphi)) \]  

\( \text{Eq. 9} \)

where \( \sigma_s^2 \) was the spatial random effect variance and \( \rho \) was an autocorrelation function with

\[ \rho(c_a, c_b \mid \varphi) = \exp[-|d_{a,b}| / \varphi] \]  

\( \text{Eq. 10} \)

where \( |d_{a,b}| \) was the distance between locations \( c_a \) and \( c_b \), and \( \varphi \) determined the rate of decay in correlation as distance increased between locations. To project the Gaussian process from the knots back onto harvest locations, we used the correction for bias in \( \varepsilon_i \) proposed in Finley et al. (2009). We defined a generic covariance function between two locations as

\[ C(c_a, c_b \mid \varphi) = \sigma_s^2 \rho(c_a, c_b \mid \varphi) \]  

and then defined \( \omega(s) \) as

\[ \omega(s) = C(c^*, c \mid \varphi)C(c^*, c^* \mid \varphi)^{-1}\tilde{\omega}(c^*) + \varepsilon_i \]  

\( \text{Eq. 11} \)

\[ \varepsilon_i \sim N(0, \text{diag}(C(c, c \mid \varphi) - C(c, c^* \mid \varphi)C(c^*, c^* \mid \varphi)^{-1}C(c^*, c \mid \varphi))) \]  

\( \text{Eq. 12} \)

We then applied the covariance functions to the supplied sets of capture sites and spatial knots, which yielded site specific estimates of harvest rate for each capture location and spatial knot.

2.2.1.3 Weekly Survival Rate. Weekly survival rates were estimated under a nest survival modeling framework (Dinsmore et al. 2002), in which we modeled whether an individual was observed alive since its previous telemetry observation \( (x) \) as a Bernoulli random variable \( (\mu) \),
\[ P(x) \sim \text{Bernoulli}(\mu) \quad \text{Eq. 13} \]

\[ \mu = s^k \quad \text{Eq. 14} \]

where \( s \) was the probability of surviving one week and \( k \) was the number of weeks since an individual was last observed alive. We modeled variation in weekly survival using a logit-linear model,

\[ \text{logit}(s) = \alpha_0 + \alpha_1 \text{Age} + \alpha_2 \text{Season} + \alpha_3 \text{Region} \quad \text{Eq. 15} \]

where \( \alpha_i \) represented individual, temporal, and spatial regression coefficients for categorical covariates Age, Season, and Region. We used a covariate for the region an individual was captured to account for spatial variation in survival. To estimate survival from banding to harvest, we linked \( S \) estimated from band recoveries to weekly survival rate (\( s \)) estimated from telemetry data of marked individuals such that

\[ S_{t,t} = s^n \quad \text{Eq. 16} \]

where \( n \) is the number of weeks between occasions. For \( n \) following the initial capture of an individual, we used the length of time from the time of marking to the beginning of the following harvest period. In subsequent occasions, we used the average number of days between the median date of capture and the first day of the hunting season to determine values for \( n \). In practice this approach allowed us to accommodate mortality of animals between capture and their first opportunity of harvest, which cannot be reconciled in a standard band recovery framework (Buderman et al. 2014). 

2.2.1.4 State Space Abundance Estimation. Abundance for each region was derived using a Lincoln estimator (Lincoln 1930, Alisauskas et al. 2013) for each region and timestep as

\[ N_{r,t} = \frac{T_{r,t}}{H_{r,t}} \quad \text{Eq. 17} \]

where \( T \) was the observed total number of individuals reported harvested, \( H \) referred to harvest rate estimated from the band recovery model, \( r \) was the region of the study area, and \( t \) was the year for
which abundance was estimated. We linked abundance through time using a state space approach. \( T_{r,t} \)

for each region were drawn from a binomial distribution

\[ T_{r,t} \sim B(\hat{H}_r, N_{r,t}) \]  

Eq. 18

where \( \hat{H}_r \) was the mean harvest rate across years for region \( r \), and was estimated as the average harvest rate at all spatial knots \( (H^*_r) \) within a region’s boundaries, such that

\[ \logit(H^*_r) = \beta_0 + \beta_1 \text{Age} + \omega(c^*) \]  

Eq. 19

We assumed each region was closed to immigration and emigration, such that total abundance at the beginning of the hunting season \( (N_{a,r,t+1}) \) was equal to the total number of adults that survived the previous year, combined with juveniles that survived from the previous year and graduated to adulthood \( (S_{a,r,t}, M_{j,r,t}) \), each of which was drawn from binomial distributions

\[ M_{a,r,t} \sim B(Q_a r, S_{a,r,t}) \]  

Eq. 20

\[ M_{j,r,t} \sim B(Q_j r, N_{j,r,t}) \]  

Eq. 21

where \( Q_r \) was the total probability of survival, estimated as

\[ Q_r = S \times (1 - \hat{h}_r) \]  

Eq. 22

As we used categorical covariates to describe regional differences in survival and therefore could not directly estimate survival in regions in which we did not band, we estimated a single value for \( S \) for all regions by averaging survival in those regions where captures occurred. We assumed that the number of juveniles recruited into the population at the beginning of each hunting season was proportional to the number of adults alive in the previous year, such that

\[ N_{j,r,t+1} \sim \text{Pois}(\lambda) \]  

Eq. 23

\[ \lambda = N_{a,r,t} \times R_t \]  

Eq. 24

\[ R_t \sim U(e^{-10}, e^{10}) \]  

Eq. 25

where \( R \) was recruitment rate. Because abundance estimates were dependent on estimates from the previous occasion, starting values \( (t = 1) \) for \( N_j \) and \( N_a \) were assumed to be equal to
\[ N_1 = \frac{T}{H} + 1 \]  \hspace{1cm} \text{Eq. 26}

2.2.2 Model Validation

In order to assess model accuracy, we simulated data that spanned a series of adjacent regions with variable abundance. We generated a 100 km x 100 km study area which was divided into 25 regions that had an area of 400 km² each (Figure 2.2). Capture sites were randomly distributed across the study area, and each capture site was randomly assigned either a high, medium, or low number of captured individuals. For each data set, we simulated banding, telemetry, and total harvest data for a given population, and used constant intercepts and beta coefficients to simulate weekly survival and harvest rates across the area, with modifications as described below to incorporate spatial heterogeneity. To prevent unrealistic population growth, we restricted the maximum regional abundance using a fixed carrying capacity of 5000 individuals. To introduce spatial variation into harvest rate and survival parameters, we generated Gaussian random fields using the “gstat” package (Pebesma 2004) in program R (R Core Team 2020) which created a location-specific beta coefficient that described spatial variation across the study area. We assessed the accuracy of estimates under variable sampling within a region and across the study area. To ensure that the simulation accurately presented a range of possible spatial heterogeneities and that the model was robust to those ranges of variation, we simulated multiple spatial configurations of harvest rate using low, medium, or high values for the partial sill, range, and nugget of the variogram used to generate the random field. In practice, this allowed us to vary the magnitude of variation in harvest rate, the maximum distance of autocorrelation, and the amount of small scale variation in harvest rates, respectively (Figure 2.3).

To evaluate model accuracy, we compared simulated values to estimates of harvest rate, survival, and abundance generated by the model. Due to wide variation in potential abundance values among simulated regions, we did not use absolute measures of error, where regions with greater
Figure 2.2. Spatial predictive processes project the underlying spatial correlation between capture sites (dots) onto an evenly distributed number of spatial knots (triangles) which leads to parameter estimates that are more representative of the area as a whole.
Figure 2.3. Spatial variation can follow many configurations, as shown by these example maps depicting potential variation in a parameter of interest according to the differences in the magnitude of variation (A-C), the maximum distance of autocorrelation (D-F), and the amount of small scale variation (G-I).
abundance would inherently have greater absolute error values. Instead, we calculated the relative bias as the difference between the true and estimated value for each region, divided by the true value.

\[
\text{Relative Bias} = \frac{\text{True} - \text{Estimated}}{\text{True}}
\]

Eq. 27

2.2.3 Case Study: Wild Turkeys in Maine

To demonstrate the applicability of the model, we used data collected from wild turkeys in Maine, USA. Maine is a large state with a variety of intermixed land use types and variable hunter densities. As such, we expected that failure to incorporate spatial variation in harvest would violate assumptions of the Lincoln estimator and lead to bias in abundance estimation (Lincoln 1930, Alisauskas et al. 2009), making it an excellent study system to apply the model. Turkeys were capture during winter using rocket and drop nets and aged as either adult or juvenile (<1 year old) according to plumage (Dickson 1992). We marked turkeys with at least 1 of 4 different marking methods with associated identification numbers, including aluminum butt end leg bands, aluminum rivet bands, plastic colored leg bands, and patagial wing tags. Nearly all individuals receiving at least 2 marks, and we assume retention of at least 1 mark was 100%. In addition to identification numbers, leg bands included contact information (toll free phone number and web form) for hunters to report the harvest of banded individuals. Hunters reported harvested turkeys directly to the project via these reporting options, or to harvest check stations when registering their turkey.

At capture sites in the greater Portland and Bangor areas, a subset of turkeys was fit with 12g VHF necklaces from Advanced Telemetry Systems (Model A3950; Isanti, Minnesota, USA), although 2 individuals were marked with 90g Litetrack GPS backpack from Lotek Wireless Fish and Wildlife Monitoring (Newmarket, Ontario, CA). We attempted to record one live/dead status for each radioed individual per week. If a transmittered individual died within the first two weeks post capture, they were censored from the data.
In Maine, hunters were required to present their harvested turkeys to a local check station for registration, which provides both a count of total harvest within each of the state’s Wildlife Management Districts (WMD), as well as age class designation. Total harvest information was available through the Maine Department of Inland Fisheries and Wildlife for all hunting seasons dating to 2006, from which we used data on total turkey harvest from 2011 through 2021. These years follow a series of changes to harvest regulations which may impact estimates of harvest rate. Due to complications related to COVID-19, MDIFW did not require hunters to register harvested turkeys during the 2020 spring hunting season. Instead, a survey was conducted to gauge success and estimate total turkey harvest. We adjusted the model to treat 2020 total harvest data as a random variable with initial values equal to the estimated harvest from survey data.

In Maine, turkeys are managed within 29 discrete WMD, which are further aggregated into 6 administrative regions. The Maine Department of Inland Fisheries and Wildlife seeks WMD-specific abundances to inform harvest management. For the distribution of spatial knots in the SPP, we used a grid with 24km spacing, with additional knots placed at the geographic center of each WMD. We eliminated knots from WMDs that did not have sufficient reported harvest to produce reliable estimates. These knot specifications ensured consistent coverage across the state, such that each WMD of interest had at least one knot within its boundaries, and that we did not predict harvest rates beyond where our data could reasonably be considered representative. The distance of 24 km was chosen by running multiple iterations of the model using various grid spacing. We then compared WMD-specific harvest rate estimates for each iteration to a model with a categorical covariate for WMD. We used root mean squared error

$$\sum \sqrt{\frac{(SPP.\text{est} - \text{Covariate.\text{est}})^2}{n}}$$

Eq. 28
to select the largest grid spacing that minimized error while also reaching convergence within the model. To compare estimates when spatial variation was not incorporated into estimates of harvest rate, we ran the model both with and without the SPP component included to compare results.

2.2.4 Computational Details

We fit the simulated data to the model as described in section 2.1, using a Bayesian approach (Hobbs and Hooten 2015). We used JAGS v.4.3.0 (Plummer 2003) via the “R2jags” package (Su and Yajima 2015) in the R v.4.0.3 programming environment (R Core Team 2020). For simulated data, models were allowed to run for 10,000 iterations, discarding the first 5,000 iterations before collecting samples. For data collected from wild turkey populations, the model was allowed to run for 50,000 iterations, discarding the first 20,000 iterations before collecting samples.

2.3 Results

2.3.1 Simulation Accuracy

Across all simulations, the average relative bias for abundance estimates was -0.04 (SD = 0.21) for adults and -0.05 (SD = -0.22) for juveniles, with each being approximately zero-centered (Figure 2.4). Relative bias in harvest rate estimates averaged -0.10 (SD = 0.18) for adults and -0.14 (SD = 0.22) for juveniles. Relative bias in weekly survival rate averaged 0.001 (SD = 0.002) for adults and 0.007 (SD = 0.006) for juveniles. We did not observe any relationship between relative bias in abundance estimates and configuration of spatial variation in harvest rates (Figure 2.5). Similarly, we did not observe any differences in relative bias in abundance associated with sampling intensity for the sample sizes we considered, both for sampling within a region and for sampling across a study area within a simulation (Figure 2.6). When we compared relative bias in abundance as it related to the portion of the population that was banded, we found that bias became more negative as the proportion banded increased, and variance increased as the proportion banded decreased (Figure 2.7).
Figure 2.4. Relative bias was consistently low for estimates of adult (A) and juvenile (B) abundance produced by a Lincoln Estimator with a spatial predictive process to account for spatial variation in harvest rates. Results shown are for simulated data sets which varied in the underlying spatial heterogeneity in the harvest rate.
Figure 2.5. Relative bias in region specific abundance estimates were consistent regardless of the spatial configuration in harvest rate. Relationship between relative bias and real abundance is depicted for each simulation set, which differed accord to their magnitude of variation (A-C), the maximum distance of autocorrelation (D-F), and the amount of small scale variation (G-I) in harvest rate.
Figure 2.6. Relative bias in region specific estimates of abundance were consistent across variable sample sizes for different data inputs, illustrated here by a summary of simulation results showing variation in bias according to sample size (x-axis) across a variety of spatial configurations in harvest rate (boxplot color).
Figure 2.7. Relative bias in region-specific abundance estimates became more negative and less variable as the proportion of banded individuals in a population increased as evidenced by the summary of results from simulation data used in a Lincoln Estimator using a spatial predictive process to account for spatial variation. The model was tested under 7 different spatial configurations of variation in harvest rate (corresponding to color of boxplots).
2.3.2 Case Study

During December through March 2018 through 2020, 408 unique male wild turkeys were trapped and banded at 72 capture sites across Maine (Figure 2.8). Of those captured, 187 were adult males and 221 were juveniles. Transmitters were deployed on a subset of 58 males. Of male turkeys captured and marked, 136 were reported as harvested during the 2018-2021 spring bearded turkey hunting seasons.

Region-specific estimates of turkey abundance averaged 677 adults and 1361 juveniles across all years and ranged from 2 – 4310 adults and 1 – 7010 juveniles (Figure 2.9). Total male turkey abundance averaged 42,797 individuals and ranged between 36,338 turkeys in 2015 and 49,238 turkeys in 2018. Region-specific estimates of adult harvest rates averaged 0.35 (ranged between 0.12 – 0.56; Figure 2.10) compared to 0.07 (ranged between 0.02 – 0.12) for juveniles. Mean weekly survival rate across years was 0.99 (ranged between 0.96 – 1.0) for adults and 0.98 (ranged between 0.89 – 1.0) for juveniles. Estimates of turkey productivity averaged 3.12 juveniles per adult and ranged between 0.13 – 109.49.

When comparing parameter estimates for models with and without the inclusion of the SPP, we found that abundance of adult turkeys was consistently lower, and had smaller credible intervals, when the SPP was included versus when it was not (Figure 2.11A). The mean difference between estimates of the two models was 286.96 (SD = 601.79) for adults and 52.88 (SD = 1072.28) for juveniles. Estimates of adult harvest rates were consistently higher when the model included a SPP compared with the model that assumed constant harvest rate (Figure 2.11C). For the juvenile age class, we observe substantially less difference in parameter estimates between models with and without a SPP (Figure 2.11B,D), consistent with a lower overall harvest rate for juvenile males, with inherently less room for variability as a result.
Figure 2.8. Spatial knots (red triangles) chosen for the spatial predictive process provide more uniform and complete coverage of the area of interest compared to capture sites (blue dots). For capture sites distributed across Wildlife Management Districts in Maine, sample size is indicated by the size of the dot, with large dots meaning larger sample sizes. Color of dots indicate whether a site had telemetry devices deployed (dark blue) or did not (light blue).
Figure 2.9. Wild turkey abundance varied across space and time for populations in Maine, USA, as predicted by a Lincoln Estimator with a spatial predictive process component. Map colors indicate mean abundance of wild turkeys adults (A) and juveniles (B) in 2021. Adult (solid line) and juvenile (dashed line) turkey abundance is shown for 2011 through 2021 (C).
Figure 2.10. Harvest rate estimates were variable among wildlife management districts across Maine, USA, for both male and juvenile wild turkeys. Regional difference in harvest are depicted for adult male turkeys with color indicating mean harvest rate for each management district.
Figure 2.11. Estimates of adult abundance and harvest rate differed between Lincoln Estimators with and without a spatial predictive process included, but juvenile harvest rate and abundance were largely similar. Estimates from both models are presented with associated error bars for abundance (A,B; shown on the log scale) and harvest rate (C,D). For C and D, triangles indicate harvest rate estimated without the inclusion of the SPP and circles indicate with the SPP.
2.4 Discussion

We found that a Lincoln estimator incorporating a SPP in the band recovery model consistently provided estimates of adult and juvenile abundance with low bias across a variety of spatial configurations of harvest for simulated data. Additionally, we found no difference in relative bias according to either sampling intensity or the underlying nature of spatial heterogeneity in harvest. When applied to real data collected from turkey populations in Maine, we observed a wide range of harvest and abundance among wildlife management districts. As expected, we found the model that did not incorporate spatial heterogeneity in harvest via the SPP underestimated harvest in some WMDs, which resulted in over-estimation of abundance in those districts, and statewide. The variation in harvest rates we observed are not irregular and should be expected across larger spatial scales (Norton et al. 2012). Most recent applications of Lincoln estimators have treated harvest rates as uniform across large areas (Alisauskas et al. 2013, Hagen et al. 2018, Shirkey and Gates 2020). While this assumption may be appropriate in some circumstances, our results suggest that future applications could consider more explicitly incorporating spatial variation in harvest rates to improve inference.

Harvest management decision must often consider populations that span considerably large spatial scales (Robinson et al. 2016). In these cases, it is not necessary to attempt inferences at individual locations because decisions are made at regional levels (Johnson et al. 2015). Instead, estimates can be aggregated to summarize relationships within a region’s boundaries, making fine scale differences in parameters at local scales less important than adequately capturing the general trend in a parameter across space. Aggregating estimates to describe parameters by region can be performed using multiple methods, with the simplest solution being to average estimates within each region. However, consideration must be given to the sampling design used, as clumped or sparse sampling within an area could lead to bias if sampled locations differ greatly from the mean across a landscape.
(Hooten et al. 2017). To some degree, SPP can mitigate such issues by using the entire data set to define a spatial correlation function and projecting it onto evenly distributed spatial knots from which estimates are then made. This will have the benefit of smoothing the prediction surface, minimizing the impact of any single sampling location which may otherwise have outsized impacts on local averages. However, if larger areas or districts have particularly high or low harvest rates, and are unsampled, the model would not be able to interpolate those relationships, meaning that adequate and representative sampling is still an important component of study design. With that said, when adequate sampling is performed, SPP has proven to be effective at identifying localized effects or “hotspots” in parameters (Viana et al. 2013), and indeed we found that model predictions were robust to a wide range of underlying spatial heterogeneity in harvest. Additionally, the placement of adequately spaced spatial knots to cover the complete area of interest overcomes some of the limitations of discontinuous data.

We observed some variation in the magnitude and direction of error across iterations, which is common when assessing IPMs (Abadi et al. 2010, Fieberg et al. 2010). We further found that relative bias became more negative, and variance decreased, as the proportion of a population that was banded increased. This shift in bias is consistent with a long-understood relationship, where accuracy of mark-recapture models depend on the ratio of the banded sample to total abundance (Robson and Regier 1964), and reinforces previous recommendations that sample size of banding studies should be informed by expected population size (Robson and Regier, 1964).

Despite the advantages of SPP, there are still opportunities for improvement. SPPs can incorporate spatial and temporal variation as separate components, but in many cases vital rates may vary according to a spatiotemporal relationship (Nichols 1996, Diefenbach et al. 2004, Rushing et al. 2017). In these instances, it would be ideal to devise a mechanism through which spatial and temporal SPPs are linked (Viana et al. 2013). Although SPP should be notably faster than alternatives, especially as the amount of data increases, using MCMC can still lead to lengthy computing times (Banerjee et al. 2010, Fieberg et al. 2010).
so alternative posterior samplers should be considered or devised to decrease processing time. As with all modeling approaches, the advantages of SPP will not overcome extremely sparse data availability or poor sampling design. As previously mentioned, the number of individuals marked should be proportional to the expected population size being sampled. While we did not observe an effect of sample size on model bias for the sample sizes we considered, which mimicked those we felt realistic for our wild turkey case study, further exploration with more limited data sets may be necessary to find a threshold at which estimates are no longer accurate. Similarly, the distribution of sampling locations as well as the configuration of spatial knots across a study area should be informed by the ecology of the system being studied. The number and placement of knots for the SPP is not trivial, and while there appears to be a wide margin for error, these decisions have an impact on estimates (Banerjee et al. 2008).

Multiple methods are currently used to monitor turkey populations. Many states approximate population trends using spring harvest data (e.g., CDEEP 2016, Harms et al. 2017), but this is only an index to population size that does not provide an estimate of overall population size which is often necessary for setting regulations (Lint et al. 1995). This method also requires accounting for changes in abundance of birds and harvest rates, both of which influence the number of birds harvested through time (Paloheimo and Fraser 1981). Expert opinion has been used to inform management decision, which is sometimes based on previous research but is more often informed by a-priori expectations rather than being data driven. Surveys such as summer sighting (PGC 2021), gobble counts (Rioux et al. 2009), and camera traps (Gonnerman 2017) can be used to produce estimates of population size at smaller scales but will be unrealistic to implement for statewide management due to restrictions on personnel time and funding. Harvest registration information is also used as an index to turkey population size by multiplying the registered spring harvest number by 10, a “rule of thumb” strategy based on the assumption that spring gobbler harvest is equal to 10% of the total population (Healy 2000). An IPM,
such as the one we have implemented, provides a data-driven alternative that can be scaled to the scope of turkey management decisions. It is relatively cost-effective as it uses often already implemented mandatory reporting of harvests and only requires periodic captures of individuals for banding. Similar IPMs have been implemented for turkey and waterfowl populations to great success (Diefenbach et al. 2012, Alisauskas et al. 2013), demonstrating that this is a feasible alternative that, with the inclusion of an SPP component, overcomes many of the shortcomings of the more common methods for monitoring turkey populations.

2.5 Conclusions

Management decisions based on biased estimates of abundance may lead to harvest regulations that exceed sustainable levels (Dillingham and Fletcher 2008). Violations of the Lincoln estimator’s assumption of representative harvest can bias estimates of both harvest rates and abundance. As Lincoln estimators become more widely applied, it is important to consider a mechanism to account for spatial variation in harvest rates. Harvest can vary according to a broad range of spatially varying ecological, environmental, and socio-economic factors that can be difficult to measure (Pope and Powell 2021). For such cases, the combination of Lincoln estimator and SPP is an especially relevant tool for capturing the magnitude and distribution of variation to reduce bias in estimates used for management. SPP functions as a component of a generalized linear mixed model framework, making it compatible with many analytical methods currently used in ecology, and therefore should be more accessible to those less familiar with spatial statistics. While we chose to apply these methods to harvest rates within a band recovery model, the use of SPP should be widely applicable across methods for vital rate estimation.
CHAPTER 3

BABY IT’S COLD OUTSIDE: DYNAMIC WINTER WEATHER MODERATES MOVEMENT BEHAVIORS AND RESOURCE SELECTION AT NORTHERN RANGE LIMITS

For wide-ranging species in northern temperate environments, populations at northern range limits are subject to more extreme conditions, colder temperatures and greater snow accumulation, compared to those in core areas. As climate change progresses, these bounding pressures may moderate on average, while extreme weather events occur more frequently. Behavioral plasticity is a potential mechanism through which animals can mitigate such extremes and continue their existence or expand at northern range limits, however relatively little work has explored how animal resource selection varies with changing weather. We applied hidden Markov movement models and step selection functions to GPS data from wintering eastern wild turkeys (*Meleagris gallopavo silvestris*) occurring near their northern range limit to identify how weather influences the transition of individuals among discrete movement states and their state-specific resource selection. We found that turkeys were more likely to spend time in a stationary state as wind chill decreased and snow depth increased, and both stationary and roosting turkeys selected for conifer forested areas and avoided areas more commonly associated with winter foraging, such as agricultural and residential areas. In contrast, mobile turkeys showed relatively weak selection for covariates considered. The degree to which turkeys altered resource selection in response to inclement weather depended both on their movement state and the specific weather variable being considered, illustrating that behavioral plasticity in response to weather was context dependent. Given our results, the potential extent of wild turkey range extension will in part be determined by availability of habitat that allows them to withstand periodic inclement weather. Combining hidden Markov movement models with step selection functions is a broadly applicable approach that can be used to identify plasticity in animal movement and dynamic resource selection in response to changing weather.
3.1 Introduction

For wide-ranging species, populations at range limits are subject to different constraints compared to those in core areas. Such constraints lay at the edge of a species fundamental niche and will influence range boundaries of a species (Soberón 2007). In the temperate regions of the northern hemisphere, colder temperatures and greater snow accumulation during winter lead to higher energetic demands (Evans 1976, Parker et al. 2009), and persistent snowpack and shorter growing seasons cause resource shortages, inhibiting individuals’ ability to meet those demands (Hou et al. 2020, Humphries et al. 2002). As climate change progresses, these bounding pressures may moderate, leading to northward expansion of certain species (Parmesan 2006, Jeschke and Strayer 2008). At the same time, the magnitude and incidence of extreme weather events is expected to increase (Easterling 2000), and the ability of individuals to persist along an expanding northern range limit will also depend, in part, on the ability to contend with extreme short term weather events (Early and Sax 2011). Thus, it is important to consider these changes in terms of both the shifting thermal niche of a species, as well as the capacity of individuals to be plastic in the face of changing weather, in order to accurately predict potential shifts in range limits.

A broad suite of physiological and life history traits enable persistence in the face of extreme weather (James 1970, Blem 1976, Geiser 2004, 2013, Ohlberger 2013, Blix 2016) but changes to such traits occur across generations, meaning selective changes that facilitate adaptation to more frequent extreme weather will occur at slower rates for species with longer inter-generational times (Noonan et al. 2018). Behavior, on the other hand, can be highly plastic (Gross et al. 2010, Hertel et al. 2020, Stewart et al. 2016) and is better suited for responding to short term variability in weather (Burger 1982, Santoro et al. 2013, Shaw 2020). For example, animals may moderate movements and activity levels in response to weather, using flexible feeding strategies to minimize foraging time and energetic costs (Daunt et al. 2006, Baylis et al. 2015, Fremgen et al. 2018), by increasing movements to gain access to
additional resources (Loe et al. 2016, Zhang et al. 2017), or by seeking out temporary refugia from extreme conditions (Shipley et al. 2019). In this way, behavioral plasticity allows animals to at least temporarily mitigate extreme cold or heavy precipitation, and may contribute to their continued existence at expanding northern range limits.

Resource acquisition is a key behavior in which animals exhibit plasticity is their decision-making. Fluctuating winter weather causes the value of local resources to vary by changing the relative risks and rewards associated with obtaining them (Parker et al. 2003). Individuals can alter their resource selection strategies to account for these changes during temporary weather events (Hall et al. 2016, Shipley et al. 2020), directly linking decisions to fitness outcomes (Leclerc et al. 2016). Despite the critical role of behavioral plasticity in resource selection for animals at northern range limits, relatively little research has evaluated dynamic resource selection under changing weather. Of the research available, there is clear evidence that animals moderate resource use according to snow depth (Courbin et al. 2017, Gilbert et al. 2017), temperature and wind speed (Sunde et al. 2014), or combinations of the two (Mayer 2019). Considering that winter weather can be highly dynamic, both within and among years, a lack of focus on plasticity in resource selection may lead to a poor understanding of how weather interacts with climate to limit a species’ range.

Understanding plasticity in resource selection is complicated by the context-specific nature of animal decision making. Functional responses, or the degree to which individuals encounter different availability of resources, may affect patterns of selection under variable landscape configurations (Beyer et al. 2010). Resource selection can also be behaviorally mediated, such that individuals make different decisions according to their current behavioral state (Cooper and Millspaugh 2001). For example, we may not expect animals to select the same landcover characteristics while foraging as they would during periods of rest or reproduction (Marzluff et al. 2004), and resident adults may differ in their selection compared with dispersing juveniles (Elliot et al. 2014). Unfortunately, quantifying variation related to
individual characteristics and experiences is difficult and often impossible to measure fully, requiring alternative approaches to incorporating such information into models (Patterson et al. 2009).

In recent years, multiple tools have been developed to provide accurate information on animal behavior from movement data. For example, Hidden Markov Models (HMM) can infer an animal’s behavioral state at a given time based on characteristics of observed movements (Langrock et al. 2012) and link variation in movement among those behaviors to environmental characteristics (McClintock et al. 2012). There are also new methods for assessing resource selection, such as Step Selection Functions (SSF; Duchesne et al. 2010) which follow a similar framework to more common resource selection functions (RSF) but use conditional regression to pair individual steps with available points to refine the scale of observation. This stepwise approach is better suited for matching the fine temporal scales at which decisions are made with the scale at which behavioral changes occur. For example, weather changes constantly over time, so the shorter time scale of SFFs makes them particularly well-suited for evaluating the effects of weather on resource selection, as they operate on an inherently shorter time scale that is more consistent with changes in weather patterns. Both HMM and SSF allow for the incorporation of random effects to account for unobserved variation (DeRuiter et al. 2016, Muff et al. 2020), which can often encompass both variable availability and differences in behavior among individuals (e.g. personality). Merging these two approaches would provide a means to identify behavior specific movement and resource selection patterns, while also accounting for how those patterns differ according to local weather.

Here we present an approach that combines HMM and SSF methods to identify how weather influences the transition of individuals among discrete movement states and their state-specific resource selection. We applied this approach to winter resource selection of eastern wild turkeys (Meleagris gallopavo silvestris; hereafter turkeys) occurring near their northern range limit in Maine, USA. Wild turkeys are a wide-ranging species that occurs across a broad suite of climate zones
throughout North America (Dickson 1992). At the northern range limit during winter, turkeys must contend with a combination of extreme low temperature, which increases energetic demands, and a scarcity of food resources as persistent snowpack obscures ground-based food resources. How turkeys moderate their behavior to contend with these conditions will influence winter survival, and may carry over to reproductive success the following spring (Lavoie et al. 2017, Porter et al. 1983). Obstruction of food sources may require more time spent foraging, but this can also lead to increased predation risk or exposure to harsh weather. Alternatively, more time spent sheltering from inclement weather will reduce energetic demands of thermoregulation but at the expense of caloric intake, which may reduce body condition and affect survival and future reproductive attempts. Turkeys roost in trees at night to avoid predators, but this may provide poor protection from the elements. Selection for roost sites that provide shelter from wind during the night may require greater distance from foraging areas, increasing the risk associated with moving between the two.

Our goal was to understand how turkeys altered daily patterns in movement in response to changing weather, and how this in turn affected their selection of resources that are potentially important for winter persistence. We did this by 1) comparing how the transition between movement states of wild turkeys changed according to local weather, and 2) identifying sources of variation in state-specific resource selection that was associated with local weather. We hypothesized that poor weather (colder wind chill and greater snow depth) would cause turkeys to spend a greater amount of time in a more stationary movement state as they sheltered from inclement conditions, and less time in a mobile state spent moving throughout their home range. We also hypothesized that poor weather would cause turkeys to alter selection in favor of landcover features that provided thermal refugia, regardless of movement state.

3.2 Materials and Methods

3.2.1 Wild Turkeys within the Study Area
Our study area in central Maine (44.804°N, -68.823°W) contained three major landcover types that were representative of general landcover gradients across much of Maine; industrial forestland, urban/suburban matrices, and agriculture. All landcover types were potentially available to turkeys throughout the study area, however agricultural land dominated the western portion of the study area, industrial forest was primarily located in the east, and the suburban/urban matrix existed in the center. Turkeys captured within this study area experienced consistent weather associated with a single climatic zone; all but one of 21 capture sites occurred within 41 km of the center of our study area, with the exception located in Monson, ME, 77 km northwest from the center.

3.2.2 Data Collection

Turkey were captured at baited sites during three winters (December 1 to March 31) in 2018 through 2020 using either rocket nets or drop nets. Captured females were chosen at random for deployment of 90-g Litetrack GPS transmitters (Lotek Wireless, Newmarket, Ontario, CA). GPS transmitters were programmed to collect hourly locations during daylight from November 1 through July 31, and one roost location was recorded each night at either 12am or 1am. We restricted our period of observation for this analysis to January 1 through March 15, with the end date corresponding to rising temperatures and increased turkey movements associated with the onset of spring. We censored all birds that died within two weeks of capture to limit the influence of trapping related effects. If two or more females were located together, we only used data from 1 individual to avoid pseudo-replication associated with correlated movements within social groups (i.e., flocks). In the case that not all marked individuals from a single flock survived the entire winter, we chose the longest-lived individual, otherwise we selected a female at random to represent the flock for that winter.

Information on local weather was obtained from the NOAA climatological database (Vose et al. 2014) for the Bangor International Airport weather station. We assumed that weather at this station was correlated with the conditions throughout our study area and could therefore be used as an index.
for changes in weather. We identified wind chill and snow depth as two major weather variables that
could influence turkey behavior, and we used daily measurements of each to describe variation in
behavior and resource selection. We calculated a minimum daily wind chill metric as $13.12 + (0.6215 \times T) - (11.37 \times V^{0.16}) + (0.3965 \times T \times V^{0.16})$, where $T$ was minimum temperature and $V$ was average wind
speed (Osczewska & Bluestein 2005).

A description of landcover covariates with associated data sources and expected correlation
with weather covariates is provided in Table 3.1. To characterize forest resources, we used
representative tree profiles derived from LiDAR point cloud data as presented by Ayrey et al. (2017) to
quantify basal area, distance to forest edge, mean tree height, and percent composition of conifer
species, each at a 10m x 10m scale. To characterize broader landscape features, we used the 2016
National Land Cover Database (Homer et al. 2020) which provided information on the amount of
agricultural (pasture/hay and row crop) land, developed land, and conifer forests at a 30m x 30m scale.
We further aggregated agricultural and developed landcover types into a single ‘food subsidy’ layer, as
these landcovers collectively reflect potential sources of anthropogenic foods available to turkeys (e.g.
waste grain or recreational bird feeders). Roosting turkeys require trees, thus we did not include
covariates for agriculture, developed, or food subsidies in models for roost site selection. We used
digital elevation models available through the Maine Geolibrary Database (Gesch et al. 2018) to
estimate the down slope within each 10m x 10m grid cell using the aspect tool in ArcMap (v10.8.1). We
then found the difference between aspect and wind direction to produce a wind exposure metric. To
characterize landcover characteristics at a local scale, we used a moving window to average each
landcover characteristic within a 90m x 90m square around each raster cell. Both weather and landcover
covariates were Z-standardized to a facilitate comparison of coefficients among variables.
Table 3.1. We hypothesized that landcover characteristics that provide shelter from decreased wind chill and increased snow depths would be selected for regardless of movement state. We provide a description of each covariate considered in our step selection function and where the data was obtained. We include the expected direction of the relationship between each landcover covariate and either wind chill or snow depth.

<table>
<thead>
<tr>
<th>Covariate</th>
<th>Description</th>
<th>Data Source</th>
<th>Wind Chill</th>
<th>Snow Depth</th>
</tr>
</thead>
<tbody>
<tr>
<td>Basal Area</td>
<td>Average amount of area occupied by tree stems (m²/ha)</td>
<td>LiDAR (Ayrey et al. 2017)</td>
<td>-</td>
<td>+</td>
</tr>
<tr>
<td>Distance to Forest Edge</td>
<td>Distance from nearest cell with basal area greater than 0</td>
<td>LiDAR (Ayrey et al. 2017)</td>
<td>-</td>
<td>+</td>
</tr>
<tr>
<td>Mean Tree Height</td>
<td>Mean tree height within a cell (m)</td>
<td>LiDAR (Ayrey et al. 2017)</td>
<td>-</td>
<td>+</td>
</tr>
<tr>
<td>Percent Conifer</td>
<td>Percent of cell covered by conifer tree species</td>
<td>LiDAR (Ayrey et al. 2017)</td>
<td>-</td>
<td>+</td>
</tr>
<tr>
<td>Proportion Agriculture</td>
<td>Proportion of cells within a 90m x 90m area categorized as pasture/hay or row crop</td>
<td>NLCD (Homer et al. 2020)</td>
<td>+</td>
<td>-</td>
</tr>
<tr>
<td>Proportion Developed</td>
<td>Proportion of cells within a 90m x 90m area categorized as developed land of any intensity</td>
<td>NLCD (Homer et al. 2020)</td>
<td>+</td>
<td>-</td>
</tr>
<tr>
<td>Proportion Food Subsidy</td>
<td>Sum of the proportion agriculture and developed within a 90m x 90m area</td>
<td>NLCD (Homer et al. 2020)</td>
<td>+</td>
<td>-</td>
</tr>
<tr>
<td>Proportion Conifer</td>
<td>Proportion of cells within a 90m x 90m area categorized as coniferous.</td>
<td>NLCD (Homer et al. 2020)</td>
<td>-</td>
<td>+</td>
</tr>
<tr>
<td>Wind Exposure</td>
<td>Difference between the slope and wind direction at a location on a given day (0°–180°)</td>
<td>Digital Elevation Map (Gesch et al. 2018)</td>
<td>+</td>
<td>-</td>
</tr>
</tbody>
</table>
3.2.3 Hidden Markov Movement Models

We constructed an HMM using the momentuHMM package (McClintock and Michelot 2018) within the R programming environment (v4.0.3, R Core Team, 2020) to categorize individual location data into three discrete movement states: roosting, stationary, and mobile (Appendix 1). Turkeys spend nights roosted in trees for safety from predators, and as such would be found in the same location during successive locations while in this state. We described stationary behavior as localized movements with little concentrated directionality, such as would be typical of birds that were loafing, preening, or sheltering (Dickson 1992). Mobile behavior differed from stationary in that distance between successive locations was greater and movement more concentrated in a persistent direction, corresponding to individuals foraging or commuting to distant food resources (Dickson 1992). We measured step length and turning angle between successive GPS transmitter locations for use as data streams within the HMM, and applied constraints to the HMM structure (as described in Appendix 1) to accommodate these three movement states.

We assumed transition between states would be influenced by snow depth and wind chill, which were treated as fixed effects using daily averages measured as previously described. We also assumed an effect of hour of the day, which we incorporated into the model using the cosinor function within momentuHMM, to account for the cyclical nature of turkey behavior throughout the day. The cosinor function estimated a coefficient for both the cosine and sine of 2×π×(hour of the day/24 hours). It was not possible to directly specify random effects within momentuHMM, so we included individual by year level covariates to account for difference in individual behavioral tendencies. The final model was visually assessed for goodness of fit using the Q-Q Plot for the pseudo-residuals of the model (Zucchini et al. 2017). To determine the significance of the relationship between weather covariates and state transition probabilities, we examined coefficient values and their 95% confidence intervals. We
used the multinomial logit link function to translate coefficient values to interpretable results. Using outputs from the HMM, we assigned the most likely movement states to each location after fitting our models.

3.2.4 Step Selection Functions

We used step selection functions (SSF; Duchesne et al. 2010) to explore how resource selection by turkeys varied among movement states generally, and within each movement state according to changing weather. Inference from SSFs are similar to the more commonly used RSFs, with the main difference being that SSF do not aggregate points for individuals but rather pair each used point with a set of available points defined by the movement between successive locations (Fortin et al. 2005). When implementing a SSF, the inclusion of random intercept terms for individuals account for unbalanced sampling among individuals (Gillies et al. 2006, Muff et al. 2020), whereas individual-specific random slopes account for variable availability of resources among individuals, which can result in functional responses in selection (Duchesne et al 2010, Gillies et al. 2006). Random slopes also accommodate an appropriate amount of uncertainty in estimates that would otherwise be overconfident without their inclusion (Muff et al. 2019). For the purposes of our analysis, random intercepts and slopes corresponded to a single winter track for each bird.

SSFs are commonly implemented using conditional logistic regression, where used and available points for each movement step made by an individual constitute a conditional stratum (Muff et al. 2019). These methods can be computationally intensive, especially with the large number of stratum associated with GPS data and the inclusion of random effects. To work around these restrictions, Muff et al. (2019) offer a simple model reformulation of the general conditional logistic regression approach that takes advantage of the fact that the conditional logistic regression is a likelihood-equivalent to the Poisson model. Thus, the probability an animal \((n = 1, \ldots, N)\) at a given time \((t = 1, \ldots, T_n)\) selects a location \((j = 1, \ldots, J_{nt})\) with habitat characteristics \((x_{ntj})\) given a set of possible locations \((x_{nt} = \{x_{nt1}, \ldots, x_{ntJ}\})\) is
E(y_{ntj}) = \mu_{ntj} = \exp (\alpha_{nt} + \beta^T x_{ntj} + u_{ntj}^T z_{ntj}), \text{ with } y_{ntj} \sim \text{Po}(\mu_{ntj})

where $\beta$ is a vector of covariates describing variation in selection, $\alpha_{nt}$ is the stratum specific intercept of animal $n$ at time $t$, $u_{ntj}^T$ is the individual-specific random slope, and $z_{ntj}$ is a design vector.

Estimating $\alpha_{nt}$ for each location becomes prohibitive for larger samples, so instead $\alpha_{nt}$ is treated as a random intercept $\alpha_{nt} \sim \text{N}(0, \sigma^2)$ where $\sigma^2$ is fixed at $10^6$. We followed a Bayesian approach for implementing our models, as it allowed a straightforward method for fixing the variance of $\alpha_{nt}$. We used integrated nested Laplace approximation (INLA; Rue et al. 2009) for its efficiency in approximating posterior marginal distributions. To fit our INLA models for turkey movement data, we used the package r-INLA in the R programming environment.

To generate available locations for each used location, we used the “random_steps” function with default arguments from the “amt” package (Signer et al. 2019). Using the full winter movement track of an individual for a given year, we generated 10 available locations for each used location. We subset the used and available points according to the movement state designations identified from the HMM, and performed separate analyses for roosting, stationary, and mobile movement states. Since turkeys require trees for roosting, available roosting locations were limited to points falling in cells with tree basal area greater than 0, indicating that trees were present in the cell. To address questions related to the effect of weather on resource selection, we created two model sets for each movement state (6 model sets total). Each model was comprised of a covariate for a single resource variable, a covariate for either wind chill or snow depth, an interaction term between the weather and resource covariates, a random intercept and slope term for individuals within a year, and a Z-standardized covariate for step length (Forester et al. 2009). We examined 95% credible intervals for each beta coefficient to determine the significance of the relationship, and approximated the relative likelihood of selection given a particular covariate value as

\[ s(x_{tb}) = \exp (x_L \beta_L + x_W \beta_W + x_L x_W \beta_I) \]
Where, for a given location \( x \) at time \( t \) for movement state \( b \), the relative likelihood of selection \( s(x) \) is affected by the resource covariate \( L \), a weather covariate \( W \), and an interaction term \( I \) (Fortin et al. 2005). To compare differences in selection among movement states, we set \( x_{\text{mean}} = 0 \) (mean weather) and varied \( x_L \) across observed values. To identify how turkeys altered resource selection within movement states as a function of changing weather, we examined the relative strength of the interaction terms for each model (Fieberg et al. 2020). Negative interaction coefficients correspond with decreased selection as weather covariates increase. As harsher weather is characterized by increased snow depth and decreased wind chill, our hypotheses predict a positive interaction coefficient for snow depth and negative for wind chill when paired with land cover covariates associated with sheltering (e.g., conifer forests, basal area).

3.3 Results

We deployed GPS transmitters on 59 turkeys during 2018 through 2020, which resulted in 26 unique movement tracks after removing flock-mates, and 11,419 locations that we used for this analysis. The number of locations for a given movement track averaged 439, and ranged from 49 to 839 locations.

3.3.1 Variation Among Turkey Movement States

The HMM estimated mean step length (distance/hour) of mobile turkeys as 133.21 m (130.47 m – 135.95 m 95% CI) compared to 11.70 m (11.16 m – 12.24 m 95% CI) for stationary turkeys (Figure 3.1a, Table 3.2). Angular concentration for stationary and mobile turkeys had overlapping 95% confidence intervals and thus were not considered significantly different (Figure 3.1b, Table 3.2). Of the 11,419 locations collected from wild turkey females in winter of 2018 through 2020, our HMM designated 8.58% within the roosting movement state, 18.58% within the stationary state, and 72.8% within the mobile state. Across all locations collected, mean wind chill experienced by turkeys during our study was 15.65°F (range -14.16°F to 40.96°F) and mean snow depth was 3.86in (0.0 in – 29.9 in).
Figure 3.1. Estimated probability distributions for step length (A) and turning angle (B) describing the movement of individual turkeys within a given movement state as estimated by a Hidden Markov Model for animal movement. Step length was assumed to follow a gamma distribution and turning angle a wrapped Cauchy distribution. Also depicted, example turkey movement path with associated movement state (C)
Table 3.2. Estimated distribution of parameters describing the step length and turning angle of wild turkeys in each movement state as determined by hidden Markov models for movement. Step length was assumed to follow a gamma distribution and turning angle a wrapped Cauchy distribution.

<table>
<thead>
<tr>
<th></th>
<th>Roosting</th>
<th>Stationary</th>
<th>Mobile</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Step Length</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean</td>
<td>2.71 (2.31 - 3.11)</td>
<td>11.70 (11.16 - 12.24)</td>
<td>133.21 (130.47 - 135.95)</td>
</tr>
<tr>
<td>Standard Deviation</td>
<td>0.90 (0.02 - 0.36)</td>
<td>10.17 (0.02 - 0.36)</td>
<td>119.84 (0.02 - 0.36)</td>
</tr>
<tr>
<td>Zero Mass</td>
<td>1.00 (1.00 - 1.00)</td>
<td>0.00 (0.00 - 0.00)</td>
<td>0.00 (0.00 - 0.00)</td>
</tr>
<tr>
<td><strong>Turn Angle</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean</td>
<td>0.00 (0.00 - 0.00)</td>
<td>0.00 (0.00 - 0.00)</td>
<td>0.00 (0.00 - 0.00)</td>
</tr>
<tr>
<td>Concentration</td>
<td>0.20 (0.02 - 0.36)</td>
<td>0.26 (0.25 - 0.28)</td>
<td>0.27 (0.25 - 0.28)</td>
</tr>
</tbody>
</table>
Daily cycles identified by the cosinor function (Figure 3.2) indicated that turkeys were most likely to start their day in a stationary state after leaving their roost, between 5am and 9am, and were most likely to transition to a mobile state by 10am. Individuals were more likely to remain in a mobile over stationary state throughout the day, with a slight increase in transition probability to a stationary state in the hours before sunset. Wind chill and snow depth both affected the rate at which turkeys transitioned among movement states; individuals were more likely to transition from a mobile to a stationary state as wind chill decreased ($\beta = -0.45; -0.58 – -0.32$ 95% CI; Figure 3.3a,c) and as snow depth increased ($\beta = 0.30; 0.19 – 0.42$ 95% CI; Figure 3.3b,d). Individual slope coefficients (Figure 3.4) indicated that turkeys were more varied in their tendency to transition from a stationary to a mobile movement state than from a mobile to stationary state.

3.3.2 Movement-state-specific Resource Selection

Differences in step selection varied among movement states according to landcover type (Figure 3.5, Table 3.3). For models comparing either snow depth or wind chill, stationary and roosting turkeys showed similar patterns of selection, which differed from the selection patterns of mobile turkeys. Comparing models for snow depth, stationary turkeys had a stronger negative selection against increased percentage of agricultural lands ($\beta = -0.98; -1.55 – -0.54$ 95% CI) compared to mobile turkeys ($\beta = -0.19; -0.38 – -0.03$ 95% CI). Turkeys selected areas with greater tree basal area for all behaviors, however the strength of selection was far greater while roosting or stationary compared with mobile (Roosting $\beta = 1.08; 0.15 – 0.79$ 95% CI; Stationary $\beta = 0.73; 0.56 – 0.90$ 95% CI; Mobile $\beta = 0.23; 0.14 – 0.33$ 95% CI). Stationary and roosting turkeys selected for increased distance from forest edge while mobile turkeys showed no strong selection (Roosting $\beta = 0.44; 0.03 – 0.85$ 95% CI; Stationary $\beta = 0.36; 0.12 – 0.60$ 95% CI; Mobile $\beta = -0.12; -0.26 – 0.02$ 95% CI). Roosting and stationary turkeys were more likely to use conifer dominated forest stands while mobile turkeys showed no strong selection (Roosting
Figure 3.2. Estimated transition probabilities (lines) and associated error estimates (ribbon) between movement states of wild turkeys during winter in Maine. Panels show probability of a turkey transitioning from a roosting (A), stationary (B), or mobile (C) state to each movement state according to hour of the day.
Figure 3.3. Turkeys were more likely to be in a stationary state as wind chill decreased and snow depth increased, as evidenced by turkey time-activity budgets (A,B) and transition probabilities between movement states (C-F). Panels C and D show probability of a turkey transitioning from a stationary state to each movement state according to wind chill (C) and snow depth (D). Panels E and F show probability of a turkey transitioning from a mobile state to each movement state according to wind chill (E) and snow depth (F). Wind chill and snow depth are each Z-standardized.
Figure 3.4. Estimated individual-specific coefficients and associated error for the probability of transitioning between movement states of wild turkeys during winter in Maine. Panels show coefficients for transitioning from a roosting (A,B), stationary (C,D), or mobile (E,F) state to each movement state.
Figure 3.5. Relative selection strength by wild turkeys for landcover covariates when weather covariates were set at the mean value. Landcover covariates assessed were distance to forest edge (A), tree basal area (B), percent tree species classified as conifer in a stand (C), wind exposure (D), proportion of area classified as agricultural land (E), and proportion of area classified as developed land (F). All covariates were Z-standardized.
Table 3.3. Estimates of coefficients for landcover as determined by step selection functions for each weather covariate. Tables shows the movement state being analyzed, the landcover and weather covariate used in the model, and present parameter estimates, standard deviation (Std.Dev), confidence limits (LCL, UCL), and whether the confidence limits overlap 0 (Sign.).

<table>
<thead>
<tr>
<th>Movement State</th>
<th>Landcover</th>
<th>Weather</th>
<th>Estimate</th>
<th>Std Dev</th>
<th>LCL</th>
<th>UCL</th>
<th>Sign.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Roosting</td>
<td>Dist. to Forest Edge</td>
<td>Snow Depth</td>
<td>0.44</td>
<td>0.21</td>
<td>0.03</td>
<td>0.85</td>
<td>*</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Wind Chill</td>
<td>0.61</td>
<td>0.21</td>
<td>0.19</td>
<td>1.02</td>
<td>*</td>
</tr>
<tr>
<td></td>
<td>Basal Area</td>
<td>Snow Depth</td>
<td>1.08</td>
<td>0.15</td>
<td>0.79</td>
<td>1.36</td>
<td>*</td>
</tr>
<tr>
<td></td>
<td>Basal Area</td>
<td>Wind Chill</td>
<td>1.34</td>
<td>0.16</td>
<td>1.03</td>
<td>1.65</td>
<td>*</td>
</tr>
<tr>
<td></td>
<td>Mean Tree Height</td>
<td>Snow Depth</td>
<td>1.43</td>
<td>0.22</td>
<td>0.99</td>
<td>1.87</td>
<td>*</td>
</tr>
<tr>
<td></td>
<td>Mean Tree Height</td>
<td>Wind Chill</td>
<td>1.44</td>
<td>0.23</td>
<td>0.98</td>
<td>1.90</td>
<td>*</td>
</tr>
<tr>
<td></td>
<td>Percent Conifer</td>
<td>Snow Depth</td>
<td>0.66</td>
<td>0.11</td>
<td>0.43</td>
<td>0.87</td>
<td>*</td>
</tr>
<tr>
<td></td>
<td>Percent Conifer</td>
<td>Wind Chill</td>
<td>0.93</td>
<td>0.12</td>
<td>0.70</td>
<td>1.17</td>
<td>*</td>
</tr>
<tr>
<td></td>
<td>Wind Exposure</td>
<td>Snow Depth</td>
<td>-0.05</td>
<td>0.08</td>
<td>-0.21</td>
<td>0.11</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Wind Exposure</td>
<td>Wind Chill</td>
<td>-0.07</td>
<td>0.09</td>
<td>-0.26</td>
<td>0.11</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Proportion Conifer</td>
<td>Snow Depth</td>
<td>0.64</td>
<td>0.13</td>
<td>0.38</td>
<td>0.90</td>
<td>*</td>
</tr>
<tr>
<td></td>
<td>Proportion Conifer</td>
<td>Wind Chill</td>
<td>0.81</td>
<td>0.14</td>
<td>0.53</td>
<td>1.09</td>
<td>*</td>
</tr>
<tr>
<td></td>
<td>Dist. to Forest Edge</td>
<td>Snow Depth</td>
<td>0.36</td>
<td>0.12</td>
<td>0.12</td>
<td>0.60</td>
<td>*</td>
</tr>
<tr>
<td></td>
<td>Dist. to Forest Edge</td>
<td>Wind Chill</td>
<td>0.31</td>
<td>0.13</td>
<td>0.07</td>
<td>0.57</td>
<td>*</td>
</tr>
<tr>
<td></td>
<td>Basal Area</td>
<td>Snow Depth</td>
<td>0.73</td>
<td>0.09</td>
<td>0.56</td>
<td>0.90</td>
<td>*</td>
</tr>
<tr>
<td></td>
<td>Basal Area</td>
<td>Wind Chill</td>
<td>0.72</td>
<td>0.09</td>
<td>0.56</td>
<td>0.89</td>
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<tr>
<td></td>
<td>Mean Tree Height</td>
<td>Snow Depth</td>
<td>0.59</td>
<td>0.14</td>
<td>0.33</td>
<td>0.88</td>
<td>*</td>
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<tr>
<td></td>
<td>Mean Tree Height</td>
<td>Wind Chill</td>
<td>0.56</td>
<td>0.14</td>
<td>0.30</td>
<td>0.85</td>
<td>*</td>
</tr>
<tr>
<td></td>
<td>Percent Conifer</td>
<td>Snow Depth</td>
<td>0.52</td>
<td>0.08</td>
<td>0.36</td>
<td>0.68</td>
<td>*</td>
</tr>
<tr>
<td></td>
<td>Percent Conifer</td>
<td>Wind Chill</td>
<td>0.47</td>
<td>0.08</td>
<td>0.32</td>
<td>0.63</td>
<td>*</td>
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<tr>
<td></td>
<td>Wind Exposure</td>
<td>Snow Depth</td>
<td>-0.07</td>
<td>0.08</td>
<td>-0.23</td>
<td>0.08</td>
<td></td>
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<tr>
<td></td>
<td>Wind Exposure</td>
<td>Wind Chill</td>
<td>-0.08</td>
<td>0.08</td>
<td>-0.24</td>
<td>0.06</td>
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\( \beta = 0.64; 0.38 – 0.90 \) 95\% CI; Stationary \( \beta = 0.65; 0.40 – 0.91 \) 95\% CI; Mobile \( \beta = -0.02; -0.11 – 0.08 \) 95\% CI).

### 3.3.3 Within Movement State Variation in Resource Selection

Turkeys in all three movements states adjusted resource selection according to changing weather, however the strength and direction of effects varied according to movement state, landcover type, and weather variable (Figure 3.6, Table 3.4). Snow depth did not affect turkey roost site selection, however as wind chill decreased, roosting turkeys selected roost sites with greater basal area (\( \beta = -0.038; -0.019 – -0.002 \) 95\% CI) and greater amounts of conifer trees (\( \beta = -0.013; -0.021 – -0.005 \) 95\% CI; \( \beta = -0.010; -0.019 – -0.001 \) 95\% CI). Wind chill did not affect selection by stationary turkeys, but as snow depth increased, stationary turkeys selected for landcover with greater proportions of agriculture (\( \beta = 0.021; 0.004 – 0.037 \) 95\% CI), greater proportions of food subsidies (\( \beta = 0.027; 0.008 – 0.045 \) 95\% CI), closer to forest edge (\( \beta = -0.022; -0.040 – -0.005 \) 95\% CI), and decreased conifer forest (\( \beta = -0.038; -0.059 – -0.018 \) 95\% CI). Mobile turkeys altered their selection according to both snow depth and wind chill. As snow depth increased, mobile turkeys selected for areas with greater amounts of developed land (\( \beta = 0.012; 0.006 – 0.000 \) 95\% CI), decreased distance to forest edge (\( \beta = -0.020; -0.031 – -0.009 \) 95\% CI), and decreased amounts of agriculture (\( \beta = -0.015; -0.024 – -0.006 \) 95\% CI). As wind chill decreased, mobile turkeys selected for areas with greater proportions of agricultural land (\( \beta = 0.007; 0.001 – 0.004 \) 95\% CI) and food subsidies (\( \beta = 0.003; 0.000 – 0.006 \) 95\% CI).

### 3.4 Discussion

#### 3.4.1 Dynamic Behavior in Response to Weather

We found that turkeys were more likely to spend time in a stationary over mobile state as wind chill decreased and snow depth increased. This reduction in movement indicates that turkeys decrease activity levels in the presence of adverse weather, potentially to limit thermoregulatory costs and predation risk as increased snow depths inhibited their movement ability and decreased foraging
Figure 3.6. Interaction term beta coefficients and associated error between landcover covariates and snow depth (A) and wind chill (B) estimated from step selection functions for wild turkeys in Roosting, Stationary, and Mobile movement states during winter in Maine.
Tables 3.4. Estimates of interaction coefficients as determined by step selection functions for wild turkey resource selection. Tables shows the movement state being analyzed, the landcover and weather covariate used in the model, and present parameter estimates, standard deviation (Std.Dev), confidence limits (LCL, UCL), and whether the confidence limits overlap 0 (Sign.).

<table>
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<th>Weather Covariate</th>
<th>Landcover Covariate</th>
<th>Movement State</th>
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<th>StdDev</th>
<th>LCL</th>
<th>UCL</th>
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efficiency. Animals must make tradeoffs in time allocation, which in winter often amount to avoiding predation and maintenance of body temperature, and obtaining the necessary energy resources to offset thermoregulatory expenditure (Lima 1986). Additional time spent foraging may increase caloric intake, but during cold temperatures may come at the cost of net energy loss through exposure. Predation risk also can increase as increased snow depths inhibit movements, making foraging an extremely risky decision (Huggard 1993, Lendrum et al. 2018). In such circumstances, it may be more advantageous to forgo foraging temporarily and instead remain in less calorie rich areas to reduce energy expenditure and predation risk until more favorable weather arise (Warkentin and West 1990).

Such an ability to incorporate information about changing environments into decision making regarding daily activities has been observed in many species (Buttemer et al. 1986, Norberg 1977) and likely influences persistence at range limits where winter weather is a limiting pressure.

We found that stationary and roosting turkeys selected for conifer forested areas and avoided areas more commonly associated with winter foraging, such as agricultural and residential areas. This may be linked to microclimate characteristics associated with forest structure, where the age, species composition, and size of trees lead to dramatic differences in local temperatures, with stands of larger, conifer trees providing increased insulation to buffer against wind and colder temperatures (Ashcroft and Gollan 2012, Latimer and Zuckerberg 2017, Suggitt et al. 2011). In the context of harsh winter weather, a reduction in movement to limit predation risk and thermoregulatory expenditure should be associated with a shift in resource selection to areas that provide shelter (Paclík and Weidinger 2007, Lustick 1983, Walsberg, 1986). Sheltering in such areas during periods of inclement weather can lead to a net improvement of overall energy expenditure despite the decreased forage potential (Villén-Pérez et al. 2013), where the associated decrease in energy expended on thermoregulation results in a net improvement on total energy lost. Failure to select for adequate shelter will increase thermoregulatory demands, which can decrease fasting endurance (Cooper 1999) and have cascading impacts on overall
energy resources and survival (Bock et al. 2013, Buttemer 1985). The observed differences in resource selection between the mobile state and the stationary and roosting states further support the hypothesis that turkeys altered behavior to adjust to environmental conditions.

We found that the degree to which turkeys altered resource selection in response to inclement weather depended both on their movement state and the specific weather variable being considered. Stationary, and to a lesser extent mobile turkeys, altered resource selection primarily according to snow depth, while roost site selection was influenced primarily by wind chill. These results show that turkeys are capable of subtle, context-specific differences in resource selection in response to dynamic weather. The relationships we observed can be attributed to primary risks turkeys experienced within each movement state. Because turkeys generally prefer walking over flying, their movements become increasingly impeded with increased snow depths in addition to increased thermoregulatory requirements and predation risk (Lendrum et al. 2018, Martin et al. 2020, Sheppard et al. 2021). In contrast, roosting turkeys are stationary and in a more exposed position, meaning thermoregulation will be of greater concern over mobility. There is considerable evidence that many species are not only capable of exhibiting plasticity in behavior according to weather, but that specific weather conditions can have variable and opposing effects on behavior depending on context (Jorde et al. 1984, Bronikowski and Altmann 1996, Wróbel and Bogdziewicz 2015). This context-specific decision making allows for individuals to maximize fitness benefits and should lead to increased persistence in a changing environment.

3.4.2 Changing Temperate Ecosystems

The ability of turkeys to adapt their movement behavior and resource selection strategies to a broad spectrum of climates and landcover types have enabled their range to extend across North America and beyond their pre-colonial distribution. The Rio Grande subspecies of wild turkeys (M. g. intermedia) has been shown to decrease movement and select for shaded areas as temperatures
increased at their southern range, where heat is a primary risk (Rakowski et al. 2019). Our results add to this growing understanding of dynamic movement and resource selection strategies, showing that these behaviors extend to cold climates as well. At northern range limits, failure to adjust behavior to increased snow depth and low temperature can impose additional metabolic costs on individuals (Coup and Pekins 2011, Haroldson et al. 1998, Oberlag et al. 1990) and contribute to lower survival compared to core species range (Kane et al. 2007, Lavoie et al. 2017, Niedzielski and Bowman 2015). For turkeys that survive winter, failure to meet metabolic demands can result in decreased body condition which can impact future reproductive efforts (Vander Haegen et al. 1988, Porter et al. 1983). These impacts on survival and more importantly reproduction can have limiting effects on wild turkey populations persistence and expansion (Pollentier et al. 2014, Roberts et al. 1995). With decreasing winter severity across their northern range limit due to climate change, there is the potential for a northward shift in wild turkey range limits, with areas farther north becoming more hospitable as deep snow cover becomes less consistent, increasing the availability of forage throughout the winter. Given our results, the extent of such changes will in part be determined by the availability of habitat that allows turkeys to withstand persistent inclement weather events.

Combining HMMs with SSFs is a broadly applicable approach that can be used to identify plasticity in animal behavior, specifically dynamic resource selection strategies. This approach should prove especially informative for the conservation of species in temperate regions, as weather patterns shift due to climate change. Given the expected changes in winter temperatures and snow accumulation over the next century, a spectrum of taxa will be impacted in a variety of ways (Williams et al. 2015). Unfortunately, many species are unlikely to incur similar benefits as turkeys, especially those that rely on consistent snow cover for survival. For example, animals use snow roosts to temporarily avoid predation risk and freezing temperatures (Shipley et al. 2019), but inconsistent and short-lived snow accumulation will limit availability of such refugia at current ranges (Pauli et al. 2013, Shipley et al.
2020). Hibernating species, which time their emergence with food availability, may also need to adjust resource selection strategies as they are met with limited resources as snowmelts occur earlier in the year (Inouye et al. 2000). Changing snow patterns may also alter predator-prey dynamics, foraging behavior, and migration (Penczykowski et al. 2017). For animals that rely on camouflage to avoid predators, reduced snow cover will lead to mismatches between animals and their environment (Zimova et al. 2016, Atmeh et al. 2018). Given that shifts in coloring will occur over generations, behavioral changes in resource selection may be one of the best short term options for continued persistence for such species. In all these cases, we can anticipate the issues related to changes in weather and climate, but we have less information about how individuals will respond in the short-term to those changes. We examined dynamic behavior in the context of thermal refugia for turkeys, but with adequate data and model construction, a variety of behavioral states and associated resource selection strategies could be identified and examined which should prove useful for conservation of many taxa.

Whether an animal maintains their current behavior or adjusts to changing external cues will influence how shifts in weather patterns impact populations and determine what actions are best suited for conservation. This information can be incorporated into planning and decision making to meet immediate or long-term conservation goals. For example, species without the capacity for plasticity in behavior will be less able to adapt to a locally changing environment (Chenard and Duckworth 2021), and may require greater immediate intervention. These species may need to be considered at greater risk and of higher priority than those that are more likely to adapt via plastic behavioral response. Information inferred from a joint HMM/SSF approach can also be used to identify key habitat necessary for the persistence of species at their current range limits. While a major focus of conservation efforts is providing breeding and foraging habitat, areas of respite from inclement winter weather can be equally important for individual fitness (Johnston et al. 2021, Shipley et al. 2020). For resident individuals in temperate climates, conservation of winter shelter should be considered in conservation assessments.
(Greiser et al. 2020, Keppel et al. 2012, 2015). Across a longer timeframe, this information can be incorporated in projections of future shifts in a species northern range limit as climate change progresses. Over the next century, temperate areas are expected to experience increased temperatures and decreased snow depths (Kreyling 2010), which are often key limits on animal distributions (Bartoń and Zalewski 2007, Kaji et al. 2000, Matthews et al. 2010). These changes will make areas that were once uninhabitable more favorable (Lenoir et al. 2017). Anticipating how these changes will impact species and their distributions in these temperate areas, will improve accuracy of species distribution models, and better inform decision making.
CHAPTER 4

EMBRACING COMPLEXITY; A MULTI-SCALE, MULTI-STAGE ASSESSMENT OF NESTING HABITAT QUALITY FOR WILD TURKEYS

Nesting habitat is often a focus of bird conservation due to the outsized impact of nesting on reproduction and population growth, but assessments are often limited to success at or selection of nest sites at a single scale. This limited scope of inference can lead to important relationships being overlooked. Here we argue for a more holistic approach to estimating nesting habitat quality, that accounts habitat selection, nest success, and adult survival across multiple scales. While each of these issues have been examined in isolation, a unified approach to evaluating nesting habitat is less common. We provide an example of such an approach using wild turkeys (*Meleagris gallopavo silvestris*) in Maine as a case study. We deployed radio and GPS transmitters on wild turkey females from 2018 through 2020 and monitored female movements and nesting activity across three years. We used resource selection functions to estimate pre-laying, laying, and nest site habitat selection, a daily survival rate model to estimate nest success and female survival during incubation, and Bayesian latent indicator scale selection to quantify and incorporate multiple scales of habitat covariate measurements for each. We found that turkeys interacted with their environment at different scales according to the stage of nesting and the landscape characteristics being selected for. We observed differences in the strength and direction of selection according to nesting phase, such opposing selection for prelaying and laying turkeys for distance to roads, the proportion of developed land in an area, and forest structural metrics. We also observed that turkeys showed stronger selection for herbaceous cover and decreased distances to riparian zones during prelaying and for increased shrub cover during laying. We found that turkeys selected nest locations with greater visual obstruction compared to available locations but largely ignored differences in broader landscape characteristics. Finally, we did not identify any relation between nest success or female mortality during incubation and the habitat surrounding a nest. When
the scope of nesting habitat is expanded beyond the nest location, a more complete understanding of how the environment influences nesting outcomes can be achieved. While each of our findings are useful and important in isolation, together they demonstrate how a management approach that ignores one component of the nesting process will be deficient in identifying the full requirements of nesting turkeys in the northeast.

4.1 Introduction

Nesting habitat is often a focus of bird conservation due to the outsized impact of nesting on reproduction and population growth (Newton 1994, Jiménez-Franco et al. 2018). However, “habitat” is not binary (Kearney 2006), as the benefits and risks associated with obtaining resources results in a gradient of quality from ideal to fully unfavorable areas. To simplify interpretation, assessments of nesting habitat often focus on a limited number of essential components, such as nest success or selection at a single spatial scale (Murtaugh 2007, Mayor et al. 2009, McGarigal et al. 2016). While pragmatic, this limited focus can result in important relationships being overlooked (Getz et al., 2018; Johnson & Lidström, 2018). Increased options to monitor nesting birds, as well as advances in modeling techniques, have made it easier to track decisions and outcomes from fertilization through the final fate of a nest and beyond (Chamberlain et al. 2018), expanding the scope of nesting and enabling a holistic assessment of habitat (Etterson et al. 2011, Lewison et al. 2018).

Despite the number of ways habitat quality can be quantified (Johnson 2007, Mortelliti et al. 2010), few studies measure both occurrence and fitness simultaneously (Johnson 2007). Failure to integrate animal decisions with their associated outcomes can lead to an incomplete picture of quality and misinterpretation of results (Battin 2004). For example, a larger number of nests within a given habitat type does not necessarily indicate greater potential for success over other habitats (Zimmerman 1982). Similarly, if females misinterpret external habitat cues, it may lead to avoidance of potential nesting areas that would otherwise yield more favorable fitness outcomes (Patten and Kelly 2010). In
both cases, the mismatch between selection and success may result in depressed fitness. Models that link the probability that a site is selected for nesting with the outcome of those decisions will identify such mismatches (Pidgeon et al. 2006, Aldridge and Boyce 2007).

Assessments that emphasize the nest site ignore the broader scale decisions that influence availability and provide context in which fine scale decisions occur (Johnson 1980, Aldridge et al. 2012). While incubation or brood-rearing are generally considered the terminal stages of nesting, these are preceded by multiple phases that can include dispersal, prospecting, nest construction, and egg laying. Nesting is therefore better thought of as a hierarchical process where each of a series of behavioral phases must take place before a successful nest can occur (Etterson et al. 2011). Resource selection may differ among each of these behavioral phases according to parental requirements that are stage-specific (Pearson and Knapp 2016). For example, while an area may provide substantial habitat for nest concealment, if there is not adequate forage available to females during the laying or nest searching periods, then overall habitat quality will be lower than when considering incubation in isolation (Catry et al. 2013). Expanding the focus of nesting habitat selection beyond the nest site may therefore capture earlier decisions that influence probability of success.

In most assessments of nest success, all failures are considered synonymous, despite the potential for different causes or outcomes (Dinsmore et al. 2002). A situation where a nest is lost to predation but the female escapes will have different fitness consequences than a case where the female was killed by a predator while nesting (Magnhagen 1991, Verboven and Tinbergen 2002). In the former, the female retains the ability to renest immediately or in following season, whereas the latter will have no additional reproductive attempts. If there is a potential association between the cause of nest failure and habitat, differentiating between multiple nesting outcomes may be necessary (Darrah et al. 2018).

Finally, the importance of spatial scale in animal-habitat relationships is widely recognized (Kristan 2006, Mayor et al. 2009, Doherty et al. 2010). However, defining biologically relevant scales
depends on a multitude of species-specific factors that may differ among habitat characteristics (Jackson and Fahrig 2012) or life-history stage (Hardy et al. 2020). For example, while establishing and moving within prelaying ranges, birds may interact with their surroundings at relatively broad scales, such that landscape-level composition and configuration is most important (Miller and Barzen 2016, Pollentier et al. 2017). As movements become more localized, such as when selecting a nest location, the importance of finer-scale habitat characteristics may be more influential (Holloran et al. 2005). Similarly, nest fate can be influenced by a variety of scale-specific factors (Chalfoun and Martin 2007, Reidy et al. 2017). Identifying the most relevant candidate scales for each nesting phase is a critical component of assessing nesting habitat.

In this study, we provide an example of a more holistic framework for assessing nesting habitat quality using wild turkeys (Meleagris gallopavo silvestris) in Maine as a case study. We present a model for wild turkey nesting habitat that 1) identifies the biologically relevant scales at which turkeys relate to landscape characteristics during each stage of nesting, 2) estimates nesting habitat quality based on both selection and success outcomes, 3) accommodates the hierarchical nature in which habitat selection decisions occur throughout the nesting period, and 4) accounts for the fate of the nest and the female during incubation. We hypothesized that turkeys would follow a hierarchical selection process, where decisions during the prelaying phase would be most influenced at broader spatial scales, and during subsequent stages turkeys would match the scale of selection to their more localized movements. We also hypothesized that turkeys would experience differential nest success as a result of habitat selection, with fine scale habitat characteristics being most impactful. Finally, we estimated nesting habitat quality in a portion of our study area to demonstrate the joint model’s predictive product.

4.2 Methods

4.2.1 Study Area
We captured and monitored radio- and GPS-marked female turkeys at two study areas located near Bangor and Portland, Maine (Figure 4.1). The Bangor study area (44.8111°N, -68.832°W) consisted of capture sites located within 93 km of the Bangor International Airport. This area was chosen as it represents three major land use types present across Maine; agricultural, industrial forest, and suburban/urban matrix. These existed as a gradient across the Bangor study area, such that agricultural landscapes dominated the western portion, industrial forests dominated the eastern portion, and the suburban/urban matrix was found between the two. In this way, all three land use types were available to all turkeys sampled in the study area, but varied in their relative abundance. Our southern study area was centered 25 km north of Portland, Maine (43.880°N, -70.339°W), spanning a gradient between rural areas and the suburban edge of metropolitan Portland, representing a variety of intermixed land use types and human activity levels. This area was chosen as it existed in areas with denser turkey and human populations, had milder winters on average, and was relevant to state management objectives.

4.2.2 Data Collection

We captured turkeys using rocket and drop nets during December through March of 2018-2020. We fit a random subset of captured female turkeys with one of three types of tracking equipment; an 80-g VHF backpack radio transmitter from Advanced Telemetry Systems (Model A1540; Isanti, Minnesota, USA), a 12-g VHF necklace radio transmitter from Advanced Telemetry Systems (Model A3950; Isanti, Minnesota, USA), or a 90-g Litetrack GPS backpack transmitter from Lotek Wireless Fish and Wildlife Monitoring, (Newmarket, Ontario, CA). We deployed transmitters with the goal of maintaining a 50:50 ratio between adult (>1 year old) and juvenile (<1 year old) turkeys. We deployed VHF transmitters across both study areas, but GPS transmitters were limited to the Bangor study area. Transmitters did not exceed 4% body mass, and all capture and handling of wild turkeys was approved by the University of Maine Institutional Animal Care and Use Committee (IACUC Protocol # A2017_11_03).
Figure 4.1. Study area map showing the general location of study areas within Maine, USA (A) and the distribution of capture sites (black points) within the Bangor (B) and Portland (C) study areas.
We monitored females for nesting behavior from April through July each year with the goal of observing each turkey twice weekly using short-distance triangulation. If we found a turkey at the same location for successive observations, we assumed the turkey to be incubating a nest. To confirm nesting status and determine the nest initiation date for each VHF-marked female, we flushed turkeys after they were suspected to be incubating for two weeks. We delayed flushing females to reduce the potential for nest abandonment, which may increase if females are disturbed early in laying or incubation (Götmark 1992). When it was not possible to locate a turkey for multiple weeks, we flushed her the day she was re-encountered to avoid missing potential nests. Upon flushing, we counted the number of eggs present and floated 3-4 eggs in water to estimate laying and incubation initiation dates (Kaj Westerkov 1950). For VHF nests that were not flushed (n=8), we set the incubation initiation date to midway between when the female was last detected off nest and when she was detected on nest. We then used the mean clutch size for all known nests to estimate laying initiation date.

We programmed GPS transmitters to collect hourly locations during daylight hours and one roost location each night through the nesting season (B. S. Cohen et al. 2018). We downloaded and reviewed location data weekly to monitor birds for potential nesting activity. If we observed a turkey at the same location for multiple successive points (i.e., 5 or more locations), we assumed incubation was initiated. Once the turkey began regular movements following a suspected nest, we visited the nest location to verify its existence and fate. We reviewed GPS location information to determine when laying occurred, which we identified as regular visits to the nest location on successive days prior to incubation initiation.

We identified covariates we hypothesized could affect one or more component of nesting (Table 4.1) and quantified each using publicly available GIS datasets. We measured covariates using the focal statistic and Euclidean distance tools in ArcGIS Pro (v2.6.0). For the focal statistic tool, we used a
Table 4.1. Covariates used to assess turkey habitat selection and nest success. For each covariate considered, we provide a description of the covariate, the cell size of the raster, and prior publications justifying their inclusion in our analysis.

<table>
<thead>
<tr>
<th>Covariate</th>
<th>Description</th>
<th>Cell Size</th>
<th>Justification</th>
</tr>
</thead>
<tbody>
<tr>
<td>Developed</td>
<td>Proportion of area categorized as any intensity of developed</td>
<td>30m</td>
<td>Spohr et al., 2004; Tinsley, 2014</td>
</tr>
<tr>
<td>Agriculture</td>
<td>Proportion of an area categorized as row crop or pasture land</td>
<td>30m</td>
<td>Lambert et al., 1990</td>
</tr>
<tr>
<td>Shrub</td>
<td>Proportion of an area categorized as shrub, which encompasses plants less than 5m tall with shrub canopy greater than 20% of total vegetation within a cell.</td>
<td>30m</td>
<td>Day et al., 1991</td>
</tr>
<tr>
<td>Herbaceous</td>
<td>Proportion of an area categorized as herbaceous. This includes areas dominated by gramanoid or herbaceous vegetation, greater than 80% of a cell</td>
<td>30m</td>
<td>Pollentier et al., 2017</td>
</tr>
<tr>
<td>Basal Area</td>
<td>Average basal area of trees within an area</td>
<td>10m</td>
<td>Pollentier et al., 2017; Thogmartin &amp; Johnson, 1999</td>
</tr>
<tr>
<td>Mean Tree Height</td>
<td>Average of tree heights within an area</td>
<td>10m</td>
<td>Pollentier et al., 2017; Thogmartin &amp; Johnson, 1999</td>
</tr>
<tr>
<td>Percent Conifer</td>
<td>Mean percent cover of cells comprised of coniferous tree species</td>
<td>10m</td>
<td>Pollentier et al., 2017; Thogmartin &amp; Johnson, 1999</td>
</tr>
<tr>
<td>Distance to Road</td>
<td>Distance from cell center to nearest public road</td>
<td>10m</td>
<td>Thogmartin &amp; Johnson, 1999; Yeldell et al., 2017</td>
</tr>
<tr>
<td>Distance to Forest Edge</td>
<td>Distance from cell center to nearest cell categorized as forested by NLCD</td>
<td>10m</td>
<td>Swanson et al., 1994</td>
</tr>
<tr>
<td>Distance to Riparian</td>
<td>Distance from a cell center to nearest stream, river, or artificial waterways</td>
<td>30m</td>
<td>Miller et al., 2000; Palmer et al., 1996</td>
</tr>
<tr>
<td>Visual Obstruction</td>
<td>Average proportion of coverboard visible at a given location.</td>
<td>-</td>
<td>Nguyen et al., 2004; Yeldell et al., 2017</td>
</tr>
</tbody>
</table>
rectangular neighborhood where the buffer radius corresponded to scales we identified as being biologically relevant to turkeys (see below). From the National Land Cover Database (Homer et al. 2020), we measured the proportion of land classified as agriculture, developed, shrub/scrub, and herbaceous within a buffer surrounding each 30mx30m raster cell. We used predictive layers derived from light detection and ranging data (LiDAR; Ayrey et al., 2017), to approximate the mean tree basal area, mean tree height, and percent softwood (i.e. coniferae) tree species within a buffer for each 10mx10m raster cell. We then summarized the 10m raster of LiDAR derived covariates for a 30m raster to match the scale of NLCD derived covariates. Using NLCD classifications for forested and non-forested land use, we measured the distance of each 30mx30m cell from a forest edge. We used public road information available via the Maine Department of Transportation to measure the distance each 30mx30m cell was from a public road. We used the National Hydrography Dataset (Geological Survey (U.S.) 2004) to measure the distance of each 30mx30m cell from the nearest riparian zone.

In addition to remotely-sensed landscape characteristics, we collected information on visual obstruction at a subset of nest sites and paired random locations using cover boards (Nudds 1977). We limited visual obstruction measurements to a subset of known nests due to limited availability to collect such information while also performing regular telemetry checks. Each nest sampled was paired with 6 random locations. For nests of GPS-marked turkeys, random locations consisted of the 3 locations visited by the turkey prior to its first arrival at the nesting location, and 3 additional locations the turkey visited 24 hours prior to its first arrival. We used the average distance between these random points derived from GPS data and their associated nest, ~130m and ~650m, respectively, to generate random locations for nests of VHF-marked turkeys. At each nest and random location, we placed a 50x50cm coverboard at the coordinates, walked 3m in each cardinal direction, and counted the number of 10x10cm squares more than 50% visible. We averaged the number of squares visible among measurements as a visual obstruction metric for each location.
4.2.3 Scale Selection

We used Bayesian latent indicator scale selection to identify the optimal scale for covariates considered (BLISS; Stuber et al., 2017). We modeled covariate scale as a latent categorical variable, which can change between iterations of a MCMC computation.

\[ y_i = \alpha + \beta x[i, sc] \]

\[ sc \sim \text{cat}(0.25, 0.25, 0.25, 0.25) \]

where \(x\) is a matrix of covariate values, the columns of which correspond to the scales covariates were quantified, \(i\) references a row in the matrix corresponding to a location, and \(sc\) is a latent categorical covariate which samples from the vector of candidate scales \(sc_1, ..., sc_n\). All scales were given a prior probability of 0.25. We identified scales relevant to our system based on the movement data collected from GPS-marked turkeys, which corresponded to mean distance between winter and nesting home ranges (~8334 m), the average width of the prelaying home range (~3360 m), mean distance traveled the 24 hours prior to nesting (~1328 m), and the immediate surroundings of an individual at a location (~120 m). We examined the correlation of covariate measurements across scales to identify which covariates did not vary greatly among scales, and present these results in the Supplementary Materials (Figure 4.2). To identify the most appropriate scale for each covariate, we used reversible-jump Markov chain Monte Carlo simulations. Each component model (i.e., prelaying, laying, nest site selection and nest success) was run independently and with only a single covariate included. We then examined the posterior samples for each model to determine the best supported scale for each covariate which would be used in the final model (Figure 4.3).

4.2.4 Resource Selection Probability Functions

We defined three behavioral states relevant to turkey nesting ecology; prelaying, laying, and nesting. For each, we modeled resource selection by turkeys using resource selection probability
functions (RSPF) under a use-available design (Lele and Keim 2006, Manly et al. 2007) which were implemented using an infinitely weighted conditional logistic regression (Fithian and Hastie 2013). We

Figure 4.2. Correlation between covariate values measured at different scales decreased as the difference in the buffer sizes used to quantify covariates increased. Plots show correlation among covariate values for the four scales considered; winter to nest (1), prelaying (2), 24 hours (3), and local (4).
Figure 4.3. Example Markov chain Monte Carlo sample trace plots showing the relative support for a given scale using the Bayesian latent indicator scale selection approach to identify the optimal scale at which to measure landscape covariates. Examples show situations where support is high (A), medium (B), and low (C) for a given covariate scale.
weighted samples such that use locations were given a weight of 1 and available locations a weight of 10,000. We used a logit link to interpret model coefficients, as the use infinite weights allowed for estimation of probability of selection (Lele and Keim 2006).

We examined GPS locations for marked turkeys to determine the start and end days for each behavioral period; pre-nesting, laying, and nesting. We first used dynamic Brownian Bridge Movement Models (dBBMM; Kranstauber et al., 2012) to estimate 95% isopleth for home ranges of GPS-marked individuals for the period of winter through initiation of incubation of the first clutch of the year for each bird. We then visually examined movement tracks in combination with the corresponding daily average of Brownian motion variance (BMV), which describes the change in movement distance and turning angle between successive locations, with higher values corresponding to longer, straight line movement. During winter, when movement was restricted and home ranges small, mean BMV was low. As the breeding season began, some birds initiated seasonal movements to breeding areas and movement in general increased, resulting in progressively higher values for BMV. For birds with overlapping winter and prelaying ranges, we began the prelaying period following when BMV estimates increased from those observed during January-March (Figure 4.4A,C). For birds that made clear directional movements away from wintering areas, we defined the beginning of the prelaying period when BMV values dropped and became consistent, indicating localized movements (Figure 4.4B,D). To identify laying periods, we used the first observation of an individual at the nest coordinates at least 15 days prior to incubation, that was then followed by regular visits to the nest.

For each RSPF, we defined use and available points for GPS-marked turkeys based on individual tracking information, and then used those observations to inform selection of use and available points for the VHF-marked turkeys, which lacked detailed movement paths (Figure 4.5). For both GPS- and VHF-marked turkeys, the number of available locations for each individual was ten times the number of use locations. We used all locations collected during the prelaying period to define use for GPS-marked
Figure 4.4. Example Brownian motion variance plots and corresponding turkey locations comparing movement behavior of turkeys in Maine, USA, which did not leave their winter home range to nest (A, C) to those that did (B, D).
Figure 4.5. Example use and available polygons used to generate use and available locations for prelaying, laying, and nest site selection by GPS-marked (A) and VHF-marked (B) turkeys. Line and point colors correspond to specific selection periods.
females. Available locations were randomly sampled from the 95% isopleth of home ranges created using dBBMM for the period from the beginning of winter until laying initiation in a given year. Laying use locations for GPS-marked turkeys were all points collected from the time egg laying was initiated until incubation began. Available locations for this period were randomly selected from within a 95% home range created from all prelaying and laying locations using dBBMM. Locations of the first nest in each year for each GPS-marked turkey were considered use locations for a nesting RSPF. Available locations were randomly selected from within a 95% dBBMM home range created from all prelaying locations.

To define prelaying available points for VHF-marked females, we created a line from the first winter location to the nest location and buffered it by a distance equal to the radius of the prelaying home range size, which approximated movement between winter and nesting ranges. For all other use and available points, we generated circular buffers with an area 125% that of the mean area of home ranges for GPS-marked individuals for the periods previously described. The number of use locations for each VHF-marked individual was equal to the mean number of use locations for GPS-marked turkeys.

4.2.5 Multi-Fate Nest Success

We estimated how landcover affects the probability of nest failure and female mortality while incubating using a multinomial logistic exposure model to account for multiple potential outcomes of a nesting event (Darrah et al. 2018). For each observation, we categorized a nest as being in one of three states; currently incubated by a female (S), failed since the previous observation, but the female was currently alive (N), and the female had died since the previous observation (H). We constructed encounter histories for each visit such that each row corresponded to an observation for a specific nest \( y_{ij} \) and each column corresponded to a possible fate. To account for nests that may have been lost due to observer influence while flushing, we truncated encounter histories at the last known visit the female was on nest for nests that failed within three days of the female being flushed. Encounter histories
began with the estimated nest initiation date, and ended when the female was observed off the nest or found dead. We modeled nest fate according to a multinomial logistic distribution:

$$ y_{ij} \sim \text{Multi} \left( \left[ P_S(t_{ij}), P_N(t_{ij}), P_H(t_{ij}), 1 \right] \right) $$

where $i$ refers to a given nest, $j$ refers to a given visit, $P$ refers to the probability that a nest would be observed with a specific fate after $t$ days since last being observed. Nest fates were assumed to be classified correctly, and fates were assumed to occur independently of one another. Effects of landscape covariates on nest failure (both with and without an associated female mortality) were modelled using linear regression with a multinomial logit link function, where $S$ was the reference state.

### 4.2.6 Nesting Habitat Quality

To estimate aggregated nesting habitat quality, we constructed a holistic model using a hierarchical Bayesian approach that included each component sub-model for selection and nest success. Within each sub-model, all ten covariates were included at the scale determined by BLISS scale selection. To estimate a final metric for nesting habitat quality, we found the product of selection and success from each component model to estimate the probability that a site would be selected for nesting, conditional on each level of selection, and that it would be successful, given that the female survived the nesting attempt. Using this holistic model, we mapped nesting habitat quality for a portion of our Bangor study area, using covariates measured at a 500m grid spacing, to illustrate how the aggregate metric could facilitate spatial predictions of habitat quality. As visual obstruction was measured at only a subset of nests and could not be predicted across study areas, we performed a separate analysis using our nest site selection and nest success models to estimate the effects of visual obstruction.

### 4.3 Results
From 2018 through 2020, we located 101 nests from 93 unique females across both study areas, of which 33 successfully hatched. Of located nests, 33 were identified from monitoring GPS-marked females and 68 were from monitoring VHF-marked females. We located 15 nests across the Portland study area and 86 across the Bangor study area.

4.3.1 Scale Selection

BLISS results indicated that scale optimization differed according to the covariate and component model being considered, with higher orders of selection having more uniform support for a single scale, while the relative support for any given scale was more equivocal for lower orders and nest success (Figure 4.6). Across models for prelaying selection, the broadest scale (8334 m) was best supported for eight covariates, the 3360 m scale was supported for one covariate, and 120 m scale was supported for one. For models of laying selection, the 8334 m scale was supported for three covariates, the 3360 m scale was supported for one covariate, the 1328 m scale was supported for four covariates, and the 120 m scale was supported for two covariates. For models of nest site selection, the 8334 m scale was supported for seven covariates, the 3360 m scale for one covariate, and the 120 m scale for two covariates. For covariates of nest failure, the 8334 m scale was supported for two covariates, the 3360 m scale for four covariates, the 1328 m scale for one covariates, and the 120 m scale for three covariates. Results for female mortality while incubating did not show clear support for any scale across covariates.

4.3.2 Nesting Habitat Quality

Coefficient estimates indicated differences in prelaying and laying selection according to habitat covariates, but little support for differences within nest site selection, nest failure, or incubating female mortality (Figure 4.7; Table 4.2). The model indicated that females in a prelaying phase selected for increased distance from roads ($\beta = 1.243; 95\% \text{ C.I.} 1.175 – 1.311$), percent cover of conifers ($\beta = 1.020; 95\% \text{ C.I.} 0.844 – 1.206$), herbaceous cover ($\beta = 0.657; 95\% \text{ C.I.} 0.611 – 0.707$), and basal area ($\beta = 0.393; 95\% \text{ C.I.} 0.351 – 0.436$).
Figure 4.6. Scale optimization results showed that prelaying selection was most influenced by covariates at the broadest scale considered while laying selection was determined by a mix of scales. There was not full support for a single scale in analysis of nest site selection, nest failure, or incubating female mortality. Within each plot, bars correspond to a specific covariate and color to a specific scale. The more support there was for a specific scale, the large the colored bar is.
Figure 4.7. Prelaying and laying selection by turkeys showed differing and sometimes opposing relationship with landscape covariates, while nest site selection and nest failure rates did not correlate with habitat characteristics beyond visual obstruction for nest site selection. Plot depicts covariate values for each habitat characteristic quantified at the scale selected by BLISS analysis.
Table 4.2. We provide full coefficient estimates for all covariates considered at the scale selected for by BLISS analysis. Here we provide the mean and median estimate from MCMC iterations along with the standard deviation (SD) and upper and lower confidence intervals (LCI, UCI).

<table>
<thead>
<tr>
<th>Component</th>
<th>Model</th>
<th>Covariate</th>
<th>Scale</th>
<th>Mean</th>
<th>Median</th>
<th>SD</th>
<th>LCI</th>
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Table 4.2 continued

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95% C.I. 0.217 – 0.585), as well as decreased mean tree height (β = -0.661; 95% C.I. -0.969 – -0.367) and distance to riparian zones (β = -0.696; 95% C.I. -0.766 – -0.625). Turkeys in the laying phase selected for areas with greater shrub landcover (β = 0.986; 95% C.I. 0.824 – 1.147) and greater tree basal area (β = 0.562; 95% C.I. 0.404 – 0.719) as well as decreased percent softwoods (β = -0.398; 95% C.I.-0.480 – -0.316), distance to road (β = -0.340; 95% C.I. -0.433 – -0.251) and distance to riparian zones (β = -0.354; 95% C.I. -0.485 – -0.223). When choosing nest site locations, turkeys selected for sites with greater visual obstruction (β = -0.165; 95% C.I. -0.223 – -0.114) but did not alter selection according to any of the landcover or forest structural covariates we considered. All coefficient estimates for nest failure and incubating female mortality widely overlapped with 0 and were considered unsupported.

Predictions of nesting habitat produced via the holistic model indicated that habitat quality was generally higher east of Bangor, an area with lower road density and a landscape primarily dominated by forests (Figure 4.8). Prediction surfaces produced from individual component models indicated little fine scale variation in prelaying selection, whereas laying selection showed greater variation at smaller scales. Variation in nest site selection and nest success showed little variation across the area considered. Error associated with nesting habitat quality estimates followed similar spatial patterns as the metric itself, where larger quality values corresponded to greater error (Figure 4.9).

4.4 Discussion

The animal-habitat relationships we observed throughout nesting support our hypothesis that turkeys follow a hierarchical habitat selection process. Pre-lying turkeys exhibited both the greatest strength of selection and the most consistent scale optimization for the largest number of landcover and forest structural variables. This suggests that turkeys interact with their landscape most prominently during the period of movement between winter home ranges and spring nesting areas. These macro-habitat selection decisions whether a females has the resources needed to successfully complete all
Figure 4.8. Nesting habitat quality estimates were largely driven by selection during the prelaying and laying periods. Plots A-D show spatial distribution of individual component model estimates for probability of prelaying selection (A), laying selection (B), nest site selection (C), and nest success (D). Plot E shows the combined probability for all component models as a single habitat quality metric. All plots are restricted to the same portion of the Bangor study area.
Figure 4.9. Uncertainty in nesting habitat quality estimates followed similar spatial relationship to the final quality metric. Plot depicts the spatial distribution of the standard deviation in quality metric estimates for the portion of the study area we assessed.
aspects of reproduction, including those that go beyond the success of the nest itself, and likely play an outsized role in shaping the distribution of turkeys during the spring breeding season. Indeed, our joint models of nesting habitat confirm the outsized role of this stage on habitat quality. These macro-scale decisions then define the availability of micro-habitat selection such as nest site, where finer-scale characteristics most influence turkey decision-making.

We found that turkeys interacted with their environment at different scales according to the stage of nesting and the landscape characteristics being selected for. Turkeys in the prelaying state generally interacted with the landscape at the broadest scale, while laying turkeys showed greater variability at the scale to which they responded. We did not observe unanimous support for a single scale for any covariates of nest site selection, nest failure, or female mortality, although this may reflect lack of significance for these effects. Differences in how prelaying and laying turkeys responded to their surroundings highlight the complex way in which animals perceive their environment at different scales (McGarigal et al. 2016, Bauder et al. 2018). Prior to nesting, an individual must establish their home range within the context of the greater landscape, requiring a broader scope of information on the availability of resources and distribution of risks (Thogmartin 1999). Once the nest is established, information collected at finer scales becomes more important as movements are restricted by the location of the nest, and individuals make decisions about how to optimize the use of space within their home range. Our results add to an ever-growing base of evidence that assessments of wildlife-landscape interactions necessitate consideration of process scale to produce unbiased results (Chalfoun and Martin 2007, Hurlbert and Jetz 2007, Boyce et al. 2017).

We also observed differences in the strength and direction of selection according to nesting phase. Comparing prelaying to laying turkeys, we observed opposing selection for distance to roads, the proportion of developed land in an area, and forest structural metrics. We also observed that turkeys showed stronger selection for herbaceous landcover types and decreased distances to riparian zones.
during prelaying, and for increased shrub-dominated landcover during laying. These differences likely correspond to variable decisions made by turkeys during each nesting phase. During prelaying, turkeys prospect the landscape as they evaluate potential nesting habitat to minimize disturbance and predation risk, leading to more time spent in areas away from roads and in denser forests (Hubbard et al. 1999, Thogmartin 1999, Yeldell et al. 2017). Prelaying turkeys selected for areas with herbaceous vegetation, which may indicate consideration for prelaying nutrition or adequate brood rearing habitat in addition to nesting substrate (Dickson 1992, Pollentier et al. 2014, Kilburg et al. 2015). In contrast, laying turkeys remained closer to roads and in areas with greater shrub availability, indicating an emphasis on increased mobility and proximity to escape cover. Such behavior-specific differences in resource selection have been observed in turkey populations (Pollentier et al., 2017; Gonnerman Dissertation Chapter 3) and are common across a broad suite of species (Ellington et al. 2020, Patten et al. 2021). When animals demonstrate shifting habitat requirements among life stages, such as those we observed, it becomes more likely that assessments of habitat quality that emphasize a single behavioral period will miss relationships that could otherwise inform management.

We found that turkeys selected nest locations with greater visual obstruction compared to available locations, and largely ignored differences in broader landscape characteristics when choosing a nest site. The importance of visual obstruction for ground-nesting birds has been shown for many galliform species (Badyaev 1995, Lautenbach et al. 2019) as nests are vulnerable to an assortment of predators (Martin et al. 2015, Melville et al. 2015). Previous research has found that turkeys select nest sites closer to roads, in larger patches with reduced edge density, and away from mature forests, and instead favor increased shrub cover (Thogmartin 1999, Streich et al. 2015, Wood et al. 2019). Except for distance to roads, these reflect our own findings for turkey prelaying selection, but not nest site selection. It is possible that previous studies of turkey nest site selection considered scales that were too broad and were instead identifying decisions related to habitat use away from the nest site.
We did not identify any relation between nest success or female mortality during incubation and the habitat surrounding a nest, which agrees with previous research on turkey nest success (Fuller et al. 2013, Little et al. 2014, Yeldell et al. 2017a, Crawford et al. 2021). Because of the number of potential nest predators that turkeys must evade, it is possible that selection for certain habitat characteristics to avoid one predator may lead to increased risk for others, resulting in comparable nest success across habitat types (Nguyen et al. 2004). It is also possible that we did not identify differences in nest success due to turkeys in poor quality habitat choosing to forego nesting altogether, or due to rapid nest failures that occurred prior to nest discovery (e.g. Blomberg et al., 2015). In either case, further research may be necessary to identify the full impact of habitat decisions on reproductive success for turkeys in the northeast United States.

Our results highlight differences in habitat selection and nest success for wild turkeys that are scale- and stage-specific, but this model is not exhaustive, and could incorporate further information to improve our understanding of nesting habitat quality. For example, extensions of this approach may incorporate survival of females throughout the nesting period, rather than solely during incubation, which can differ with landscape characteristics (Hubbard et al. 1999, Pollentier et al. 2014b). Additionally, while we found no relationship between nest success and habitat characteristics at the nest site, other metrics of productivity beyond success could be quantified to determine habitat impacts on fitness. Clutch size and egg mass are also important characteristics of a nesting attempt that affect recruitment, and may vary according to habitat and resource availability (Jetz et al. 2008, Blomberg et al. 2014, Bailly et al. 2016). Finally, as successfully hatching a nest does not ensure recruitment into the breeding population, information on brood habitat selection and survival may provide important insights into how habitat affects recruitment of individuals following a successful nesting attempt (Spears et al. 2007, Gibson et al. 2016). A comprehensive understanding of nesting habitat could incorporate some or all these metrics to better inform management.
4.5 Management Implications

When the scope of nesting habitat is expanded beyond the nest location, a more complete understanding of how the environment influences nesting outcomes can be achieved. A more holistic approach requires considering the various behavioral stages from fertilization through incubation. By incorporating resource selection during prelaying and laying phases with nest site selection and nest success, we were able to identify multiple scales of selection important for turkeys nesting in the northeast United States. At broader scales, differential selection between prelaying and laying indicated a need for a variety of forest structures and compositions with variable proximity to roads and riparian zones. Additionally, providing forage and escape cover in the form of shrubs and herbaceous vegetation will be important during both behavioral states. At the local scale, turkeys selected for areas of increased visual obstruction, likely in an effort to avoid predation and disturbance, although the impact of these decisions on nest success appears minimal. While each of these findings are useful and important in isolation, a management approach that ignores one component of the nesting process will be deficient in identifying the full requirements of nesting turkeys in the northeast.
CHAPTER 5
AN INDIVIDUAL BASED MODEL TO ESTIMATE POPULATION CONNECTIVITY FOR HARVESTED EASTERN WILD TURKEYS

The administrative boundaries used in wildlife management are often a product of political and social influences and therefore there should be little expectation that animal movements will be restricted to human-defined management regions. To assess assumptions of population closure common in wildlife management and monitoring, multiple data sources can be used to build and calibrate individual based models for animal movement from which inferences can be made. We built an IBM for wild turkey spring seasonal movements to simulate individual responses to landscape connectivity and identify emergent migratory connectivity dynamics between harvest management regions in Maine. We found that male turkeys were more likely to initiate seasonal movements than females but were also less selective in their settling decisions, resulting in similar rates of immigration between sexes. We calculated a low degree of migratory connectivity between WMDs which, in combination with the substantial number of boundary crossings observed, indicated a more diffuse distribution of turkeys with limited correlation between winter and spring WMDs. While defining management regions for such a dispersed population may be difficult, information on the total number of turkeys moving between districts can delineate where immigration is strongest and therefore which WMDs share the most animals and should therefore be considered as a singular unit. Transition probabilities between WMDs can identify uneven immigration patterns and therefore where source-sink populations likely exist, so that harvest regulations can be considered with both in mind.

5.1 Introduction

The administrative boundaries used in wildlife management are as much a product of political and social influence as they are defined by knowledge of ecological processes (Meisingset et al. 2018). If management units do not closely match the distribution of a population, immigration and emigration
between units can impact the effectiveness of management decisions (Gordon et al. 2004, Hebblewhite et al. 2006, Limiñana et al. 2012). For example, the regulation of harvested populations is often determined at regional scales, where agencies make local management decisions based on the distribution of populations across a defined area (Williams et al. 1999, Robinson et al. 2016). If uneven immigration exists among management areas, changes in regional abundance are likely and therefore warrant adjustments to harvest regulations (Novaro et al. 2000, Brøseth et al. 2005, Moore and Krementz 2017). To limit the exchange of individuals between areas with differing regulations or objectives, it may be useful to divide or group management units such that regulations match the underlying population structure, which requires knowledge of the distribution of animals and movement patterns within a population (Allen and Singh 2016, Porreca et al. 2016).

How best to assess the motivations and consequences of animal movements depends on the spatial and temporal scales being considered. Individual animal movement patterns are often studied in the context of the functional connectivity of a landscape, or the degree to which a landscape enables or impedes movement (Taylor et al. 2006), which provides insight into the ecological processes that drive fine-scale movement among habitat patches (Tischendorf and Fahrig 2000). In contrast, migratory connectivity provides a framework for studying the relationship between individual movements and abundance and how they interact to affect populations at larger temporal and spatial scales (Webster et al. 2002). Where functional connectivity considers a continuous decision process at the scale of individual movements, migratory connectivity addresses how individual movements result in the exchange of individuals among discrete populations (E. B. Cohen et al. 2018). While they may be considered opposing end of a spectrum, there is utility in integrating the two approaches for the purposes of understanding the movement of harvested species amongst management regions. Functional connectivity can provide insight into the propensity of individuals to move and disperse across landscapes (Bélisle 2005), while migratory connectivity can describe how those movements
manifest in broad scale changes to populations or across regions (Ambrosini et al. 2009, E. B. Cohen et al. 2018). By combining the two approaches, we improve our understanding into how individual movement decisions lead to population scale dynamics (Nathan 2008, Hawkes 2009).

Individual based modeling (IBM) has grown increasingly common in connectivity research due to its capacity to link the interactions between individuals and their environment to population scale patterns of movement (Chon et al. 2009, Pe’er et al. 2011). When normal parametric approaches are not viable due to complex or unmeasured influences on animal movement, it can be simpler to simulate individual movements and make inferences about the resulting broad-scale dynamics (Grimm and Railsback 2013). An IBM approach provides additional benefits related to data availability, as assessments of connectivity tend to be resource intensive. Direct measures of landscape connectivity often rely on costly fine scale individual movement information (Richard and Armstrong 2010, Keeley et al. 2017, Merrick and Koprowski 2017) while migratory connectivity studies must capture large numbers of individuals to obtain adequate recapture samples from which inferences can be made (Ambrosini et al. 2009, E. B. Cohen et al. 2018). IBM provides a means to integrate multiple data types and maximize the value of limited data to overcome potential resource limitations (Rushing et al. 2014). For example, fine scale movement information collected from a small number of individuals can be used to train an IBM, which is then calibrated on a larger number of coarse scale data such as band recoveries or genetic assignments (Hauenstein et al. 2019). This would be especially useful in the harvest management of mobile, resident species, such as ungulates and upland game birds, where multiple types of movement information, such as banding and tracking data, are available.

One current management scenario that would benefit from an improved understanding of connectivity is the management of eastern wild turkeys (hereafter turkeys; *Meleagris gallopavo silvestris*) in the Northeastern US. Turkey populations across the United States are managed by state agencies, with most setting harvest regulations within discrete regions (Healy 2000). In the northeast,
turkeys must contend with winter conditions that limit forage availability, leading turkeys to establish winter ranges in areas that provide food but potentially don’t meet other ecological needs such as breeding habitat. In such situations, turkeys move between seasonal home ranges to acquire necessary resources for persistence, which will impact management decisions (Jarnemo 2008, Hörnell-Willebrand et al. 2014). For example, harvest management objectives, such as limiting nuisance turkey encounters in human populated areas, could become more complicated by substantial movements between regions. If turkeys are being sourced from other regions or if they temporarily leave an area during the harvest season avoiding removal, then increasing harvest to reduce density in the areas affected may prove unsuccessful due to source-sink dynamics (Slough and Mowat 1996, Novaro et al. 2000). In all cases, better understanding the prevalence and magnitude of turkey movements between regions would improve management for turkeys in the Northeast.

We assessed the seasonal movement patterns of turkeys to determine functional connectivity between winter and spring home ranges for populations at their northern range limit. As connectivity is determined by a complex series of decisions surrounding animal movement behaviors, it is often advantageous to simplify into three distinct processes: initiation, movement through the landscape matrix, and settling (Bowler and Benton 2005, Baguette and Van Dyck 2007). As each may have unique drivers that influence animal movement decisions, we assessed each process separately and then integrated observed relationships into a final model simulating connectivity between seasonal ranges. Our objectives were to 1) model propensity to initiate seasonal movements according to characteristics of a turkey’s winter range, 2) simulate individual seasonal movement decisions made between winter and spring ranges using an individual based model trained on GPS location data and calibrated using harvest and nesting observations, 3) model settling decisions made by turkeys that initiated seasonal movements between their winter and spring ranges according to landcover characteristics, and 4) assess
connectivity of turkey populations using a simulation model that integrates the three decision processes to predict movement amongst management regions.

5.2 Methods

5.2.1 Study Area

Capture sites were distributed across Maine, USA, according to observed turkey wintering locations. Maine contained a variety of land use types, ranging from agricultural to suburban/urban matrix to industrial forests. Much of the human population of Maine was distributed within its southern and coastal counties, near the cities of Portland, Augusta, and Bangor (USDC, 2018). Beyond these urban and suburban areas, the northern and western portions of Maine were predominantly characterized by low human density (<50 individuals per sq mile) and heavily forested areas, with over 83% of Maine’s landscape being classified as forested (USDA Forest Service 2020). Maine’s topography consisted of hilly to mountainous areas shaped by the formation of the Appalachian Mountain range and glacial drift (Maine Geological Survey 2005). Within Maine, we designated two study areas within which we deployed transmitters in addition to bands to collect nesting (Gonnerman Chapter 4) as well as seasonal home range and movement (Gonnerman Chapter 3 & 4) data distributed within Maine according to objectives central to previous chapters.

5.2.2 Data Collection

We captured turkeys from December through March of 2018-2020 and marked each with one or two unique leg bands with information for reporting recovered birds. We fit a subset of captured female turkeys with either a GPS or VHF transmitter for the purposes of monitoring nesting activity. We programmed GPS transmitters to record hourly locations throughout daylight hours and an additional roost location at midnight each day from November 1 through July 31 each year. From late April to early June of 2018-2020, Maine allowed for the harvest of bearded turkeys across most of the state. When banded turkeys were reported, we asked hunters to identify the town of harvest, which we used to
define the locations of recoveries. During April through July of 2018-2020, we located VHF-marked turkeys and used triangulation to approximate their location to identify nesting behavior according to methods described in chapter 4.

We used observed movements between capture and either harvest or nesting locations to assess movement of wild turkeys between their winter and nesting home ranges. We created a sampling grid of hexagonal cells sized to approximate the average area of all Maine towns (~104 km²). We defined seasonal movements as any instance where a turkey that was observed in a different grid cell than the one it was captured within. We subset our observations to only harvests and nests that occurred in the same year as when the turkey was captured.

5.2.3 Habitat Covariates

Using datasets from remotely sensed data products, we measured landscape characteristics to assess hypotheses for wild turkey seasonal movement patterns. We used raster data available through the National Land Cover Database (Homer et al. 2020) and Natural Resources Canada (Latifovic 2015) to identify forested, agriculture (row crop and pasture land), developed, wetland, and grassland landcover at a 30m resolution. Forested landcover is an essential component of wild turkey habitat, providing shelter, foraging opportunities, and roost locations at night (Chamberlain et al. 2000, Pollentier et al. 2017). Agricultural lands, developed areas, and grasslands are all potential foraging areas for turkeys (Vander Haegen et al. 1989, Lambert et al. 1990, Niedzielski and Bowman 2016, Pollentier et al. 2017) but some of these areas may exhibit greater potential for disturbance and predation (Spohr et al. 2004), leading to opposing forces of selection that may influence movement. Wetlands in the northeast become inundated and potentially impassable as snow melts in the spring and water accumulates, which may cause turkeys to avoid such areas. We used the Euclidean Distance tool in ArcGIS Pro (v2.6.0) to measure distance to forest edge for each raster cell. We used public road information available through the Department of Transportation to measure distance from nearest road for a 30m scale.
raster. Roads and forest edges have been shown facilitate movement by animals (Holbrook et al. 1987, Trombulak and Frissell 2000) and may provide convenient corridors between winter and spring ranges for turkeys. We used digital elevation maps and the slope tool in ArcGIS Pro to quantify the average slope for a 30m resolution raster. Despite their ability to fly, turkeys’ primarily move by walking and thus may avoid areas with steep slopes which inhibit movement. We used the “landscapemetrics” package (Hesselbarth et al. 2019) in program R (v.4.0.3, R Core Team, 2020) to generate an aggregation index, edge density, and a connectance index for forested habitat within each sampling grid cell. Forest configuration, specifically increased fragmentation and edge density, may lead to an increases in nest predator abundance in an area (Fleming and Porter 2015), leading turkeys to avoid these areas in the spring. To identify trends in the propensity to initiate seasonal movements and selection for settling locations, we summarized landcover covariates within hexagonal sampling grid cells. To identify patterns of fine scale movement between winter and spring ranges, covariates were measured at locations along a 30m raster.

5.2.4 Modelling Overview

To make inferences about turkey migratory connectivity between WMDs, we used models for movement propensity and settling decisions in combination with an IBM describing landscape connectivity between winter and spring ranges constructed using GPS tracking data and calibrated on banding and nesting information (Figure 5.1). Models initiated seasonal movements according to the probabilities determined from movement propensity models based on landcover covariates. Given that a turkey initiated seasonal movements, the IBM simulated movement decisions according to individual behavior parameters and a habitat suitability surface created from GPS tracking data (Figure 5.2). IBM simulations were terminated probabilistically according to results from models describing settling decisions. We distributed simulated turkeys according to WMD specific abundance estimates and used the resulting start and end locations to calculate migratory connectivity metrics.
Figure 5.1. Directed acyclic graph showing which data was used by each component model to simulate connectivity of WMDs for turkeys in Maine.
Figure 5.2. Example movement decisions demonstrating how weights are derived from movement data and a habitat suitability surface within the Individual Based Model for wild turkey seasonal movements between winter and spring ranges. Turkeys could choose to move to any available raster cell within their perceptual range (A). Selection for a given cell was weighted according to habitat suitability as well as step length (B) and turning angle (C), the weights of which were defined by individual specific distributions based on behavioral parameters.
5.2.5 Propensity for Seasonal Movement

We assessed the influence of landscape characteristics on the propensity for turkeys to initiate seasonal movements away from their established winter range using generalized linear mixed models (Resano-Mayor et al. 2020) in program R (v.4.0.3, R Core Team, 2020). We set the response variable as a binary outcome for whether a turkey nested or was harvested in a different sampling grid cell than the one in which it was captured. We limited our analysis to only include nests or harvests that occurred within the same year as when the turkey was captured. For all covariates considered, we created separate linear and quadratic models with and without a sex interaction. We compared models using Akaike Information Criterion (AIC; Burnham & Anderson, 2002) and considered all models that performed better than the null model to be initially supported, and then combined them into a single global model. If multiple models for the same covariate performed better than the null, we used only the model with the lowest AIC score. We examined the p-value for coefficients within the global model and removed relationships that were not considered significant (p < 0.05) to create a final model for seasonal movement propensity. If only one component of a covariate relationship was supported (e.g., the quadratic but not linear term for a polynomial relationship being supported), we retained all components within the final model. Using the final model, we predicted the probability a turkey located within each sampling grid cell would choose to initiate a seasonal movement outside of its current grid cell, given the mean characteristics within that cell.

5.2.6 Individual Based Model Development

To assess decisions made by turkeys while moving between winter and spring home ranges, we simulated potential movement paths using an individual based model (IBM; Pe’er et al. 2011, Allen et al. 2016) of turkey movement that was informed by our GPS tracking data. The overall workflow of model construction and calibration was based on Hauenstein et al. (2019), with adjustments made to accommodate our particular data types. Below, we follow the presentation format (i.e., overview,
design concepts, detail protocol) suggested by Grimm et al. (2010) to provide a standardized description of the IBM.

**Purpose** – The IBM was designed to simulate turkey movement decisions in response to landscape connectivity as they move between winter and spring home ranges. A calibrated version of the IBM was used to assess migratory connectivity among management districts in Maine.

**Agents, state variables, and scales** – Agents within the IBM were individual turkeys whose movement behaviors were determined by independently assigned parameter values that defined movement distance and direction as well as habitat specialization. We assumed step lengths were distributed according to a gamma distribution (Avgar et al. 2016) specified by agent-specific shape (k) and rate (θ) parameters. Similarly, we assumed turning angle would be best described by a wrapped-cauchy distribution (Bailey and Codling 2021) with a common mean (μ = 0) and agent-specific directional persistence (γ). Habitat specialization was defined by a weighting parameter (p) which defined the influence habitat characteristics were given when making movement decisions. We defined an agent’s perceptual range (i.e., the maximum distance it could move between steps) as 95% quantile of the unique gamma cumulative distribution function defined by step length parameters. Movement locations were chosen from a 30m raster for habitat suitability. While real turkeys exhibit consistent movement patterns throughout a day, the IBM simulates movement at discrete time intervals to better match the format of collected data.

**Process overview and scheduling** – Agents selected for daytime locations and roost sites according to the same IBM movement decision process (see below), with differences in daytime and roost location selection being associated with differences in their respective habitat suitability surfaces. For each movement decision, an agent assessed available habitat within its perceptual range and weighted each potential location according to their step length, turning angle, and habitat specialization parameters. The available locations were then sampled according to their weight to determine the next
location. Agents made 15 movement decisions per day for up to 30 days, with the 15\textsuperscript{th} decision each day being for a nighttime roost location.

5.2.6.1 Design Concepts

\textit{Basic Principles} – The IBM described wild turkeys at their northern range limit traveling between winter and spring ranges. While previous research has described the localized movement of turkeys within wintering and breeding ranges (Badyaev et al. 1996, Niedzielski and Bowman 2016), there is comparatively little information available describing observed movements between the two. Thus, we used direct observations of GPS-marked female turkey movement tracks monitored from 2018-2020 to define parameter distributions during the initial construction of our IBM. To simulate these movements, agents within the IBM traveled via a series of short distance movements and were limited in the total distance that they could realistically travel within a given period. Additionally, while turkeys are considered a generalist species able to persist in many ecosystems (Dickson 1992), they exhibit predictable patterns in habitat selection throughout the year (Miller and Conner 2007, Pollentier et al. 2017, B. S. Cohen et al. 2018), thus we incorporated information on habitat structure into the IBM. Turkeys are a tree roosting species, using a heightened position to avoid predators at night (Chamberlain et al. 2000, Sasmal et al. 2018), meaning selection for adequate roost locations were included as a component of movement decisions. Finally, while previous studies of wild turkey movements indicate some tendencies to return to previous nesting locations (Badyaev and Faust 1996), we were limited in our ability to assess nest site fidelity and instead chose to ignore this aspect of movement as it affected long term directional patterns and not short distance movement decisions.

\textit{Emergence} – Primary results from each simulation were the simulated movement tracks, which are produced from the sequential decisions made from an agent’s origin to the final destination realized after up to 30 days of movement.
Sensing – Agents sensed habitat structure at available raster cells within their perceptual range via the habitat suitability surfaces. Additionally, they collected information on the distance to each cell and the change in direction that would result from moving to each cell.

Stochasticity – Agent movement decisions were based on a weighted random sampling of available points within their perceptual range. These decisions were influenced by the behavioral traits of each agent, which were defined by randomly sampling from prior distributions describing potential parameter values for the population.

Observation – Model outputs included the coordinates for each selected location and the order decisions were made in, which together were used to produce a single movement track per agent. Additionally, the habitat suitability score, step length, and direction from previous location were recorded for each selected location within a track.

Initialization – Parameter values defining agent movement behavior were initialized independently by sampling from prior distributions with replacement. To define the initial prior distributions for calibrating the model, we used GPS tracking data of wild turkeys near Bangor, Maine. We fit observed step lengths and turning angles from seasonal movement tracks, after removing steps of length zero, to a gamma distribution and wrapped Cauchy distribution respectively and used parameter estimates to inform prior distributions. To account for potential differences in movement patterns across Maine, we widened the estimated confidence intervals for each distribution parameter by a factor of 20 and used these as the limits for a uniform prior distribution. For parameters that were limited to positive values (i.e., shape and rate of a gamma distribution and scale of a wrapped Cauchy), we truncated distributions to only sample values greater than zero. We used an uninformative uniform prior \((U(0.1, 5))\) for habitat specialization (Hauenstein et al. 2019). Following calibration (see below), priors were adjusted according to rejection sampling results (see below) for use in estimating WMD connectivity in Maine.
During calibration, agent starting locations were chosen from a set of 101 observed seasonal movements derived from nesting and harvest datasets. We generated 1000 agents for each observed turkey movement, with starting locations set to the capture location of a turkey. Starting locations were randomly shifted up to 70 meters to limit the influence of starting position on an agent’s initial trajectory. For estimating of WMD connectivity, starting locations were randomly distributed across Maine in proportion to the estimated abundance of turkeys in each WMD (Gonnerman Dissertation Chapter 2). For WMDs where abundance estimates were not available, we used an average of estimates from all adjacent WMDs.

**Input Data** – Two habitat suitability surfaces were used as inputs in the IBM for daytime and roost site selection respectively. These surfaces were generated using a step selection function (SSF; Duchesne et al., 2010) based on GPS location data for female turkeys traveling between winter and spring ranges. The SSF included categorical covariates for agricultural, developed, and wetland land cover types as well as continuous covariates for slope, distance to road, and distance to forest edge all quantified across a 30m raster. The SSF was implemented via conditional logistic regression with random slopes for individual (Muff et al. 2020) using “r-inla” (Rue et al. 2009) in program R (v.4.0.3, R Core Team, 2020). Coefficient values from the SSF were used to generate a resistance surface for Maine and surrounding land (Osipova et al. 2019), which was then inversed to produce the final habitat suitability surface (Zeller et al. 2012). The final surfaces were modified such that the probability of selecting a water body was zero. Additionally, the roost site selection surface was further modified so only cells that were forested could be selected.

**5.2.6.2 Submodels**

**Movement Decisions** – For each movement decision, agents selected from all raster cells within their perceptual range, which was the 95% quantile of the gamma cumulative distribution function defined by their step length parameters. For each cell, the agent assessed the habitat suitability value
(\(H\)), the distance from its current location to each cell \((d)\), and the change in direction from its previous trajectory \((\alpha)\). A selection weight, \(\omega\), was calculated for each cell based on these values and an agent’s movement parameters, such that

\[
\omega_{i,j} = H(x_i, y_i) \frac{1}{\Gamma(k_j) \theta_j^k j} d_i^{k_j - 1} e^{-\frac{d_i}{\theta_j}} \frac{1}{2\pi \cosh(\gamma_j)} \sinh(\gamma_j) \cos(\alpha_i - \mu)
\]

where \(i\) refers to an available locations and \(j\) refers to an agent. Put simply, the resulting weight, which was agent- and location-specific, was the product of the weighted habitat suitability, the probability density of a gamma distribution for step length, and the probability density of a wrapped Cauchy distribution for turning angle (Hauenstein et al. 2019). The agent then performed a weighted random sample of the available locations to select its next location.

5.2.6.3 IBM Calibration

Our initial model was based on a relatively small sample of GPS-marked female turkeys located in a limited portion of the total area of interest. As such, the IBM may not be representative of male turkeys or turkeys located in other portions of the state. To produce results that better represented turkey populations across Maine, we used approximate Bayesian computation rejection sampling (Sunnåker et al. 2013) in conjunction with observations of nests and harvest locations to calibrate the model for a wider array of potential movement behaviors (Figure 5.3). We compared capture locations to subsequent harvest or nest locations that occurred in the same year to identify individuals that initiated seasonal movements. Using only these individuals, we simulated 1000 movement tracks for each observed seasonal movement. For all simulations, we identified whether, at any time during the movement track, the agent entered the sampling grid cell in which the nest or harvest occurred. If it did not, the movement track was removed from the sample. Using the movement parameters of agents from the remaining tracks, we used the “pdqr” package (Chasnovski 2021) in program R.
Figure 5.3. ABC rejection sampling was performed on IBM simulations using harvest or nesting locations to define likely seasonal movement paths made by turkeys in Maine. Simulated tracks were accepted as plausible if at any time the entered a sampling grid cell which contained the termination of an observed seasonal movement.
(v.4.0.3, R Core Team, 2020) to generate new prior distributions for use in simulating turkey movements to assess connectivity between WMDs.

5.2.7 Settling Decisions

We used resource selection functions (RSF; Manly et al., 2007) to identify landscape characteristics that influenced turkey settling decisions. We specified used locations as the sampling grid cell in which a turkey was harvested or nested within, restricting observations to those that occurred in the same year as when capture occurred. To designate available locations, we created a line from the capture location to observation location and then buffered it by grid cell radius. All grid cells that intersected with the buffer were then considered available to a turkey during their seasonal movement period. We compared the effect of landscape characteristics using conditional logistic regressions via the “survival” package (Lin and Zelterman 2002) in program R (v.4.0.3, R Core Team, 2020) where individual turkeys were the strata identifier. For all covariates considered, we created linear and quadratic models and followed model selection and model building approaches as described above under “Propensity for Seasonal Movements.” Using the final model for settling decisions, we estimated the probability of selection for each sampling grid cell within the area of interest.

5.2.8 Predicting Connectivity of Turkey Populations

We estimated the probability to initiate and terminate seasonal movements in combination with the calibrated IBM to generate simulated tracks of turkey movement which were then used to estimate connectivity between WMDs in Maine. Agents of the IBM were initialized at random starting locations within WMDs according to the variation in turkey abundance across the state (Gonnerman Dissertation Chapter 2). Agents then chose whether to leave their starting sampling grid cell according to a Bernoulli random trial

\[ P(\text{Seasonal Movement}) = B(n, m_y) \]
where \( n \) is the number of trials (1), and \( m \) is the probability a turkey initiated a seasonal movement, which was dependent on habitat covariates within sampling grid cell \( g \). If a turkey did not initiate a seasonal movement, it was randomly placed at a forested location within its initiate sampling grid cell. Otherwise, the calibrated IBM is used to simulate movement steps. For each step, the agent assessed whether it had entered a new sampling grid cell. If so, then the agent decided whether to end its seasonal movement according to a Bernoulli random trial

\[
P(\text{Settle}) = B(n, s_g)
\]

where \( s \) is the probability a turkey would select sampling grid cell \( g \) to establish its spring range, given the characteristics of the cell and our best-supported model above. If a turkey chooses to settling in a cell, it is randomly placed at a forested location within the cell. Otherwise, the IBM continues simulating movements for the agent. If the agent reaches 30 days and has not chosen to settle, the simulation ends at the final roost location on the last day. We then used the start and end location of each movement track to identify the associated origin and destination WMD for each simulated bird.

We calculated a measure of connectivity among WMDs using the “MigConnectivity” package (E. B. Cohen et al. 2018) in program R (v.4.0.3, R Core Team, 2020). Using the start and end locations for each simulation, we subset the data to birds with different origin and destination WMDs. To quantify total change in abundance attributed to turkey movements, we subtracted the total turkeys that started in a WMD from the total that ended in a WMD. We also quantified the percent change in abundance as the total change divided by the initial abundance of turkeys within a WMD. To quantify the likelihood a turkey would move between WMDs, we quantified a transition probability for movement between each pair of WMDs as the total number of individuals that ended in a given destination WMD divided by the number of individuals that began in a given origin WMD. To quantify the total number of turkeys moving between WMD pairs, we summed the total number of turkeys that moved between a given WMD pair.

### 5.3 Results
From 2018 through 2020, we captured and banded 890 unique wild turkeys across the state; 406 males and 484 females. We observed 24 unique seasonal movement paths from GPS marked hens. Seventy-four male turkeys were harvested in the same year as they were captured, with 23 being harvested in the sampling grid cell they were captured in compared to 51 that were harvested in a different cell. We identified 91 nests that were initiated in the same year as the hen was captured, with 41 occurring in the same sampling grid cell as capture compared to 50 in a different cell.

5.3.1 Seasonal Movement Propensity

The final model describing propensity for seasonal movements included coefficients for sex, proportion agriculture, connectance index, edge density, aggregation index, a quadratic term for proportion developed, and latitude (Figure 5.4 A,B). When all landcover covariates were set to the mean, male turkeys had a 75.1% (±10.9%) probability to initiate seasonal movements compared to 18.0% (±7.6%) for female turkeys (β = 2.618; 95% C.I. 1.505 – 3.730). As proportion agriculture within a sampling grid cell increased, the probability of seasonal movements decreased (β = -1.243; 95% C.I. -2.041 – -0.480). As the connectance index of a grid cell increased, the probability of seasonal movements decreased (β = -32.068; 95% C.I. –14.018 – -5.012). As the edge density of a grid cell increased, the probability of seasonal movements decreased (β = -4527.017; 95% C.I. –2112.103 – -6.942). As the aggregation index of a grid cell increased, the probability of seasonal movements decreased (β = -4503.905; 95% C.I. –2102.025 – -6.906). Probability of seasonal movements was lowest near 12% developed landcover within a grid cell, and increased as the proportion either increased or decreased. As latitude increased, the probability of seasonal movements increased (β = 0.787; 95% C.I. 0.102 – 1.472). When extrapolating model estimates for all sampling grid cells within Maine, the mean probability of seasonal movements was 56.4% for females and 70.1% for males, and ranged between 0% and 100% among WMDs for both sexes.
Figure 5.4. Both the probability to initiate seasonal movements (A,B) and selection for settling locations (C,D) varied across Maine according to relationships between observed female (A,C) and male (B,D) turkey movements and remotely-sensed habitat covariates.
5.3.2 Step Selection Function (Habitat Suitability)

For the SSF describing selection by female turkeys during seasonal movements, only coefficients for wetland cover, slope, and distance to forest edge were supported (Figure 5.5). Habitat patches categorized as wetland were 0.519 (95% C.I. 0.363 – 0.715) times as likely to be selected than those not categorized as wetland. For every 10 degree increase in slope, a habitat patch was 1.271 (95% C.I. 1.083 – 1.507) times as likely to be selected. For every 100 m increase in distance to forest edge, a habitat patch was 0.670 (95% C.I. 0.549 – 0.741) times less likely to be selected.

5.3.3 Individual Based Model Calibration

Mean step length of GPS-marked females during seasonal movements was 272.4 m (1 m – 3004 m and mean turning angle was 0.1 radians (-3.14 – 3.14). Observed step lengths were best described by a gamma distribution with a $k$ of 0.848 (SE = 0.017) and $rate$ of 0.003 (SE = 0.0008). Observed turning angles were best described by a wrapped Cauchy distribution with a rho of 0.082 (SE = 0.026).

For the 101 observed seasonal movements between capture and either harvest or nest location, we generated a total of 101,000 simulated seasonal movement paths to calibrate the parameter priors for the IBM, of which 34,708 overlapped with their paired destination sampling grid cell and were accepted. For 6 of the 101 observed seasonal movements, we did not observe a simulated path overlap with their destination sampling grid. Of parameters defining movement of accepted simulations (Figure 5.6), $k$ averaged 0.855 (0.500 – 1.197), $rate$ averaged 0.003 (0.002 – 0.005), $rho$ averaged 0.269 (0.0 – 0.525), and $p$ averaged 2.280 (0.1001 – 5.000).

5.3.4 Settling Decisions

The final model describing selection for settling locations included interactions between sex and quadratic relationships for both proportion wetland and proportion agriculture (Figure 5.4 C,D). For proportion wetland, probability to terminate seasonal movements was highest near 20% wetland landcover within a grid cell for males and near 32% for females (Figure 5.7A). For proportion agriculture,
Figure 5.5. Variable habitat suitability resulted in areas of concentrated turkey movements. Here we present a portion of the habitat suitability surface estimated from a step selection function using female turkey GPS tracking data (A), the resulting simulated movement steps produced during the calibration of the IBM (B), and an estimate of turkey location density produce from a kernel density estimator (C).
Figure 5.6. Calibrated parameter distributions (red dotted line) were a result of individual movement characteristics (grey dotted line) and were narrower than the proposed prior distributions (solid black line) based on GPS movement data. Parameters correspond to habitat specialization (A), turning angle concentration (B), and step length (C,D).
Figure 5.7. Selection for sampling grid cells when establishing spring ranges following seasonal movements differed between male (pink) and female (purple) turkeys according to the proportion of wetland (A) and agriculture (B) within a grid cell.
probability to terminate seasonal movements was lowest near 6% agriculture landcover within a grid cell for both males and females (Figure 5.7B). When extrapolating model estimates for all sampling grid cells within Maine, the mean probability of terminating seasonal movements was 76.5% (48.7% – 99.8%) for females and 80.2% (49.2% – 100%) for males.

5.3.5 WMD Connectivity

Of the 86,950 simulated agents used to estimate connectivity between WMDs, 46,011 (52.9%) initiated seasonal movements away from their winter range (Table 5.1). A total of 10,988 (12.6%) simulated tracks ended in a different WMD than the one in which they started, and 1,407 of these (1.6%) ended outside of state boundary lines. 38.2% of females initiated seasonal movements compared to 67.6% of males. Of turkeys that ended their movement in a different WMD than they started, 5,591 (50.9%) initiated seasonal movements while 5,397 (49.1%) did not. 12.6% of both males and females ended their movements in a different WMD than the one in which they started. Mean net distance traveled between starting and ending points by all simulated turkeys was 4,963 m and ranged from 9 m to 29,972 m.

Migratory connectivity calculated from simulated seasonal movements was 0.380. Total change in turkey abundance within a WMD attributed to seasonal movements averaged -48.52 (-646 – 497). Mean percent change in abundance attributed to seasonal movements was 7.35% (-12.43% – 85.40%; Figure 5.8A). Excluding WMD pairs where no turkeys were shared between origin and destination, the average transition probability was 0.192 (0.002 – 0.727; Figure 5.8B). The mean number of individuals exchanged between WMDs was 136.9 (1 – 867; Figure 5.8C).
Table 5.1. Immigration rates were similar among turkeys that did and did not initiate spring seasonal movements. Here we show the total number of simulated turkeys that initiated seasonal movements and whether they emigrated to new WMDs by each sex. We also provide the mean, minimum, and maximum distance traveled for each grouping.

<table>
<thead>
<tr>
<th>Initiated Movement</th>
<th>Emigrated</th>
<th>Sex</th>
<th>Total</th>
<th>Mean Distance</th>
<th>Min. Distance</th>
<th>Max Distance</th>
</tr>
</thead>
<tbody>
<tr>
<td>N</td>
<td>N</td>
<td>F</td>
<td>23215</td>
<td>4924.8</td>
<td>13.4</td>
<td>11841.6</td>
</tr>
<tr>
<td>N</td>
<td>N</td>
<td>M</td>
<td>12327</td>
<td>4857.2</td>
<td>27.0</td>
<td>11874.0</td>
</tr>
<tr>
<td>N</td>
<td>Y</td>
<td>F</td>
<td>3623</td>
<td>6358.0</td>
<td>376.0</td>
<td>12408.5</td>
</tr>
<tr>
<td>N</td>
<td>Y</td>
<td>M</td>
<td>1774</td>
<td>6361.3</td>
<td>391.1</td>
<td>11867.3</td>
</tr>
<tr>
<td>Y</td>
<td>N</td>
<td>F</td>
<td>14767</td>
<td>4535.7</td>
<td>9.4</td>
<td>22057.6</td>
</tr>
<tr>
<td>Y</td>
<td>N</td>
<td>M</td>
<td>25653</td>
<td>4712.2</td>
<td>18.6</td>
<td>17866.8</td>
</tr>
<tr>
<td>Y</td>
<td>Y</td>
<td>F</td>
<td>1870</td>
<td>6351.2</td>
<td>521.7</td>
<td>29972.7</td>
</tr>
<tr>
<td>Y</td>
<td>Y</td>
<td>M</td>
<td>3721</td>
<td>6273.0</td>
<td>357.4</td>
<td>26516.6</td>
</tr>
</tbody>
</table>
Figure 5.8. Simulations of WMD connectivity indicate that uneven immigration rates resulted in net changes to turkey abundance for most WMDs. Here we present the percent change in WMD turkey abundance (A), the individual transition probabilities for each WMD pairing (B), and the total number of individuals exchanged between WMDs (C).
5.4 Discussion

We observed uneven exchange of individuals among WMDs, resulting in net changes to WMD abundance that were mediated by seasonal movements. Such movement dynamics are important to consider when evaluating population response to management (Johnson et al. 1992, Anthony and Blumstein 2000, Morales et al. 2010), particularly for harvested species where local emigration and immigration may produce additive or opposing pressures to harvest, respectively (Pedersen et al. 2004, Sedinger et al. 2010). For example, in our system the spatial configuration of net change in abundance largely imitated fall harvest regulations. In the southwestern portion of the state, more liberal regulations intended to stabilize generally larger turkey populations (MDIFW, 2017) aligned with a predicted a net emigration of turkeys. In the northwest and southeaster portions of the state, where turkey abundance was lesser and harvest regulations more restrictive, net immigration was present and consistent with management objectives to stabilize and grow these populations. In contrast, in the northeastern portion of the state, the combination of emigration and minimal fall harvest currently allowed may make these populations more sensitive to changes in harvest and therefore warrant a more conservative management approach. To more directly predict how harvest and movement interact to affect population growth, our results can be integrated into existing population estimation models (Gonnerman Chapter 2) to simulate response to various harvest management regimes.

Unbalanced immigration and emigration among harvested populations can lead to the emergence of source-sink dynamics (Naranjo and Bodmer 2007, Andreasen et al. 2012) which often require consideration to reach desired management outcomes. For example, the Maine Department of Inland Fisheries and Wildlife turkey management plan lists decreasing human-wildlife conflicts and disease spread among turkey populations as key objectives (MDIFW, 2017), both of which call for the reduction of turkey densities through harvest or relocations under normal assumptions of a closed population (Dickman 2010). However, if populations are open, emergent source-sink dynamics can
broadly influence management outcomes by altering optimal harvest limits (Lundberg and Jonzén 1999) and inhibiting the ability to monitor for regional population declines (Robinson et al. 2008). Region specific consequences may also arise in the presence of harvest, such as in areas with high animal density that are supplemented by emigration from neighboring populations. If harvest is increased in such areas, then a population sink may occur and density will not be reduced, although demographics of the population might shift (Novaro et al. 2000, Robinson et al. 2008). Conversely, if a densely populated area serves as a source for other populations, then increasing harvest within that region could have destabilizing demographic effects and lower long term population viability for supported sinks (Lundberg and Jonzén 1999). As populations aren’t defined by their WMD boundaries, the spatial configuration of source and sink populations stemming from harvest can further impact these dynamics (Novaro et al. 2005). In all cases, a more complete knowledge of the rate of immigration and emigration between management districts will inform effective implementation of harvest regulations.

Parameter distributions from the calibrated IBM indicated a range of movement behaviors explained observed seasonal movements by turkeys in Maine. Step length parameter distributions supported tendencies for both short- and long-distance movements and turning angle concentrations showed a tendency for greater directionality in movement, both of which describe dispersal and seasonal movement behaviors (Byers 2001, Grovenburg et al. 2009). Simulated turkeys placed a moderate emphasis on landscape structure as indicated by a wide distribution for $p$ which decreased at low and high values. As turkeys in Maine exist across a variety of landscape compositions, a more moderate consideration for habitat structure may facilitate movement better than high or low specialization strategies, which are more dependent on the amount and configuration of available habitat for success (Püttker et al. 2013, Martin and Fahrig 2018).

All parameter distributions calibrated on nest and harvest data were wider than those derived from GPS data alone, indicating that integrating additional data sources allowed the IBM to simulate for
a broader, more representative range of movement strategies associated with turkey location and sex.

As movement behavior has been shown to vary within and among populations for a variety of reasons (Bélisle 2005, Singh et al. 2012), models based on few individuals from a limited area may result in overly specific inferences not applicable across an entire population. For example, as functional connectivity is a product of landscape structure (Goodwin and Fahrig 2002, Day et al. 2020), our inclusion of data from more heavily forested areas and from areas with higher human population densities capture movements that better represented the movement across landcover available in Maine. Movement tendencies are also a result of behavioral and biological traits of an individual which can vary within a population (Hyslop et al. 2014, Harrison et al. 2015, Bastille-Rousseau and Wittemyer 2019, Mariela et al. 2020), further increasing the need to collect data that is representative of the whole population. Failing to account for the range of possible movement strategies present in a population can result in bias of connectivity estimates which misinform management (Palmer et al. 2014).

Our simulations illustrated that male turkeys were more likely to initiate seasonal movements than females, but were less selective in their settling decisions, resulting in similar rates of dispersal among WMDs between the sexes. Most females that moved between WMDs in spring began closer to management boundaries and crossed during within-home range movements, whereas most males did so during seasonal movements and traveled greater distances. While these movements resulted in similar connectivity outcomes, the differing mechanisms by which they arose warrant consideration. Greater selectivity by females was likely a result of nesting habitat selection, as female turkeys select for a variety of resources throughout the nesting process (Gonnerman Chapter 4, Little et al., 2016; W. F. Moore et al., 2010; Pollentier et al., 2014), which impact movement between winter and nesting ranges. The decreased tendency for females to initiate seasonal movements may indicate that many are able to access winter and nesting resources within overlapping or proximate areas. Despite this, we still observed management boundary crossing by female turkeys that did not initiate seasonal movements,
likely due to overlap of home-ranges and management management boundaries, increasing the chance of being observed in a different WMD that an individual was captured (Bischof et al. 2016). Thus, as a greater amount of winter habitat occurs along WMD boundaries, we would expect increased exchange of individuals, especially for females. Our simulations randomly distributed turkeys within WMDs, but an approach that adjusts starting locations according to winter habitat may better represent movements of turkeys in Maine. While females responded to habitat during seasonal movements, male turkeys during spring may make movement decisions to improve reproductive opportunities (Hurst et al. 1991), leading to an emphasis on hen density over habitat. The IBM treated turkeys as independent agents that did not interact with one another, but if male movements respond to turkey density, then an approach that allows agents in the IBM to interact may more realistically mimic such dynamics.

Seasonal movements simulated by the IBM took place immediately prior to the spring turkey hunting season, when most male harvests occur. As such, the distribution of male turkeys following seasonal movements is unlikely to change prior to the hunting season. However, as there is a greater amount of time between seasonal movements and the fall either-sex hunting season, the IBM likely does not capture movements that define fall turkey distributions. During the summer, successfully nesting turkeys shift home ranges to include brood rearing habitat (Pollentier et al. 2014b, Streich et al. 2015) and further changes to turkey distributions may occur in the fall as individuals move to winter ranges (Vander Haegen et al. 1989, Kane et al. 2007). If turkeys exhibit fidelity for wintering grounds like some do for nests and roost sites (Badyaev and Faust 1996, Caveny et al. 2011), then initial changes in abundance due to spring seasonal movements may be negated by turkeys returning to their original wintering grounds. Should these additional movements occur, it is unlikely that inferences can be directly made about fall turkey distributions from the current IBM results. Further information on how turkeys move throughout the summer and fall are likely necessary to identify how harvest management must account for turkey movements for the fall hunting season.
In addition to harvest management, our results provide an example for why movement of individuals should be considered for monitoring population abundance. While a portion of simulated individuals that moved across WMD boundaries did so during local movements, most were a result of directional seasonal movements away from wintering grounds. Such non-random movement among populations may introduce bias into abundance estimates due to violation of closure assumptions, affecting both accuracy and precision (Kendall 1999). If individual movements occur between areas with uneven detection probabilities, as has been observed for turkeys across WMDs in Maine (Gonnerman Chapter 2), further bias may arise (Chadœuf et al. 2018). Fortunately, extensions of commonly-implemented abundance estimation procedures have been developed to account for animal movements that violate closure assumptions (Otis et al. 1978, MacKenzie et al. 2002, Royle 2004), although they often require estimation of movement behavior or rates of immigration and emigration (Horton and Letcher 2008, Ketz et al. 2018). When budget limitations prevent collecting individual movement information, models such as the IBM presented here can be constructed using expert knowledge and calibrated on available data types to better account for model violations (Hauenstein et al. 2019).

As calls to distinguish between wildlife management and political boundaries grow more numerous (Linnell et al. 2001, Bischof et al. 2016, Meisingset et al. 2018), information on which new boundaries can be defined also grows more readily available (Thums et al. 2018). Direct observations of animal movement via GPS and radiotelemetry (Walton et al. 2018, Mckinnon et al. 2019) or simulated movements from IBMs (Philips 2020) are all capable of providing insight to guide ecologically relevant management guidelines. For example, we calculated a low degree of migratory connectivity between WMDs which, in combination with the substantial number of boundary crossings observed, indicated a more diffuse distribution of turkeys with limited correlation between winter and spring WMDs. While defining management regions for such a dispersed population may be difficult, information on the total number of turkeys moving between districts can delineate where immigration is strongest and therefore
which WMDs share the most animals and should therefore be considered as a singular unit. Transition probabilities between WMDs can identify uneven immigration patterns and therefore where source-sink populations likely exist, so that harvest regulations can be considered with both in mind. Animal movement patterns can even inform the shape of management units, such as maximizing the ratio of a WMD’s area to its perimeter to increase the maximum potential distance from a management boundary and decrease the likelihood of immigration to other WMDs.
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Appendix 1: Description of Hidden Markov Models for Turkey Movement

We used HMM to categorize individual location data into discrete movement states. For the purposes of HMM, the observed data is a simplification of animal movements, usually in the form of step distance and turning angle (Adam et al. 2019, DeRuiter et al. 2016, McKellar et al. 2015), but they can include many other metrics related to an individual’s movement such as speed, depth, or altitude (McClintock et al. 2013, van Beest et al. 2019). The observed movement data is assumed to be generated from one of a number of distributions, each corresponding to a latent movement state, which is modeled as a Markov chain that determines which distribution is selected for a given timestep (Langrock et al. 2012). We measured step length and turning angle between successive GPS transmitter locations for use as the observed data streams within the HMM.

We identified roosting, stationary, and mobile as the three primary movement states that turkeys could exist in during the time period considered. Turkeys spend nights roosted in trees for safety from predators, and as such would be found in the same location during successive locations while in this state. We described stationary behavior as localized movements with little concentrated directionality. This type of behavior could encompass loafing, preening, and sheltering behaviors (Dickson 1992). Mobile behavior differed from stationary in that distance between successive locations would be greater and movement would be more concentrated in a given direction, behavior that may correspond to individuals foraging and searching for necessary resources (Dickson 1992). We applied constraints to the HMM structure (described below) to accommodate these three movement states.

We used the momentuHMM package (McClintock and Michelot 2018) in the R programming environment (v4.0.3, R Core Team 2020) to fit individual turkey movement tracks to the specified movement states. momentuHMM requires that data streams be collected at uniform time intervals, which does not describe our data due to missed location fixes, slight irregularities in the timing of fixes, and the time gap between roost fixes and daytime fixes. To account for the nighttime periods without
fixes, we set the single roost location collected each night to the location for each nighttime hour when a location was not otherwise scheduled to be collected. To account for all other irregularities in location data timing, we used the crawlWrap function in momentuHMM, which fits a continuous-time correlated random walk (Johnson et al. 2008) to predict regularly timed locations that are interpolated across any periods of missing data. We assumed that step length was distributed according to a gamma distribution and turning angle concentration was distributed according to a wrapped Cauchy distribution (McClintock & Michelot 2018).

User defined boundaries can be implemented within momentuHMM to better define the distributions that describe each movement state. Based on a-priori assumptions about the three movement states, we set limits on the mean and zero-mass parameters for step length and on the concentration of the turning angle. It was assumed that mean step length was greatest for Mobile and lowest for Roosting. Turning angle concentration was assumed to be lowest for Roosting and highest for Mobile. To better identify Roosting behavior, we restricted the zero-mass parameter to >0.98 and the mean step length to <5. We restricted turning angle concentration to less than 0.94 for all three movement states to avoid pooling within one of the movement states. As we were interested in periods when turkeys were least active, we restricted mean step length for the stationary state to be less than the first quartile of daylight step lengths collected (20 m).

momentuHMM also allows for the inclusion of additional environmental and individual covariates to better describe variation in the transition probabilities between states (McClintock et al. 2012, Pirotta et al. 2018). This allows for the identification of factors that influence behavior. We assumed that transition between states would be influenced by snow depth, wind chill, and hour of the day. We used the cosinor function within momentuHMM to account for the cyclical nature of behavior throughout the day. The cosinor function estimates a coefficient for both the cosine and sine of 2π×(hour of the day/cycle length) which in our case was 24 hours. We included individual by year level
covariates to account for difference in individual behavioral tendencies. By specifying the “retryFits” argument, which we set to 5, we were able to use random perturbations of parameter estimates to iteratively improve model fit and return the model with the largest log likelihood. The final model was visually assessed for goodness of fit using the Q-Q Plot for the pseudo-residuals of the model (Zucchini et al. 2017). To determine the significance of the relationship between weather covariates and state transition probabilities, we examined coefficient values and their 95% confidence intervals. We used the multinomial logit link function to translate coefficient values to interpretable results. Using outputs from the HMM, we assigned the most likely movement states to each location after fitting our models.
BIOGRAPHY OF THE AUTHOR

Matthew Gonnerman was born in Dallas, Texas on May 11, 1989. He graduated with a bachelor of science degree in biology from Saint Louis University in 2011 before getting a master of science in wildlife management at Auburn University in 2017. Between his undergraduate and master’s degree, Matthew spent his time working an assortment of field technician jobs where he performed prescribed burns to rehabilitate native grasslands, assessed the wintering and stopover habitat of endangered whooping cranes, and worked on an assortment of upland game bird projects across the country. His first publication was completed while working on his doctorate at the University of Maine and discusses the nesting phenology of wild turkeys in relation to hunting activity in Maine. He is a candidate for the Doctor of Philosophy degree in wildlife ecology from the University of Maine in December of 2021.