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Modeling autumn migration of a rare soaring raptor identifies new movement corridors in central Appalachia

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ABSTRACT

Understanding animal movements is fundamental to ecology and conservation, yet direct measurement of movements of birds is both challenging and costly. Raptor behavior and demography are especially difficult to monitor, but models of movement can provide information toward this goal. The golden eagle (*Aquila chrysaetos*) in eastern North America is an apex predator of regional conservation concern, and little is known about its population ecology, movements, or behavior. We designed an agent-based model to simulate autumn migration of eagles in Pennsylvania, USA. Inputs to the model included information on regional topography, known flight behaviors (i.e. slope-soaring and thermal-soaring and gliding), estimated uplift, and a principal axis of migration. In total, we modeled 6094 flight routes, averaging 2191 (±1281; ±SD; range: 3–5373) moves. Simulations were spatially comparable to historic flight route data collected via telemetry and generally followed topography that provided uplift. In our model, orographic uplift available to migrant eagles was stronger and more frequent than thermal uplift, and uplift forms were not correlated with one another ($r = -0.145$). Modeled golden eagle migration in autumn follows a narrow-front pattern as individuals are concentrated in areas that produce orographic uplift. Simulated flights were more concentrated on days when historic counts of golden eagles were high at monitoring sites. In contrast, simulations were more dispersed on days when fewer actual eagles were recorded. We used output from our simulations to select new sites that could be used for monitoring migratory raptors. Relatively large numbers of golden eagles were observed at these sites, thus validating performance of our model. This work identifies a novel, cost-effective method for modeling migration patterns of and furthering conservation goals for a rare, low-density raptor species.

1. Introduction

Movement ecology seeks to explain the intrinsic and extrinsic factors that influence movements and spatial distributions of animals (Nathan et al., 2008). Movements and distributions of birds are of particular interest as many of their populations worldwide are characterized, in part, by their migratory behavior (Mandel et al., 2008; Zalles and Bildstein, 2000). Migratory behaviors are often expansive in scale, and such behaviors can have real consequences for population biology. For example, for some species, most mortality occurs during migration (Klaassen et al., 2014; Newton, 2010; Sillett and Holmes, 2002). Consequently, this period is important for study and monitoring of species of conservation concern (Bildstein, 2006; Bowlin et al., 2010; Dunn and Hussell, 1995; Hahn et al., 2009; Thorup et al., 2006).

Monitoring is difficult when focal populations are composed of secretive, low-density individuals. These challenges are compounded when individuals are sensitive to human activity and when conservation efforts are inhibited by logistics and finances (Zalles and Bildstein, 2000). Among birds, raptors present some of the most significant monitoring challenges. For example, birds of prey are not highly vocal and are not amenable to surveys with techniques developed to monitor songbirds. However, monitoring their populations can be important to effective conservation management because birds of prey are apex predators that are often indicative of ecosystem health (Bildstein, 2001; Sergio et al., 2005, 2006, 2008).

During migration, raptors are observed at hawk-count sites, often where the landscape concentrates their flights (Geyer von Schweppenburg, 1963; Kerlinger, 1989; Zalles and Bildstein, 2000). Concentration points allow for more efficient data collection, and

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in some circumstances, hawk-count data can provide demographic estimates for ecological and management applications. For example, hawk-counts are used to estimate trends in raptor populations and to make inference about demographic parameters such as population size (Dennhardt et al., 2015; Hawk Migration Association of North America, 2013; Hull et al., 2010; Lewis and Gould, 2000). Because hawk-count data are so readily available, using them in concert with agent-based movement models may lead to important insights into individual behavior and into where and when populations might best be monitored.

Agent-based simulation models are commonly used to predict how individual animals respond to factors in their environment. These models are useful for predicting risks associated with behaviors of rare species, especially when those behaviors interact with anthropogenic processes (Ainslie et al., 2014; Goss-Custard and Stillman, 2008; Gschweng et al., 2012). Agent-based models are advantageous for modeling animal movements because of their utility for predicting aggregated behaviors at the population-level (Bauer and Klaassen, 2013; Goss-Custard and Stillman, 2008). Migration is one such aggregate behavior that is of great interest to species monitoring, conservation, and management (Eichhorn et al., 2012). In order to better understand migration decisions made at the individual-level, it is important to incorporate weather information into agent-based models of migration (Ainslie et al., 2014; Shamoun-Baranes et al., 2010; Van Loon et al., 2011). This is especially true for those species that rely on updrafts to subsidize energetic costs associated with long-distance migration.

Golden eagles (*Aquila chrysaetos*) rely heavily on environmental updrafts during migration (Bohrer et al., 2012; Brandes and Ombalski, 2004; Lanzone et al., 2012). These raptors are rarely observed in eastern North America and little is known about their population ecology, movements, and behavior (Katzner et al., 2012a; Kochert and Steenhof, 2002). Eastern golden eagles breed in remote areas of northeastern Canada (Kochert et al., 2002; Watson, 2010), and most migrate through the central Appalachian Mountains to overwinter in the eastern United States (Brodeur and Morneau, 1999; Brodeur et al., 1996; Millsap and Vana, 1984; Morneau et al., 1994). Despite reports of continental population declines (Hoffman and Smith, 2003; Smith et al., 2008), there are indications that the size of this eastern subpopulation may be increasing (Farmer and Smith, 2010; Farmer et al., 2008). However, the number of individuals in this population is unknown.

Although eastern golden eagles are rarely seen on their remote breeding grounds, they are counted in the hundreds at hawk-count sites throughout the Appalachian region. Therefore, hawk-count data may provide a foundation for insight toward conservation management of this species. The main objective of this study was to use simulation models to evaluate southbound golden eagle migration within central Appalachia and to relate spatial patterns in those movements to the locations of existing hawk-count sites. Because entry and exit points into this system are largely known, our model focuses on characterizing more local-scale phenomena, specifically how eagles move through the landscape and how that information may inform monitoring. In particular, we used our model to answer the following questions: (1) how does regional topography and weather influence eagle migration routes? and (2) are there gaps in the spatial distribution of hawk-count sites where migrant eagles are concentrating that could support new hawk-count sites?

2. Materials and methods

2.1. Study area

We focused our research on an area of the central Appalachian Mountains roughly defined by the state of Pennsylvania, USA (Fig. 1a). Topography in Pennsylvania is diverse and includes long-linear ridges, lowland valleys, forested highlands, and mountain foothills spread throughout multiple physiographic provinces (United States Forest Service, 2007). Local, autumn weather is temperate, windy, and overcast. Easterly and westerly winds are most prevalent, and both interact with the steep topography of mountain ridges to generate orographic uplift, which the eagles use in slope-soaring flight (Bohrer et al., 2012). On warmer days with little wind, downward solar radiation heats the land surface and produces thermal uplift, which the eagles use in thermal-soaring and gliding flight (Duerr et al., 2012). Peak migration for eastern golden eagles occurs in November (Katzner et al., 2012a, 2012b).

2.2. Overview

We describe our computer model based on the updated overview, design concepts, and details (ODD) protocol (Grimm et al., 2010).

2.2.1. Purpose

We designed an agent-based movement model (hereafter, migration model), written in the Visual C# 4.0 coding language (Microsoft Corporation, 2010). The primary purpose of this model was to simulate migratory movements of golden eagles. Previous models of golden eagle movements focused on migration influenced by one form of uplift (Brandes and Ombalski, 2004). Due to recent evidence implicating a role for multiple flight modes (Duerr et al., 2012; Lanzone et al., 2012), we designed our computer model to incorporate multiple forms of uplift. The subsequent conservation goal of our work was to use output from the migration model to evaluate spatial relationships between simulated flights and existing hawk-count sites.

2.2.2. Entities, state variables, and scales

We modeled southbound, autumn migration for golden eagles. A simulated eagle comprises an entity in this model, whose states are the grid-cells through which it moves. The scale of each grid-cell corresponds to the spatial resolution of the input National Elevation Dataset (NED, 90 m^2 resolution; United States Geological Survey, 2012). We chose to simplify our model by simulating migration at 90 m^2 resolution in order to assess intensity of movements at a scale relevant to regional migration and to avoid modeling local-scale interferences (e.g., from forest tree lines and man-made structures) with uplift generation. Before an eagle moves to any grid-cell, the environmental state (estimated uplift, in m/s) of the grid-cells around its current position (i.e., due west, east, southwest, south, and southeast) is determined from input weather data.

To create meteorological inputs for the model, we randomly selected 33 weather days from November 2002 to 2011. We obtained meteorological data for those days from the North American Regional Reanalysis (NARR; Mesinger et al., 2006). We assigned the weather data from NARR's 32 km^2 resolution to the scale of the NED using a spatial join in ArcGIS 10 (ESRI Inc., Redlands, CA). On each of our randomly selected days, we chose 3 separate, 3-h blocks of data (i.e., 1500, 1800, 2100 Greenwich Mean Time, equivalent to 1000, 1300, 1600 Eastern Standard Time) and pulled the following weather variables for that day: wind, heat flux, boundary layer, and air temperature conditions. Our complete sample comprised 495 weather files (i.e., 33 days × 3 h × 5 variables), of which 15 (i.e., 1 days × 3 h × 5 variables) were randomly selected as input for each model run.

Each grid-cell has its own unique state. We assigned a probability to each grid-cell adjacent to the simulated eagles' current position and assumed that each probability represents the likelihood of the bird moving to any one cell. We constrained movement to the west (W), east (E), southwest (SW), south (S), or

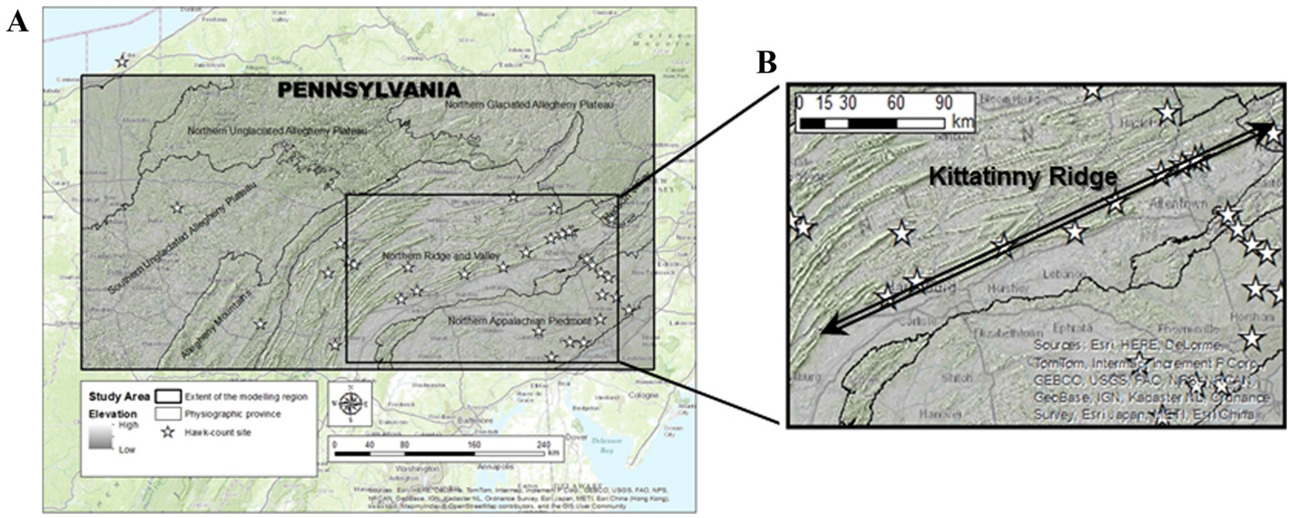

Fig. 1. (a) Study area and model system in the central Appalachian Mountains of Pennsylvania, USA. (b) General location of the Kittatinny Ridge in the study area (i.e., represented by the arrow), an important corridor for migrant raptors in autumn.

southeast (SE) directions. We weighted the grid-cell probabilities such that the highest probability of movement was in the southwest direction because we know that raptors in this region tend to migrate in this direction (i.e., termed the principal axis of migration (PAM); Brandes and Ombalski, 2004; Kerlinger, 1989). We initially set these probabilities as follows: W = 0.225, E = 0.05, SW = 0.300, S = 0.225, SE = 0.200, but subsequently adjusted those probabilities based on the amount of uplift in each cell. We accounted for uplift as follows: (1) grid-cells are first assigned their initial movement probability; (2) grid-cells are then populated with the estimated total uplift (i.e. thermal plus orographic uplift) based on weather and topographic conditions; (3) total uplift across all grid-cells is averaged among the grid-cells; (4) total uplift per grid-cell is then divided by the average uplift; (5) adjusted total uplift per grid-cell is then multiplied by each cell's movement probability; and (6) resulting probabilities are normalized by the sum of adjusted total uplift. In effect, this produces grid-cell probabilities weighted by localized uplift, and these probabilities determine an eagle's next movement.

Simulated eagles could only move one grid-cell per time step, except for when lift was ≤ 0 m/s in the five nearest cells. When that occurred, we allowed the simulated eagle to move several grid-cells to the southwest. To do this, lift was averaged among four groups of nine grid-cells between 90 and 500 m in the southwesterly direction from the current position. The eagle then immediately moved to the furthest (southwest) grid-cell in the group containing the highest average lift. This "looking ahead" behavior mimics direct, powered (i.e., flapping) flight between positions (Brandes, 2009). For example, an eagle might see a distant ridgeline, perceive current wind conditions as favorable (e.g., from behavior of nearby conspecifics), and fly directly to a point on that ridgeline to use the orographic lift there. In addition, autumn migrants neither follow ridgelines nor move east or west indefinitely; instead, they often leave ridgelines to advance migration, especially when topography leads away from the migration goal, even though uplift may be strong (Bildstein, 2006). Therefore, any time an eagle moved more than five grid-cells consecutively in the east or west direction, movement probabilities for the E and W grid-cells were cut in half in order to ensure that migration proceeded southward. For example, when an eagle traveled more than five eastbound moves, then both east and west grid-cell probabilities decreased, while the other probabilities (i.e., SW, S, or SE) increased, causing the chance of southbound migration to increase.

2.2.3. Process overview and scheduling

Each flight route is simulated one at a time in the migration model. The elevation state for grid-cells is fixed, based on the NED, while input weather data, used to derive uplift, is dynamic with respect to weather hour. That is, after each 100 km of modeled flight, the input weather dataset changes to a new set that has the same weather day and the next consecutive weather hour. Thus, the initially selected weather date stays fixed over an eagle's migration period, whereas the weather hour changes deterministically. Changes in weather (i.e., uplift) operate in this way for each eagle; therefore, weather is modeled as a discrete process with respect to time. After a flight route completes, the route is saved and stored in computer memory until all other flight routes are completed.

2.3. Design concepts

2.3.1. Basic principles

We modeled individual eagle movements as a response to the amount of uplift available in the environment (Van Loon et al., 2011). At every step in the model, each grid-cell has a value of orographic uplift and thermal uplift whose sum is the total uplift available to a migrating eagle. In the model, total uplift at any one time does not solely determine to the overall migration density of flight routes because total uplift: (a) is dynamic regionwide; (b) is evaluated by the eagle only in the context of their immediate neighborhood (i.e., the five grid-cells in the W, E, SW, S, and SE directions); and (c) changes with each 100 km of modeled flight based on changing weather. This approach is, we believe, broadly representative of the environment that eagles face and the decision making required of them. We chose to simulate movements based on total uplift because high magnitudes of orographic and thermal uplift typically do not co-occur. This is because high winds that favor orographic lift tend to disintegrate thermals (Stull, 1988).

We established the following rules of motion for the migration model:

1. Eagle movements are based on deterministic patterns (direction of migration) and stochastic variation due to topography and weather (i.e., uplift). Simulated eagles ignore conspecifics, terrestrial habitat cover, and individual experience.
2. Eagles accurately perceive strength of uplift in cells that they have not yet visited.

3. Eagles use slope-soaring and thermal-soaring and gliding whenever possible while on migration and engage in flapping flight only when uplift is not available.
4. Eagles migrate across the study area within a 24-h time period.
5. Eagles do not stop to forage or roost (i.e., flights are continuous and uninterrupted).
6. Weather conditions (e.g., wind speed, wind direction, thermal activity) shift after each 100 km of modeled flight.
7. Within November, eagles always migrate regardless of the weather conditions.

2.3.1.1. Estimating orographic uplift. Local topography deflects horizontal surface winds to generate orographic uplift that eagles use to subsidize flight. We estimated orographic uplift (w_o) based on the following relationship of terrain slope and aspect (from the NED) to wind speed and direction (Bohrer et al., 2012; Brandes and Ombalski, 2004):

$$w_o = \nu C_\alpha, \tag{1}$$

$$C_\alpha = \mathrm{Sin}(\theta)\mathrm{Cos}(\alpha - \beta), \tag{2}$$

where ν is the horizontal wind speed at ground-level (m/s), C_α is an updraft coefficient with a constant angle of terrain slope, θ (degrees, level = 0) per grid-cell, and terrain aspect, β (degrees, North = 0), and horizontal wind direction at ground-level, α (degrees, North = 0). We did not consider orographic uplift on the leeward side of the terrain, and all negative values of w_0 were set to 0 (Bohrer et al., 2012; Brandes and Ombalski, 2004). We calculated terrain slope and aspect as follows (Zevenbergen and Thorne, 1987):

$$\theta = \arctan\left[(dz/dx)^2 + (dz/dy)^2\right]^{1/2}, \tag{3}$$

$$\beta = \arctan[(dz/dx)/(dz/dy)], \tag{4}$$

where dz/dx and dz/dy are the eastward (x) and northward characteristics (y) of the local terrain, respectively.

For every 90 m^2 grid-cell of the NED within the study area, we estimated a value of w_0 based on the input NARR wind conditions. The NARR dataset provides wind data at several atmospheric pressure levels as well as wind data at specific heights above ground level. Therefore, we used the U-wind and V-wind data, measured at 30 m above the ground surface to identify wind speed and wind direction. We calculated all wind speeds and wind directions from the U- and V-wind data as follows:

$$\nu = \sqrt{U_i^2 + V_i^2}, \tag{5}$$

$$\alpha = 57.29578 \times \arctan 2(U_i + V_i) + 180, \tag{6}$$

where ν and α represent the wind speed and wind direction, respectively, U_i and V_i are the U- and V-wind components in radians at grid-cell i, and 57.29578 is a conversion factor from radians to degrees.

2.3.1.2. Estimating thermal uplift. Downward solar radiation during the daytime heats the ground surface, which can produce strong heat flux for thermals that eagles use to subsidize flight (Bohrer et al., 2012). Values of thermal uplift velocity can be estimated by the convective velocity parameter, $w^\bullet$ (Spaar et al., 2000; Stull, 1988):

$$w^\bullet = [gz(H/T)]^{1/3}, \tag{7}$$

where g is the acceleration due to gravity (m/s^2), z is the flight altitude (m), H is the surface sensible heat flux (W/m^2), T is the potential air temperature (K), and $w^\bullet$ represents the mean uplift velocity (m/s) at any height within the boundary layer. We set all negative values of $w^\bullet$ to 0.

For each 90 m^2 pixel of the NED, a value of $w^\bullet$ was estimated using the height of the planetary boundary layer (HPBL, corresponding to z in Section 2.1), sensible heat flux (SHF, H), and potential air temperature (POTT, T) from the NARR data.

2.3.2. Emergence

Migratory flight routes, and the overall spatial density thereof, are modeled as emergent behaviors of individual eagles in the model. This output is expected to vary with respect to changes in environmental uplift. For example, when orographic uplift is greater than thermal uplift, then eagle flight routes should be more tightly clustered, around mountain ridgelines. When thermal uplift is greater than orographic uplift, then eagle flights should be more spread out, away from the ridgelines and in the valleys.

2.3.3. Stochasticity

Stochasticity is used in the migration model in three distinct ways. First, the initial selection of a starting location by an individual eagle is a random process. Variability in starting position on the northern boundary of the study area is known from existing telemetry data (n = 21 tracked eagles; Miller, 2012) and roughly follows a Gaussian distribution. Entrance into the study area on the northeastern side of Pennsylvania is poorly understood. Because we lacked prior knowledge on the distribution of this process, we modeled it as a uniform random process, as that seemed most biologically plausible given what we do know about the situation. Second, stochasticity is used to model eagle movement steps via the procedure that weights movement probabilities by each grid-cell's localized uplift. Variability in eagle movement decisions with respect to local uplift on the landscape-level is largely unknown, and thus we chose to model the total migratory process as a directed random walk. Finally, selection of initial weather hour and weather date was also a random process.

2.3.4. Observation

Observations from the migration model include complete flight routes (i.e., total simulations) with eagle moves that are spatially referenced for mapping, and these data are stored in individually identified comma separated value files. In addition to basic reference information, output files include the magnitude of uplift, by total uplift and uplift form, in each grid-cell moved to by the eagles. File path names for weather data files are also stored in output files by date and hour. We only analyzed those simulations that contained greater than three moves in total. Whenever simulated eagles started too close to an edge of the study area, they often stopped their migration after only a few moves (i.e., once they reached the edge boundary). We decided to exclude these short flight routes from our spatial analyses and instead focus on paths with greater numbers of movements.

2.4. Details

2.4.1. Initialization

Model initialization always followed the same process for each flight route simulated. Eagles first begin outside of the boundary of the study area. Upon entrance into the study area, selection of a starting position is made along with the weather date and hour. Once the weather time period is selected, the associated data are used to build an uplift field. After model initialization, the majority of flight routes begin along the northern Pennsylvania border. We also simulated a proportion of flight routes on the northeastern boundary of the study area to gain insight into movements along the Kittatinny Ridge System, an important migration corridor in autumn (Fig. 1b). The proportion of simulated birds starting on the northeastern boundary matched the proportion of real birds

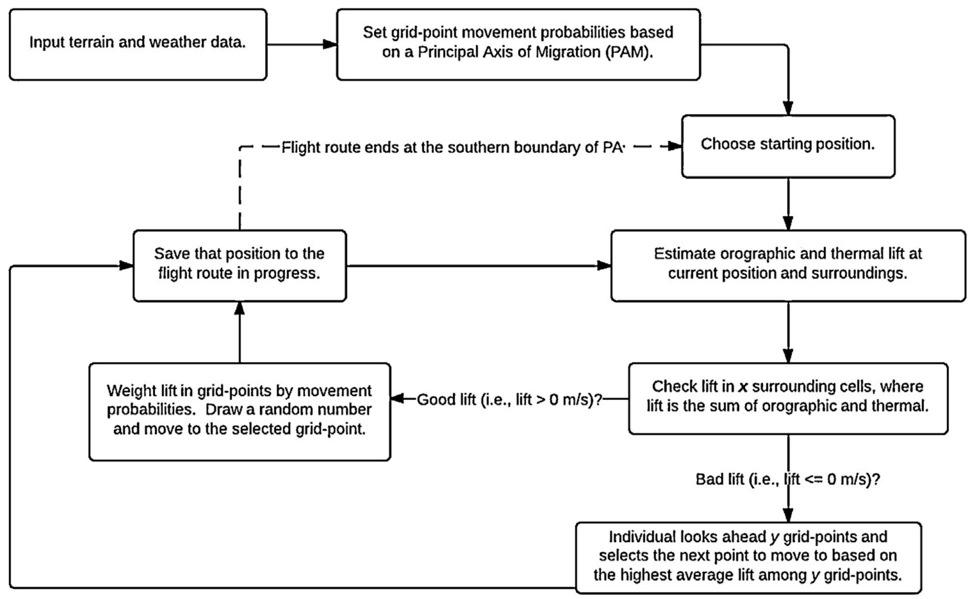

Fig. 2. Conceptual model describing the general steps involved in modeling migration routes across the study area. Eagle movement steps occur in consecutive, 90 m steps corresponding to the spatial resolution of the NED (1 arc second). When uplift is good (>0 m/s) then the eagle chooses among 5 (x) grid-cells, and moves 1 grid-cell at a time (a). When uplift is bad (0 m/s) then the eagle chooses among 36 (y) grid-cells, and moves to 1 grid-cell in a group of points containing the highest average lift, compared among 4 different groups of grid-cells (b). Lift is averaged over 9 grid-cells per group to compare average lift among the 4 groups. When an eagle reaches the southern boundary of the study area, its flight route completes and a new flight route initiates (see Fig. 4). The process repeats until a predetermined number of flight routes are built.

counted on the Kittatinny to the total counted within Pennsylvania (Hawk Migration Association of North America, 2014).

After choosing a starting point, the simulated eagle evaluates total uplift in the five surrounding grid-cells and selects a destination grid-cell based on a random number draw. The random number drawn is used to select among grid-cells with probabilities weighted by total uplift per grid-cell. This adjusted number represents the probability of movement to the respective grid-cell. Finally, the model process, operating as a directed random walk, is repeated until the simulated eagle reaches a border of the modeling region (south, east, or west; Fig. 2).

2.4.2. *Input*

To begin simulation of a desired number of flight routes, the model requires the following inputs: the total number flight routes to simulate, mean and standard deviation of starting locations (i.e., from telemetry) along the northern boundary of the study area, fixed movement probabilities in the W, E, SW, S, and SE grid-cells around any one eagle location, the NED representing the entire study area, and all weather files required to estimate both orographic and thermal uplift. The NED and weather data files are stored in the file working directory for access by the computer program, while the remaining inputs are set manually.

2.5. *Sensitivity analysis*

We analyzed simulated responses to changes in the three main inputs to the model: choice of starting position along the northern boundary, magnitude of orographic uplift, and magnitude of thermal uplift. In each set of simulations, we allowed only one of these three inputs to vary while the other two were kept constant at their mean value. We evaluated the difference in mean ending position of each route between the sets as an index of sensitivity to values per input variable using Welch's two-sample t-tests with unequal variances (Appendix A). We also evaluated spatial patterns in the simulated flight routes to assess the degree to which they were clustered. To do this, we used the Spatial Autocorrelation Tool (Moran's I test) in the Spatial Statistics package within ArcGIS 10 (ESRI Inc., Redlands, CA).

We simulated 100 flight routes for each value of each variable we considered. For example, we simulated 100 routes using the mean starting position and the mean thermal uplift and with orographic uplift set to 0.0 m/s. Then we simulated another 100 routes with the same mean starting position and thermal uplift, but with orographic uplift set to 1.0 m/s. We repeated this process, incrementally increasing values of orographic uplift by units of one, up to the maximum uplift value we observed (9.0 m/s). Thus, for 10 different starting positions (evenly spaced along the northern border of our region), 10 values of orographic uplift (0.0–9.0 m/s), and eight values of thermal uplift (0.0–7.0 m/s), we generated 2800 flight routes in total.

2.6. *Spatial analysis*

We mapped movement paths in ArcGIS 10 (ESRI Inc., Redlands, CA). We computed the density of flight routes per unit area to characterize migration hot- and cold-spots. To assess whether either uplift form was more available to eagles, we compared the strength and frequency of the modeled distributions of orographic and thermal uplift available to eagles. We were also interested in whether or not the magnitude of each uplift form was correlated. To evaluate this, we conducted a Pearson's correlation on each uplift form with the total number of simulated movements. To evaluate model performance, we compared the density of routes from actual autumn flights (2006–2012) of golden eagles ($n = 21$) collected via telemetry (Miller, 2012), to the density field of our simulated flights. To determine how simulated eagles interacted with the distribution of topographical land forms, we examined the proportion of modeled flight routes that intersected with regional physiographic provinces (United States Forest Service, 2007) and the Kittatinny Ridge System (Hawk Migration Association of North America, 2014). We conducted all statistical analyses using R Statistical Software 2.15.2 (Core Development R Team, 2013).

The probability of a golden eagle migrating increases with weather conditions that produce uplift (Duerr et al., 2014).

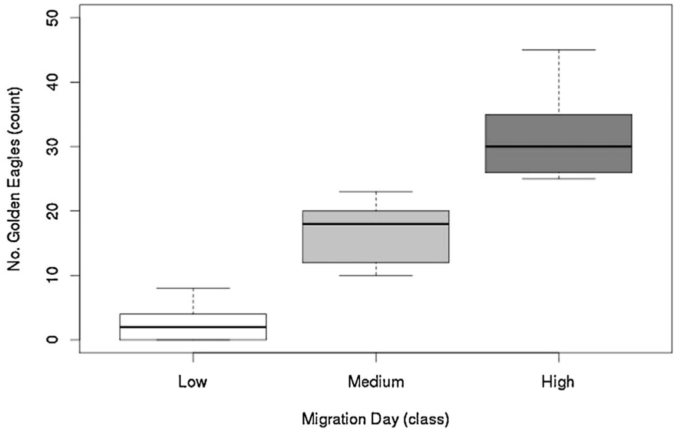

Fig. 3. Variation in counts of golden eagles based on classes of migration days. We classified our NARR weather datasets ($n = 33$ days) by natural breaks in hawk-count data collected on each type of day in the study area. We used November data from the following hawk-counts: Allegheny Front, Stone Mountain, Waggoner's Gap, Second Mountain, and Hawk Mountain Sanctuary (Hawk Migration Association of North America, 2014). We used the three classes as a proxy for the quality of weather conditions on a given day.

Although weather patterns shift as the autumn season progresses in the Appalachians (Maransky et al., 1997), we modeled eagle movements using days only in the month of November, which helps us avoid any potential confounding effects of migration phenology with migration intensity. To analyze how weather influences our simulations, we used real data from Pennsylvania hawk-count sites on each of our NARR weather days ($n = 33$) to define classes of eagle migration days (Fig. 3). We defined three classes of days (i.e., high-, medium-, and low-migration) by natural breaks in the data. A high-migration day occurred when ≥24 golden eagles were counted at sites in Pennsylvania. On a medium-migration day, between 9 and 23 golden eagles were counted. During a low-migration day, between zero and eight eagles were counted. We then assigned modeled flight routes to a migration day type based on the weather day in which the simulation occurred. We then compared distribution of flight routes among categories of migration days and we extracted the hot-spots (i.e., locations of greatest density) to estimate the land area covered by highest flight densities on each category of migration day. This allowed us to evaluate whether golden eagles migrate on a broad- or narrow-front during such types of days (Murray, 1964).

2.7. Model validation

We used output from the density of simulated flight routes to find potential gaps in the distribution of existing hawk-count sites (Hawk Migration Association of North America, 2014) and to identify sites for field work to validate models. Our process for picking validation sites was as follows. First, we extracted migration hot-spots from the flight routes' density field and from these hot-spots, picked potential sites for model verification. Second, we restricted verification sites by choosing only those nearest to statistically significant clusters (>95% confidence) of high values of flight route density using the Hot Spot Analysis Tool (Getis-Ord *Gi** test) in the Spatial Statistics package (ESRI Inc., Redlands, CA). This tests whether the spatial clustering of high values is more apparent than one would expect in a random distribution. Third, we defined the number of potential sites to survey by only including those with open land-cover (Fry et al., 2011) and elevated topography (e.g., preferably on long-linear ridgelines) to aid our ability to sight migrants. Next, we limited sites to visit based on their proximity to public roads (i.e., <1 km) using the Digital Base Map of Pennsylvania County Road dataset (Pennsylvania Department of Conservation and Natural Resources, 2007). After that, we excluded all sites <5 km from an active hawk-count site. Finally, we randomly sampled from this collection of potential sites to collect data on migrant golden eagles. We also mapped our survey data alongside data collected at nearby hawk-count sites on the same days in order to compare recordings of migrant golden eagles. This served as another verification of model performance.

Lastly, we compared output from our simulation model to that of an existing raptor migration model, *FlightPath v. 1.1* (Brandes, 2009). *FlightPath* uses only modeled estimates of orographic uplift to simulate eagle migration. Our model uses empirically derived estimates of both orographic and thermal uplift in simulations. The two models are similar in that they both model migration at 90 m^2 grid-cell resolution, use terrain-based orographic uplift estimation, involve a southwesterly PAM, apply a look ahead function in areas of low lift, and select from ranges of potential starting positions. The models are different because *FlightPath* models movement over a smaller area, includes an option for declaring eagle random movements (e.g., in scale and frequency), and uses a minimum uplift threshold to limit eagle movements to areas only where uplift is great enough to keep a soaring eagle aloft.

We simulated an identical number of flight routes with each model under the same weather conditions and with similar starting constraints. In each model, simulations started in the northeastern corner of their respective modeling region. We then mapped the output from each model, and compared spatial differences in the simulated flight routes from each model to understand influences of regional topography and similar weather conditions on their simulations. Finally, to evaluate how well each model simulated flight routes near hawk-count sites, we compared the number of simulations per model that passed through 3 km buffer zones (i.e., mean distance for observers to see and identify migrating raptors; Ainslie et al., 2014; Farmer et al., 2010) around hawk-count sites in Pennsylvania.

3. Results

3.1. Model output

Our migration model produced 25,481,796 individual moves, comprising a total of 6378 simulated flight routes, which required ~588 h of computer time. Of this total, 5000 routes started along the northernmost boundary of the model system, while 1378 started along the northeastern boundary (~27% of the preliminary set). Some simulations comprised fewer than three moves because they started too close to an edge of the model system, and we excluded these routes ($n = 284$) from spatial analyses. Therefore, our final sample of simulations contained 6094 complete flight routes. Mean (±SD) number of moves per flight route was 2191 (±1281; range: 3–5373 grid-cells).

3.2. Sensitivity analysis

Our sensitivity analysis showed that the start and end points of simulated flight routes were largely influenced by starting position and PAM, rather than the magnitude of uplift or its form. When assessing the sensitivity of flight routes based on uplift forms, the spatial patterns in density of flight routes overall remained the same (Appendix A). Not surprisingly, given the limits to variation imposed in the sensitivity analysis, less variation was present in the general spatial pattern of these flight routes compared to that of our original set of simulations. Flight routes were also random in their distribution for each set of sensitivity analysis simulations (Appendix A).

Table 1
Summary statistics of estimated uplift forms compared with the total number of simulated movements (n = 25,481,796) for golden eagles in Pennsylvania, USA during November 2002–2011. Zero values of each uplift form represent those 0 m/s and non-zero values represent those >0 m/s.

Statistic	Orographic uplift (m/s)	Thermal uplift (m/s)
Raw count of zero values	6,817,057	16,988,977
Raw count of non-zero values	18,664,739	8,492,819
Correlation between uplift forms (Pearson's r)	−0.145	–
Minimum	0.00	0.00
Maximum	9.06	7.17
Median	0.35	0.00
Mean (±SD)	0.70 (±0.91)	0.89 (±1.45)
Skewness	1.96	1.41
Kurtosis	7.50	3.79

3.3. Spatial analysis: influences of topography and weather

The geographic distribution of modeled eagle flight routes was non-uniform. The majority of eagle flights were concentrated in the Ridge and Valley physiographic province of the central Appalachians (Fig. 4a). Distributions of orographic and thermal lift were non-normal and right-skewed. Orographic uplift was stronger and occurred more frequently than thermal uplift, and uplift forms were not correlated with one another (Pearson's r = −0.145; Table 1).

Proportions of flight routes intersecting different physiographic provinces were also non-uniformly distributed across the study area (Table 2). The greatest proportion of flight routes intersected the Allegheny Plateaus with lower proportions crossing the Allegheny Mountain, Blue Ridge Mountain, and Northern Piedmont regions. The majority of routes crossed the Ridge and Valley province, which contains most of the hawk-count sites in Pennsylvania (Hawk Migration Association of North America, 2014). More than 25% of routes passed within 3 km (i.e., mean distance for observers to see and identify migrants; Farmer et al., 2010) of the Kittatinny ridgeline, near sites like Hawk Mountain Sanctuary (Table 2; Hawk Migration Association of North America, 2014).

On high-migration days (those weather days in which real hawk-counters observed many golden eagles), simulations were most clustered over the central portion of the study area (Fig. 4b). On medium-migration days (Fig. 4c), the highest density of simulations was less clustered than that of high-migration days. On low-migration days (Fig. 4d), the highest density of simulated routes was less concentrated than on both high- and medium-migration days. Regardless of the migration day class (high-, medium-, or low-), the majority of routes passed through the Ridge and Valley province. The amount of area for hot-spots was least on high-migration days (5203.18 km^2; 84% of maximum), most on low-migration days (6152.87 km^2; 100% of maximum), and in between the other two on medium-migration days (5386.98 km^2; 87% of maximum). In each subset of simulations, three major areas consistently expressed the highest density of routes. These groups of mountains (listed with Pennsylvania counties) are: (1) Bald Eagle (Centre, Clinton, and Lycoming), Tussey (Huntingdon, and Blair; Fig. 5b), and Allegheny (Bedford); (2) Brush, Canoe, and Evitts (Blair and Bedford); and (3) Endless, Jacks, Stone, and Tuscarora (Susquehanna, Union, Mifflin, Huntingdon, and Fulton).

Table 2
Proportions of total simulated flight routes (n = 6094) intersecting physiographic provinces and the Kittatinny Ridge System in Pennsylvania, USA.

Physiographic province	Number of flight routes	Proportion of total
Allegheny Plateaus	6071	0.99
Allegheny Mountains	2017	0.33
Blue Ridge Mountains	618	0.10
Northern Piedmont	1150	0.19
Ridge and Valley	4310	0.71
Migration corridor		
Kittatinny Ridge System	1638	0.27

3.4. Model validation

We identified 129 potential hawk-count sites and randomly chose 11 sites for model validation. We counted migrating raptors at these sites for 121 observer hours over 13 days (Appendix B), during the peak migration period for golden eagles in 2013 (15 October–04 December; Appendix C). Sites had a mean elevation of 630 m, and the majority (n = 9) had an easterly aspect. Overall, we recorded 56 migrating golden eagles at six of the sites. These migrants comprised 72% of the total number of eagles counted (n = 78; 56 golden eagles + 19 bald eagles (*Haliaeetus leucocephalus*) + 3 unidentified eagles). In addition to observing eagles, we recorded other raptors (n = 330; e.g., *Cathartes aura*, *Coragyps atratus*, and *Falco* spp., *Buteo* spp., and *Accipiter* spp.) at nine test sites. We did not observe any migrating raptors of any species at the other two sites.

3.5. Model comparisons

We simulated 90 flight routes with both our model and *FlightPath*, using similar starting constraints and weather conditions (Appendix D). The majority of simulations from *FlightPath* passed through the Ridge and Valley province. However, very few *FlightPath* simulations crossed the Kittatinny Ridge System. In contrast, more routes from our migration model passed sites along that corridor. Many of our routes were closer to other sites outside of *FlightPath*'s modeling area (e.g., Hawk Mountain Sanctuary). In general, *FlightPath* simulations more closely followed ridgelines in the Ridge and Valley province than did simulations our model produced. Our simulations do follow some major ridgelines (e.g., Jacks and Stone Mountain), but they also follow more minor ridgelines (e.g., areas north of Second Mountain and Hawk Mountain Sanctuary) than do routes from *FlightPath*. Finally, both model sets had exactly the same number of simulations (n = 44) pass within 3 km of hawk-count sites in Pennsylvania. In *FlightPath*, those 44 simulations passed near seven hawk-count sites, while the 44 simulations from our migration model passed near nine hawk-count sites. Five of those sites were shared between the models.

4. Discussion

This modeling exercise provides insight into how an apex predator of high conservation priority migrates and how this species responds to variation in topography and weather during migration. Furthermore, our model also highlights both the utility of movement models in providing such insights and also how these models can incorporate citizen-science data for conservation.

4.1. Spatial analysis: influences of topography

Modeled simulations also reflect movement patterns observed via telemetry (see Duerr et al., 2012; Katzner et al., 2012b; Lanzone et al., 2012; Miller et al., 2014), as many simulations concentrate along prominent Appalachian ridgelines and existing hawk-count sites (Fig. 5a). Furthermore, the direction of topography in the Appalachians is important to general patterns in eagle migration. Flight routes from the telemetry data and our simulations confirm that eagles tend to frequent the long-linear topography of the central Appalachians during autumn migration. Our modeling also highlights the importance of the Ridge and Valley province to golden eagle migration. In fact, an overwhelming majority of

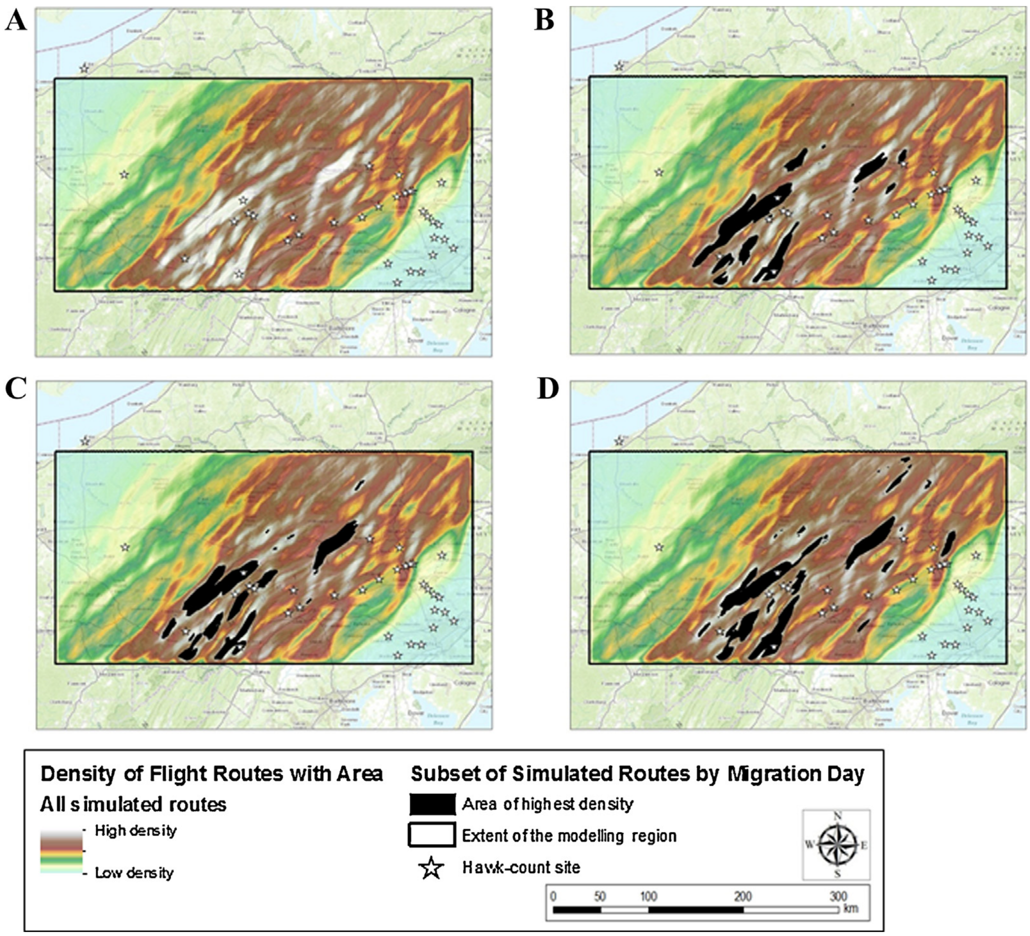

Fig. 4. (a) Density of simulated golden eagle flight routes (n = 6094) in Pennsylvania, USA during November 2002–2011. This overall density of flight routes is paired with subsets of simulations classified by high-, medium-, and low-migration count days. We used these types of migration days as a proxy for different weather conditions. (b) Regional comparison with flight routes (n = 1755) modeled on high-migration days. (c) Regional comparison with flight routes (n = 1329) modeled on medium-migration days. (d) Regional comparison with flight routes (n = 3010) modeled on low-migration days. Overall, we classified "area of highest density" (i.e. hot-spots) as the top category, based on three classes of natural breaks, in the complete density of flight routes per migration day. The size of hot-spot area varied by migration day class with 5203.18 km^2, 5386.98 km^2, 6152.87 km^2 for high-, medium-, and low-migration days, respectively.

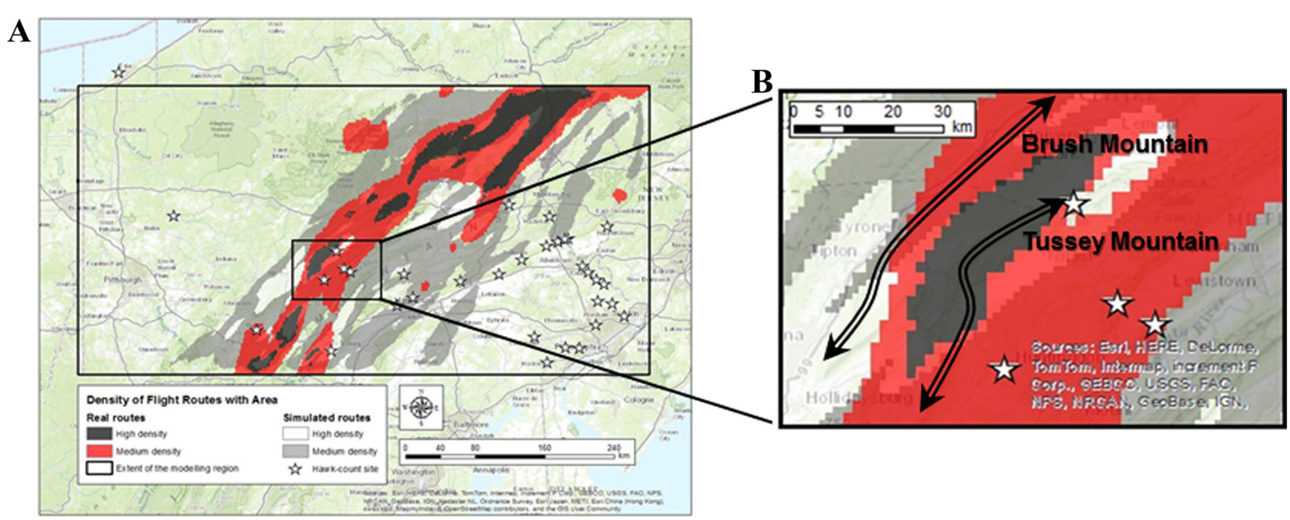

Fig. 5. (a) Regional comparison of density fields between modeled movement (n = 25,481,796 data points from 6094 simulated flight routes) and movement observations during autumn 2006–2012 (n = 16,348 data points for 21 telemetered eagles; Miller, 2012). (b) General locations of two nearby mountains, Brush and Tussey (i.e., represented by individual arrows), which both concentrate large densities of real migrants (i.e., telemetry data) and simulated migrants in autumn. It is important to note that the Tussey Mountain hawk-count (i.e., white star on north side of its arrow) does not operate during the autumn migration season. For each collection of route density, we classified "high" and "medium" areas as the top two categories of each route type (i.e. real or simulated) based on three classes of natural breaks in the data. We also excluded the third category of each density dataset (i.e. "low"); therefore, we do not present those here.

our simulated eagle migrations (71%) intersected this province. The Ridge and Valley is not only a hot-spot for eagle migration, but it is also a focal point for wind energy development (American Wind Energy Association, 2013; Miller et al., 2014). Areas for wind energy development are typically near major ridgelines that eagles use to migrate regionally and travel locally (Brandes et al., 2009; Katzner et al., 2012b).

4.2. Spatial analysis: influences of weather

Our analysis of weather data corroborates previous findings that conditions in autumn are conducive to producing more orographic than thermal uplift (Duerr et al., 2014). Nevertheless, both forms of uplift were available to simulated eagles. Although eagle flights should be more direct when birds are using thermal lift (Duerr et al., 2012), our modeled migration pathways were of similar length regardless of weather. This suggests that either our model does not accurately reflect eagle movement or that one form of uplift predominates in the environment. Because we know the latter is true (i.e., orographic uplift predominates), this gives credence to the biological relevance of the rest of the processes we modeled.

The surface area of hot-spots for medium- and low-migration days informs about the different roles and frequency of use of orographic and thermal uplift by eagles. Differences between the three categories of eagle use likely are explained by variation in the real conditions observed on those weather days. For example, on a low-migration day, the weather might be least-favorable for generating orographic uplift (e.g., weak, directed winds; Bohrer et al., 2012; Brandes and Ombalski, 2004). At the same time, on those days use of thermal lift may produce a broad-front in eagle migration where individuals are spread across a larger area (Murray, 1964).

If eagles are using thermal lift, they are typically farther away from hawk-count sites on ridgelines, out of sight of observers (Ainslie et al., 2014; Farmer et al., 2010). On a medium-migration day, weather conditions might be moderately favorable for generating orographic uplift (e.g., moderate, directed winds inhibiting weaker thermals), causing some eagles to use the ridgelines in sight of hawk-count observers, while more eagles could still be using weaker thermals. On a high-migration day, weather conditions might be most-favorable for orographic uplift (e.g., strong, directed winds dissipating thermals; Stull, 1988).

Our evaluation of hot-spot area on high-migration days suggests that golden eagle migration in autumn may be in a narrow-front, rather than in a broad-front. This narrow-front migration could be attributable to the relatively greater availability of orographic uplift and the limited nature of thermal updrafts on such days. On each type of migration day, thermal updrafts cover a larger amount area throughout the lowland valleys (broad-front), while orographic uplift is constrained at the mountain ridgelines (narrow-front). New research should investigate these migration front patterns alongside environmental uplift. Greater understanding of weather conditions and consequential migration patterns could be used to curb wind energy production at concentration points (e.g., high-elevation locations) in uplift-conducive areas and time periods when migrating eagles are at greater risk of collision with active turbines.

4.3. Verifying model output

Satellite telemetry and modeled flight both suggest that there are several corridors eagles use when entering Pennsylvania. Golden eagles follow these pathways into the Ridge and Valley province to the east and northeast of State College, Tyrone, and Altoona, Pennsylvania. This eastern portion of the Ridge and Valley lacks hawk-count sites, making it a good place for local conservation groups to establish new monitoring sites.

We observed migrating golden eagles at 55% of sites we visited. Several of these days we observed more golden eagles than any other raptor species. Data collected at nearby hawk-counts also reflected those patterns (Appendix C). As a result, we suspect that there is connectivity between our ridgeline sites and some of the other (established) sites elsewhere in Pennsylvania (Teter et al., 2003). The effectiveness of our model at accurately predicting sites closely associated with existing hawk-counts suggests that the model is correctly predicting eagle behavior. This pattern also gives us more confidence in the assessment of proposed sites not associated with an existing hawk-count site and in the overall utility of our model for assessing autumn migration of golden eagles in Pennsylvania.

4.4. Model comparisons

FlightPath simulates eagle flights with a minimum uplift threshold that limits movements in areas of too little uplift. Our model does not take into account such a threshold, and the magnitude of uplift available in the environment may limit movements of large soaring migrants like golden eagles. A small golden eagle weighs about 2.5 kg, has a 1.8 m wingspan, 0.52 m wing chord, and 0.936 m^2 wing area (these are minimum measures for North American golden eagles; Watson, 2010). When an eagle of this size migrates at mean ground elevation (368.01 m; NED) in Pennsylvania, the estimated minimum sink speed is 0.90 m/s (minimum sink speed is roughly equal to the amount of uplift required to keep a bird in level flight, and it is calculated with the Glide Polar function in Program FLIGHT 1.24; Pennycuick, 2008).

Our mean simulated estimates for each uplift form (0.70 m/s (orographic) and 0.89 m/s (thermal) were close to the minimum sink speed of 0.90 m/s). Because mean values were close to this minimum on many days in which we simulated migration, uplift was likely less than the minimum larger eagles require. This may, in fact, inhibit the accuracy of the migration model in predicting eagle movements. For example, omission of a minimum uplift threshold (or sink speed) from our models could explain why some simulated eagles migrated west of Laurel Ridge in the Allegheny Mountains. These areas likely have low updrafts and migration there may not accurately represent eagle movements in that portion of Pennsylvania.

4.5. Sensitivity analysis and limitations of the migration model

Our sensitivity analysis demonstrates that when inputs are constrained, simulated eagle flights are less clustered in space and largely driven by PAM and the choice of starting position in Pennsylvania (Appendix A). Evaluation of simulations outside of our sensitivity analysis indicates that the inclusion of dynamic weather conditions, randomized starting positions, and more complex behavior rules allows simulated eagle flights to more closely mimic reality than do those produced in the sensitivity analysis. This suggests that our migration model is useful for assessing variation in spatial patterns of golden eagle migration.

Our migration model is limited in that it does not include some eagle behaviors known to occur in the wild. First, our model does not allow for stopover or roosting episodes. Second, we modeled golden eagle flights in a continuous, day-long manner (i.e., with respect to NARR weather day in November; Mesinger et al., 2006); true movements may occur over several days. Third, our model did not incorporate movements related to feeding forays. These simplifications are useful for visualizing and interpreting movement, but they may constrain our ability to understand certain details of migration. For example, it is well known that many migrants are energy-limited (Hedenström, 1993). Energy-limited migrants may stop frequently to forage, especially when weather is not suitable for migration. Likewise, the "look ahead" function in our model simulates an aspect of eagle behavior (i.e., flapping flight when on migration) that is poorly understood. As a consequence, our model could misrepresent this behavior. Future models would benefit from more effective parameterization of this potentially critical input variable.

The small proportion of simulations (~27%) that intersect the Kittatinny Ridge System may be lower than the real proportion of eagles that migrate down this ridge. We expected more routes to pass through this area because it is a well-known migration corridor along which many golden eagles migrate every autumn (Broun, 1935; Teter et al., 2003; Hawk Migration Association of North America, 2014). However, hawk-count data suggest that this area is relatively better for migratory hawks (e.g., *Buteo* spp.) than for golden eagles. To this point, many golden eagles using the Kittatinny arrive early and are generally young in age. For instance, at Hawk Mountain Sanctuary in Novembers 2002–2011, 54% of golden eagles counted were pre-adults along with 37% adults and 9% unaged (Hawk Migration Association of North America, 2014). Furthermore, adult golden eagles migrate later in the autumn, while younger eagles migrate earlier in the season (Duerr et al., 2014). Together, these data lead us to believe that our migration model might better represent movements by adult golden eagles.

Our migration model also forced birds to migrate regardless of weather conditions. Therefore, the migration behavior we modeled may represent the best a simulated eagle can do, rather than the behavior that a real eagle may prefer (e.g., waiting out bad weather conditions). As a result, forcing migration despite the quality of weather conditions likely drives individuals exclusively in the direction of PAM, which does not always agree with the changing direction of some Appalachian ridgelines. Despite these issues, the telemetry data provide support for modeling eagle migration in a directed random walk fashion as most flights are directed south-southwest. An improved model might incorporate weather only from days on which a certain minimum number of actual eagles migrated historically.

4.6. New opportunities for simulating migration with implications for continued monitoring

Golden eagles are a good model species for understanding raptor movement because their flight behaviors are similar to that of other species (i.e., *Accipiter* and *Buteo* spp.) that also migrate through and are counted in the thousands in the central Appalachians. We also identified several, key migration corridors for potential new hawk-count sites in Pennsylvania. Many of the sites we describe are close to public roads, and thus of high potential for citizen-science data collection. Ease-of-access is important for attracting volunteers and the public to participate in ongoing research—creating opportunities for increased conservation education (Bildstein, 1998).

Future migration modeling efforts should incorporate foraging and roosting (i.e., stopover) behaviors into modeling eagle movements. Inclusion of these parameters could help us to understand the relative influence of such behaviors on migration trajectories. In addition, it would be especially important to know the role of minimum uplift thresholds (or sink speeds) in migrating raptors and their paths. An in-depth evaluation of the nature and degree of connectivity between hawk-count sites would also be useful. Furthermore, other studies could focus on migratory directionality, and the process that governs it, to give greater insights into the use of directed random walks in movement models. With this new information, more comprehensive research projects might focus on making stronger inference to demographic parameters.

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Appendix A–D. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ecolmodel.2015.02.010.

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