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MODELING RAPTOR MIGRATION PATHWAYS USING A FLUID-FLOW ANALOGY

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ABSTRACT.—We describe an approach to mathematical modeling of raptor migration under conditions in which terrain updrafts are the primary source of lift. The model is based on the analogy of laminar fluid flow to raptor migration, with the assumption that migration flux at a particular location is proportional to terrain conductivity and the local energy gradient driving migration. The terrain conductivity parameter is taken to be the relative updraft strength, which is calculated using wind direction, terrain slope, and terrain aspect data determined from a digital-elevation model of the area of interest. By imposing a directional energy gradient (a preferred axis of migration [PAM]) across the resulting conductivity field, flow (i.e., migration) is generated, and the predominant migration paths through the region are determined. We apply the model by simulating the spring migration of Golden Eagles (*Aquila chrysaetos*) through central Pennsylvania under eight different wind scenarios. The locations of the simulated migration tracks depended on wind direction, PAM direction, and the spatial arrangement and orientation of terrain features. Migration tracks showed a marked tendency to converge toward a small number of preferred pathways as the migration proceeds. The overall pattern of simulated migration was consistent with available count data. Model results showed that south/southeast and north/northwest winds provided the best conditions for rapid migration across the region, as was suggested by field data.

KEY WORDS: *Golden Eagle;* Aquila chrysaetos; *migration; pathways; modeling; updrafts; terrain.*

MODELACIÓN DE LAS RUTAS DE MIGRACIÓN MEDIANTE EL USO DE UN MODELO DE ANALOGÍA DE FLUIDO DE FLUJO

RESUMEN.—Describimos un enfoque para la modelación matemática bajo condiciones en las cuales las corrientes termicas son la fuente primaria para elevarse. El modelo esta basado en la analogía del flujo laminar aplicado a la migración de rapaces asumiendo que el flujo migratorio en una localidad particular es proporcional a la conductividad del terreno y el gradiente de energía local que guía la migración. El parámetro de conductividad del terreno es asumido como la fuerza relativa de las corrientes ascendentes el cual es calculado usando la dirección del viento, la pendiente del terreno, determinados a partir de un modelo de elevación digital del area de interés. Mediante la imposición de un gradiente direccional de energía (un eje seleccionado de migración) a través del campo de conductividad resultante, el flujo (migración) es generado, y las rutas de migración son determinadas a través de la región. Aplicamos el modelo para simular la migración de primavera del águila dorada (*Aquila chrysaetos*) a través del centro del Pennsylvania bajo ocho escenarios de vientos diferentes. Las localidades de simulación de las rutas dependieron de la dirección del viento, del eje de migración y del arreglo espacial y de la orientacion de las características del terreno. Las rutas de migracion

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mostraron una marcada tendencia hacia la cobertura de un pequeño numero de rutas preferidas tal como la migración ocurre. El patrón general de la migración simulada es consistente con los datos de los conteos disponibles. Los resultados del modelo demuestran que los vientos sur/sureste y norte/noreste proveen las mejores condiciones para una rápida migración a través de la región tal como lo sugieren los datos del campo.

[Traducción de César Márquez]

It is widely held among raptor biologists and hawk watchers that some mountain ridges concentrate raptors in greater numbers than others (e.g., Haugh 1974). Why this is true is an interesting question, especially in areas like the northern Appalachians, where there is a network of ridges and many hawk watches where counts have been conducted (Zalles and Bildstein 2000). The factors that concentrate migrant raptors on one ridge, while leaving a nearby ridge of similar morphology with few migrants, have only been discussed in a qualitative sense. Detailed quantitative modeling of topographic and landscape structure effects on raptor-migration pathways at the regional scale has not been conducted.

Here we describe a raptor migration model based on a fluid-flow analogy and digital-elevation data. The overall premise is that raptors migrating over the landscape are analogous to fluid flowing through a variably conductive medium. Fluid flows are driven by directionally-oriented energy gradients, much as raptors are driven by an innate urge to migrate in a particular direction, termed the preferred axis of migration (PAM; Kerlinger 1989). Fluid flows tend to channel along connected pathways of high conductivity (i.e., "the path of least resistance"). Similarly, raptors use pathways along which migration can be obtained at the lowest energy cost, by using thermals, ridge updrafts, and other sources of lift (Kerlinger 1989). Productive inland count sites like Hawk Mountain, PA (Broun 1935) and the Goshute Mountains, NV (Hoffman 1985), are often on long or converging geographic features known as "leading lines" (Mueller and Berger 1967). In our analogy, these can be thought of as thin layers of sand (high conductivity) in an otherwise silty or clayey medium (low conductivity). Because the equations of groundwater flow are well developed, the analogy is useful in creating a quantitative model of raptor migration.

The model is applicable to conditions where updrafts or deflection currents resulting from horizontal surface winds deflecting off sloping terrain are the primary source of lift, rather than thermals or other ephemeral atmospheric phenomena discussed by Haugh (1974). Updrafts are often the primary source of lift during early spring and late fall migration in temperate latitudes, and on overcast days. We apply the model to simulate the early spring Golden Eagle (*Aquila chrysaetos*) migration through central Pennsylvania and determine its primary migration pathways through the region. The paper concludes with a discussion of the utility, limitations, and possible additional applications of the model.

METHODS

Model Equations. Fluid flows are modeled with the continuity equation (mass conservation) and a momentum equation or equation of motion. Continuity also applies to migrating raptors, meaning that the same number of raptors arrives at a location as leaves that location For laminar flow (e.g., groundwater flow), the equation of motion is linear and is known as Darcy's law (Bear 1972):

$$q_s = K\frac{\partial h}{\partial s} \tag{1}$$

where q_s is the flux velocity (dimensions of length [L]/time [T]) in the s-direction (s is a spatial coordinate x, y, or z having dimension L), K is the hydraulic conductivity (dimensions of L/T), a material property which describes the ease of flow, and h is the fluid energy per unit weight (the symbol h is used because energy is expressed as an equivalent height (h) of water with dimension L) Restated in words, the velocity of fluid in a particular direction is directly proportional to the local conductivity (K) and the energy gradient in that direction. Analogous equations describe a variety of physical transport phenomena (e.g., heat, electricity).

The first assumption in our model is that an equation of the same form applies for raptor migration; that is, migration velocity at a particular location is directly proportional to "terrain conductivity" (defined below), and the magnitude of the local energy gradient driving migration. Clearly, raptor migration is complex and quite possibly nonlinear, but it is not unreasonable to assume this form as a first approximation. For example, migration should be rapid where terrain conductivity is high in the desired direction (i.e., the PAM) and the energy gradient (i.e., urge to migrate) is strong. Conversely, migration should be slow where terrain conductivity is low and the energy gradient is weak. Other combinations of conductivity and energy lead to intermediate migration rates.

In groundwater flows (and presumably raptor migration across a diverse landscape), the parameter K is highly variable in space and may range over several orders of magnitude. For simulating flow through such a domain, it is necessary to divide the region of interest into a grid of conductivity values, and approximate the derivative term in equation (1) ($\partial h/\partial s$) by difference at each point. For example, the velocity from point i to point j was written as:

$$q_{i-j} = K_{i-j}\frac{h_i - h_j}{s_i - s_j} \qquad (2)$$

where K_{i-j} is a mean conductivity for flow between points i and j (it is standard practice in groundwater modeling to use the harmonic mean, because the range of variation between gridpoints is typically quite large). Note that if $h_i > h_j$, the flux calculated from (2) will be positive; however, if $h_j > h_i$, the flux calculated from (2) will be negative, meaning that velocity (migration) is in the opposite direction (from j to i). Thus, equation (2) gives the direction of flow as well as its rate.

Now consider a gridpoint (point 0) surrounded by four gridpoints (points 1–4) an equal distance away in the east-west and north-south directions. The continuity equation for point 0 is written as:

$$q_{0-1} + q_{0-2} + q_{0-3} + q_{0-4} = 0 \qquad (3)$$

Substituting equation (2) into equation (3), and solving for the energy at point 0 gives:

$$h_0 = \frac{h_1 K_{0-1} + h_2 K_{0-2} + h_3 K_{0-3} + h_4 K_{0-4}}{K_{0-1} + K_{0-2} + K_{0-3} + K_{0-4}} \qquad (4)$$

When equation (4) is written for all the gridpoints in the model domain, the result is a set of algebraic equations that can be solved simultaneously (a variety of matrix solution methods can be used) for the unknown energy values.

To apply the model, a directional energy gradient is created to drive the flow by assigning different energy values to the model boundaries (for example, a higher value on the southern boundary will cause northward flow). The magnitude of this applied energy gradient relates to the biological drive to migrate, and thus, is difficult to quantify. However, to the extent that relative differences in fluxes or velocities between locations are desired rather than the flux value at each location, the magnitudes of the boundary energy values are essentially arbitrary, so long as these values create flow in the desired direction. Throughout the paper we are interested in such relative differences in migration and do not attempt to predict actual numbers of migrants.

The Conductivity Field. The second assumption in our model is that the conductivity (K), or ease of migration, at a particular location on the landscape is given by the updraft strength, which can be parameterized from the terrain orientation and slope, and direction of surface winds. Empirical support for the correlation between updraft strength and migrant airspeed is given by Kerlinger (1989). He found that lift (wind component perpendicular to the ridge) was the most important predictor of air speed for raptors migrating along the Kittatinny Ridge at Hawk Mountain, PA and Raccoon Ridge, NJ.

Updrafts will be strong where wind is perpendicular to the terrain and the terrain is steeply sloped and weak where the wind is parallel to the terrain, or the terrain is relatively flat. For a particular wind direction, we use the product of two parameters to determine the relative updraft strength (conductivity) at each location: (1) the cosine of the angle between the terrain aspect and the wind direction (ranging from 0 for parallel winds to 1 for perpendicular winds), and (2) the terrain slope. This algorithm determines the relative conductivity of different points of the landscape as a function of wind direction. In general, steeply sloping ridges that are oriented perpendicular to the wind direction will provide connected areas of high conductivity.

The calculations can be performed using a digital-elevation model of the area of interest. A digital-elevation model is a two-dimensional matrix of elevations representing a topographic map. At each gridpoint, the local terrain aspect and slope can be determined by calculating the maximum slope value from the eight principal directions (north, northeast, east, southeast, south, southwest, west, and northwest). Because the cosine of the terrain/wind angle becomes negative where the terrain slopes away from the wind, resulting in negative conductivity, it is necessary to correct these off-wind values to zero or a small positive value (conductivity cannot be <0). Note that in reality, lift may exist due to vertical eddies on the off-wind side of a ridge; however, such turbulent features are beyond the scope of the model. The resulting grid of conductivity values (one value for each point of the digital-elevation model) serves as the connection between the migration model and the modeled region.

Interpretation of Results by Particle Tracking. Once the matrix of equations is solved, equation (2) can be used to determine the magnitude and direction of the migration flux at each gridpoint in the domain. A useful final step is to conduct "particle tracking" to trace out individual migration paths through the domain. Particle tracking is often used in fluid mechanics to help visualize and interpret complex flow fields. There are several possible algorithms for particle tracking; a simple form consists of using equation (2) to calculate the velocity in the eight possible directions from a starting point and then choosing the next cell in the highest velocity direction (termed the D8 method; O'Callaghan and Mark 1984) The calculation is repeated from the new cell, and then continued until a model boundary is eventually reached One can also determine the travel time or velocity of a particular path through the flow field as part of the tracking algorithm.

Model Application. In this paper we apply the model to simulate the spring Golden Eagle migration through Pennsylvania. This season, species, and location were chosen as an initial test for the model because the migration occurs during a period of minimal thermal lift, count data are available for comparison with model simulations, and the flight occurs through a relatively small region of highly-variable terrain. To test the model, we summarized Golden Eagle data from spring hawk watches in northeastern North America, separated into full-time and part-time sites (Table 1). Recent full-time count data from Tussey Mountain hawk watch, 11 km southwest of State College, PA, show a substantially larger spring Golden Eagle flight than at the long-term Lake Ontario shoreline sites. Data from other part-time sites in the

Table 1. Summary of spring Golden Eagle migration count data, northeast North America. Based on data reported in *Hawk Migration Association of North America Hawk Migration Studies* and BIRDHAWK (listserv.arizona.edu/archives/birdhawk.html). Hawk Mountain data provided by L. Goodrich (pers. comm.).

Site Name	Description	Location	Years	Annual Count Maximum: Range (Mean)	Annual Count Maximum: Daily Counts[a]
Full-time sites					
Braddock Bay, NY	Lake Ontario shore	Central NY	1979–2002	6–53 (22)	11, 9, 7
Derby Hill, NY	Lake Ontario shore	Central NY	1980–2002	13–92 (31)	25, 23, 16
Niagara Peninsula	Niagra Escarp./Penin.	Southern ON	1980–2002	3–13 (7)	4, 4, 3
Raccoon Ridge, NJ	Ridge	Northwest NJ	1975–76	1–3 (2)	1, 1, 1
Ripley, NY	Lake Erie shore	Western NY	1987–99	2–12 (4)	7, 3, 2
Tussey Mountain, PA	Ridge	Central PA	2001–02	119–166 (143)	22, 22, 14
Part-time sites					
Allegheny Front, PA	Edge of Allegheny Plateau	Southwest PA	1990–2002	2–75	22, 21, 19
Hawk Mountain, PA	Kittatinny Ridge	Eastern PA	1969–2002	0–2	2, 1, 1
Hook Mountain, NY	Hudson River bluff	Eastern NY	1976–2002	0–5	5, 1, 1
Jacks Mountain, PA	Ridge	Central PA	1995–99	1–11	10, 8, 3
Mount Pleasant, NY	Allegheny Plateau	West central NY	1992–93	6–34	10, 8, 3
Second Mountain, PA	Ridge	East central PA	1993–97	0–2	1, 1, 1
Sideling Hill, PA	Ridge	South central PA	1997–98	18–43	15, 5, 5
Tuscarora Summit,	Ridge	South central PA	1977–2002	0–9	3, 2, 2
Tussey Mountain, PA	Ridge	Central PA	1995–2000	16–95	20, 16, 15
Valleyfield, QE	River crossing	Southern QE	1980–2002	2–55	19, 8, 5
White Deer Ridge, PA	Ridge	Central PA	2000–01	25–33	13, 11, 6

[a] The three highest counts on record are listed.

western portion of the ridge-and-valley region suggest similar numbers of migrating Golden Eagles. However, Golden Eagles are rarely seen along the Lake Erie and Lake Ontario shorelines to the northwest, or along the Kittatinny Ridge to the east. Based on a comprehensive review of such data, Brandes (1998) suggested a narrow spring migration route through the ridges of central Pennsylvania west of Harrisburg, which is distinct from the fall migration route across the state, documented extensively at hawk watches along the Kittatinny Ridge (e.g., Hawk Mountain, Waggoner's Gap). Available satellite telemetry data (Brodeur et al. 1996) are consistent with a spring route through central Pennsylvania. Approximately 80% of the spring Golden Eagle flight at Tussey Mountain occurs from late February through March with a median date of 10 March, and only 11 of 285 Golden Eagles for which flight path data were recorded during spring 2001 and 2002 were crossing and leaving the ridge (D. Ombalski, D. Brandes, and M. Lanzone unpubl. data). Thus, the model assumption that eagles primarily use terrain updraft-dominated lift is reasonable for this application.

To create the conductivity field for simulating spring Golden Eagle migration through Pennsylvania, we used the 1:250 000 scale (ca. 100-m resolution) state digital-elevation model available from the United States Geological Survey (http://edc.usgs.gov/geodata/). Higher resolution data are available, but are unnecessary for simulating migration over scales of several hundred kilometers. Mountain ridges in this region are on the order of 2–3 km wide, therefore such terrain features are well represented at the 100-m resolution. The size of the digital-elevation model (2860 × 4950 gridpoints for the entire state) requires that the equations be solved at more than 14 million locations; to reduce the computer memory requirements, we focused on a 2400 × 2400 grid (240 km × 240 km) of the central portion of Pennsylvania (Fig. 1) where Golden Eagles are known to migrate. Satellite telemetry data from the eastern U.S. (Brodeur et al. 1996) gave an average spring migration distance of 68 km/d, indicating it takes Golden Eagles several days to traverse the study region.

Note the contrasting topography of the Allegheny Plateau (northwest portion), the ridge-and-valley (central portion), and Piedmont physiographic provinces (southeast) in Fig. 1. Slopes are maximized in deeply incised canyons of the Appalachian Plateau, and along the ridges of the ridge-and-valley province. The terrain aspect through the study area is dominated by the southeast and northwest directions, due to the southwest to northeast trend of the Appalachian Mountains.

Slope and aspect at each point of the digital-elevation model were determined using the Spatial Analyst package of the ArcView Geographical Information System (Environmental Systems Research Institute, Redlands, CA U.S.A.), and the conductivity was determined using

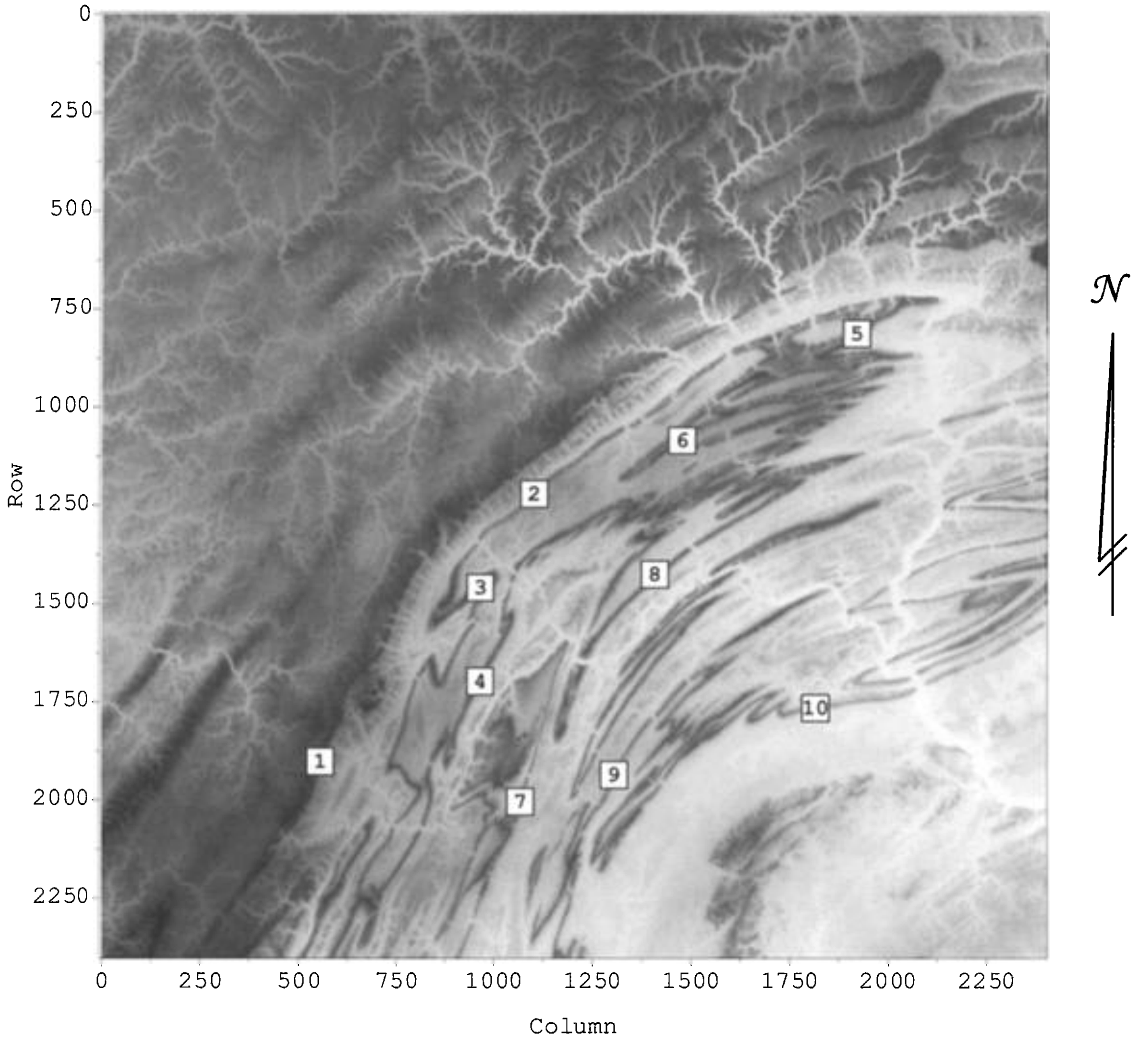

Figure 1. 100-m resolution shaded digital-elevation model (dark = high elevation, light = low elevation) of central Pennsylvania covering a 240 × 240 km area centered on the town of State College. Landscape features are designated by numbers: 1 = Allegheny Front, 2 = Bald Eagle Mountain, 3 = Brush Mountain, 4 = Tussey Mountain, 5 = White Deer Ridge, 6 = Nittany Mountain, 7 = Sideling Hill, 8 = Jacks Mountain, 9 = Tuscarora Mountain, 10 = Kittatinny Ridge.

the method outlined above in the Map Calculator function of ArcView. All negative conductivity values were set to a constant value of +0.01, several orders of magnitude below typical windward terrain conductivity values. We also investigated the application of a nonlinear scale factor to the conductivity values to widen their range of variation; however, this had no significant effect on the simulated migration tracks. The results were exported from ArcView as a text array for input to the model, which was implemented as a FORTRAN program. To reduce the number of required simulations, model runs were made for four combined wind directions (south/southeast, west/southwest, north/northwest, and east/northeast) rather than all eight, by summing the respective conductivity fields. This was felt to be a reasonable approach since winds are deflected locally by the terrain and often shift over the course of a day as weather systems move across the region.

To generate flow across the model domain, constant energy values were imposed along the southern (high energy) and northern (low energy) boundaries of the region to create a northward (PAM = 0°) energy gradient. We used energy values of 1000 and 0 for the south and north, respectively (we also investigated northward

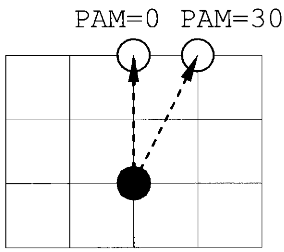

Figure 2. Schematic of imposed migration used for traversing low-velocity zones of the model domain. The migration track is deflected 200 m to the north for principal axis of migration (PAM) = 0°, and 225 m to the north-northeast for PAM = 30°.

gradients of 100–0 and 10–0, but these had no effect on the relative differences in flux values between locations or on the simulated tracks).

A 30° (north/northeast) PAM was also simulated, because spring interthermal glide directions were found to be ca. 20–30° in central New York where leading lines are absent (Kerlinger 1989). Furthermore, relative to the spring counts in central Pennsylvania, few Golden Eagles appear along the southern shore of Lake Ontario in March (Brandes 1998), which suggests a northeastward migration heading from central Pennsylvania. This was implemented by imposing an additional set of constant energy values to the north and south boundaries incorporating the 30° deflection.

Once the flow field was solved, particle tracking was done from a series of equally spaced points along a portion of the southern boundary of the model (column 200–1100 at 50 column [5 km] increments; Fig. 1). This 90-km span encompasses the region where hawk-watch data show that Golden Eagles enter Pennsylvania during spring migration (Brandes 1998). We note that the distribution of Golden Eagles entering Pennsylvania is almost certainly nonuniform; thus each starting point represents different numbers of migrants. The maximum velocity tracking algorithm described previously was used throughout. For each track, velocity data at each step was recorded so that travel times and mean velocities of different tracks could be compared.

In preliminary model runs, we found that in low-velocity regions of the model domain, such as flat terrain, this algorithm tends to produce unrealistically circuitous migration tracks and dead-ends in terrain coves and dips. Such issues are common in digital-elevation model-based analysis when the scale of terrain variation is smaller than the grid resolution, and are often solved by applying a pit-filling routine to artificially smooth the terrain (e.g., Jenson and Domingue 1988). To prevent such dead-end tracks and ensure continued migration across low conductivity regions, at each gridpoint where the maximum velocity from equation (2) dropped below a threshold velocity of 1 (typical velocities along ridges were 15 to 150), a PAM-directed migration of two gridpoints was imposed (Fig. 2). Our reasoning is that where sources of lift are lacking, raptors will expend energy to continue migrating in the desired direction.

RESULTS

Conductivity Fields. The mountain ridges create a network of high conductivity pathways relative to the surrounding terrain (Fig. 3). Although the deeply incised river valleys of the northern Appalachian Plateau also show high conductivity, these are generally not well aligned or continuous over large distances (Fig. 3). Note the similarity in the south/southeast and north/northwest fields, and the east/northeast and west/southwest fields; this reflects the general longitudinal symmetry of the ridges. There are important exceptions to this symmetry, such as the Allegheny Front (Fig. 1) on south/southeast appearing as a long streak of high conductivity that all but disappears on north/northwest winds. The ridges in the southern portion of the study area are oriented at ca. 20–25°, and show high conductivity on east/northeast and west/southwest winds (due to the east and west components, respectively). Near the center of the study area the ridges generally bend more easterly to ca. 50–60°, and thus their conductivity is much reduced on east/northeast and west/southwest winds compared to south/southeast and north/northwest winds.

Simulated Migration Tracks. Based on simulated trends there is a marked convergence of flight paths across the region, from 19 entering to 4 exiting (Figs. 4–7). The model clearly shows the influence of the ridges in directing the migration pattern, particularly for the PAM = 30° case. In many cases the simulated flight paths follow ridges for 10s of km (in some cases >100 km), including ridges such as the Allegheny Front, Tussey Mountain, Sideling Hill, and Jacks Mountain (Fig. 1). At the termination of the ridges in the northeast part of the study area for the PAM = 0° case, flight tracks bend northward across the intervening valleys, whereas for PAM = 30°, the tracks head north-northeast.

Figure 5 shows the simulated migration tracks for north/northwest wind directions. Overall, the particle tracks for north/northwest winds (Fig. 5) are similar to those on south/southeast winds, with the flight even more confined to the ridge-and-valley region. Convergence of the flight to a few paths through the central part of the study area is again apparent. For the PAM = 30° case, the flight tends more toward the eastern ridges and away from the Allegheny Plateau. The difference in PAM can be influential in changing the flight pattern at a spe-

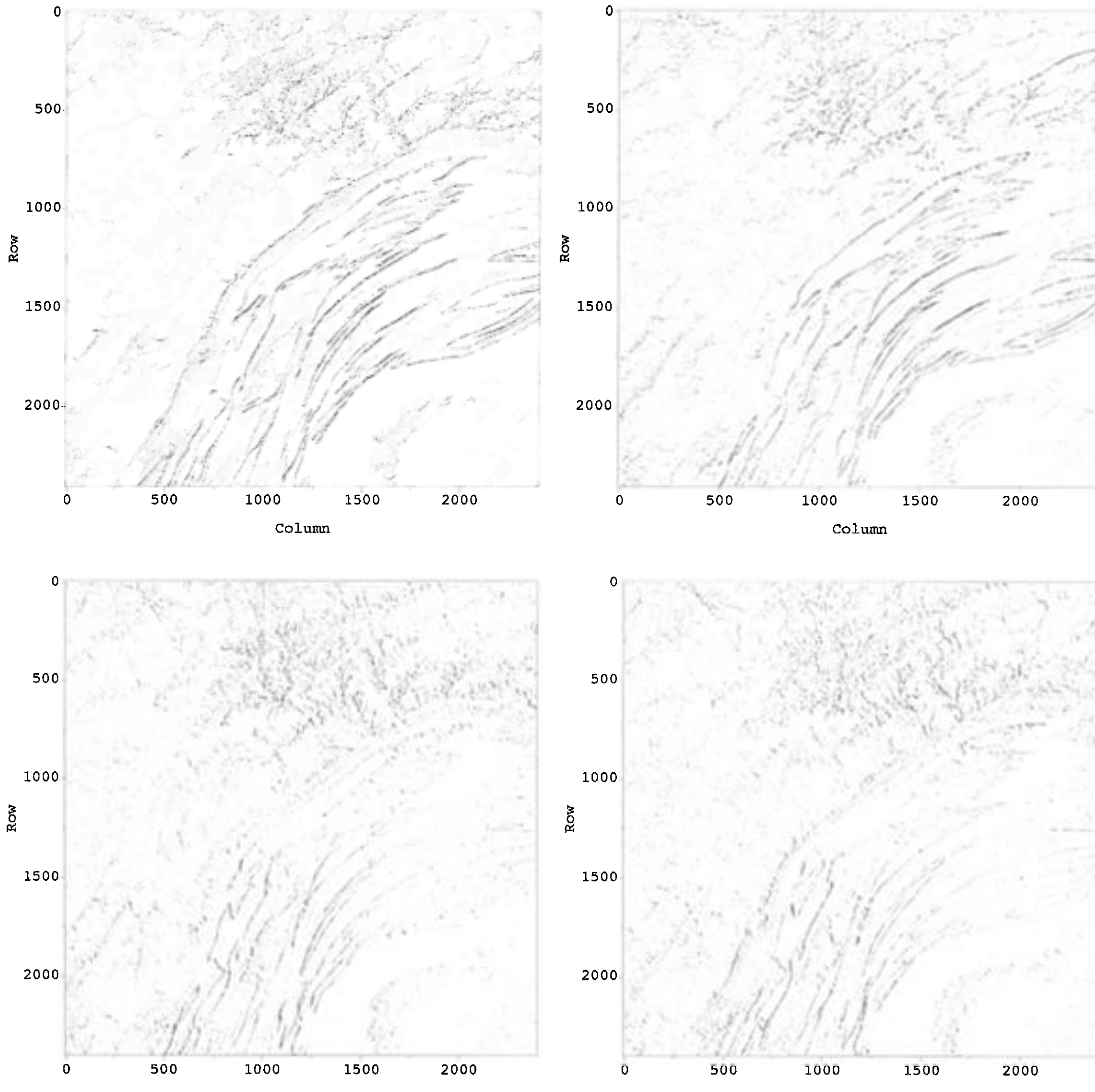

Figure 3. Relative conductivity (i.e., updraft strength) of central Pennsylvania for south/southeast winds (top left), north/northwest winds (top right), west/southwest winds (bottom left), and east/northeast winds (bottom right). Regions of high conductivity are dark and regions of low conductivity are light.

cific location, such as the northern end of Brush Mountain (Fig. 1). For PAM = 0°, the track heads northward across the 12-km wide Nittany Valley, while for PAM = 30°, it crosses the 5-km wide gap northeastward to Tussey Mountain. Note that this effect did not occur on south/southeast winds, showing the sensitivity to both wind direction and PAM.

The overall pattern for west/southwest wind directions (Fig. 6) trends more along the PAM under these conditions than for the south/southeast and north/northwest winds, with more tracks crossing the Allegheny Plateau, where conductivity is generally lower and the terrain is not as directionally oriented. Although there is some ridge deflection in the southern portion of the study area where

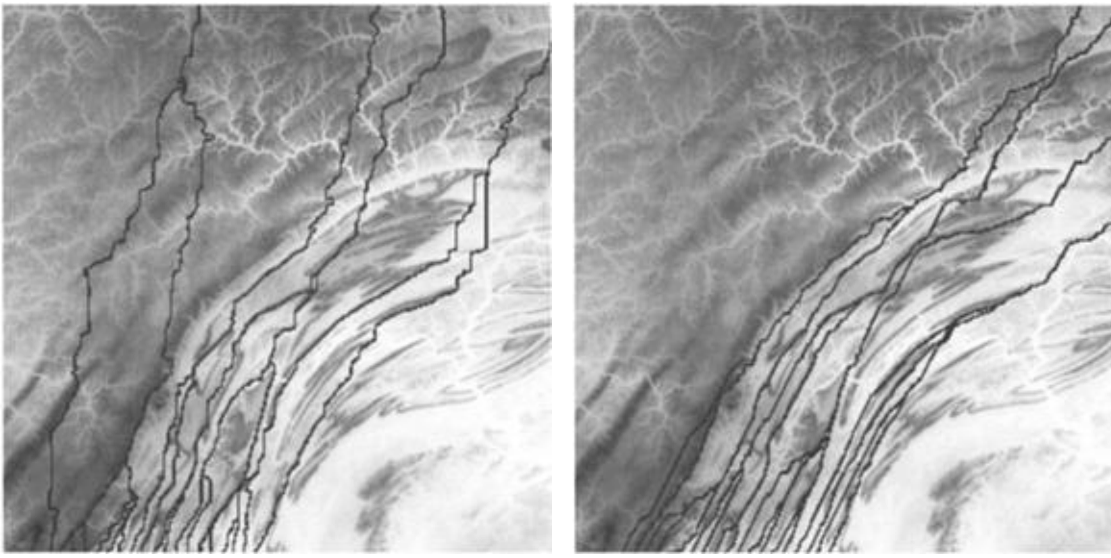

Figure 4. Simulated migration tracks through central Pennsylvania for south/southeast winds. Left image for principal axis of migration (PAM) = 0°, right image for PAM = 30°.

the ridges are oriented more northerly (20–25°), the ridges are not as effective in deflecting the migration as for the previous cases, particularly where the ridges bend eastward near the center of the study area. As a result, the convergence of flight paths is not as strong as for the south/southeast and north/northwest winds.

The model results for east/northeast wind directions (Fig. 7) are similar to those for west/southwest winds, again showing a more PAM-oriented pattern with less convergence than for south/southeast or north/northwest winds. Several tracks can be seen to cross the ridges without deflection. One dead-end track is shown in Fig. 7 (PAM =

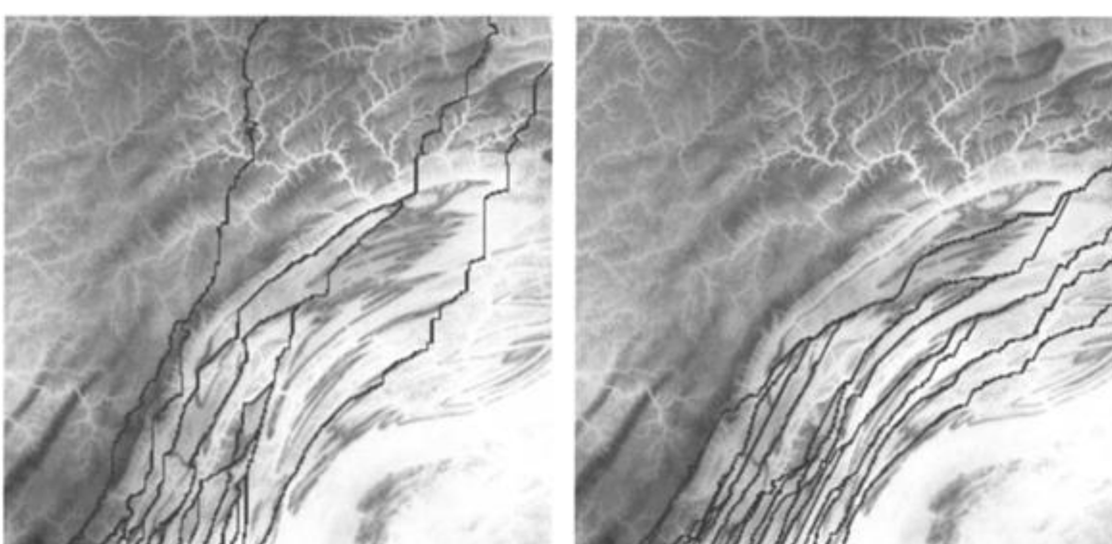

Figure 5. Simulated migration tracks through central Pennsylvania for north/northwest winds. Left image for principal axis of migration (PAM) = 0°, right image for PAM = 30°.

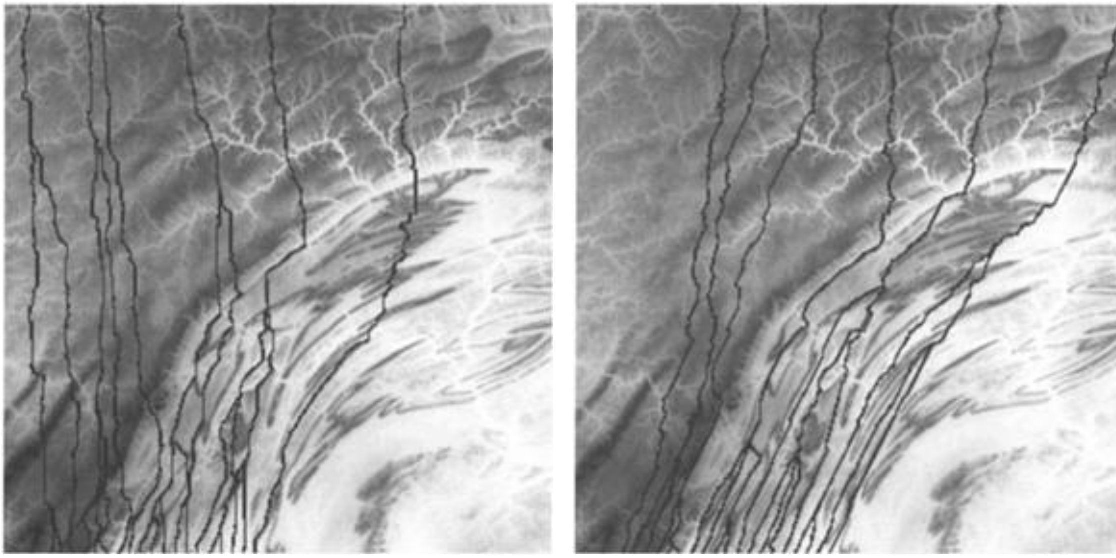

Figure 6. Simulated migration tracks through central Pennsylvania for west/southwest winds. Left image for principal axis of migration (PAM) = 0°, right image for PAM = 30°.

30°); this is a result of local "pits" in the energy field due to dips and southward-facing coves in the terrain.

For the two PAM values used, higher mean track velocities through the study area are realized on south/southeast and north/northwest winds than on west/southwest and east/northeast winds (Table 2). This is due to the flight being more confined to high-conductivity pathways extending across the study area. A further point of interest is that the tracks that enter west of the ridge-and-valley region (west of column 500) are significantly

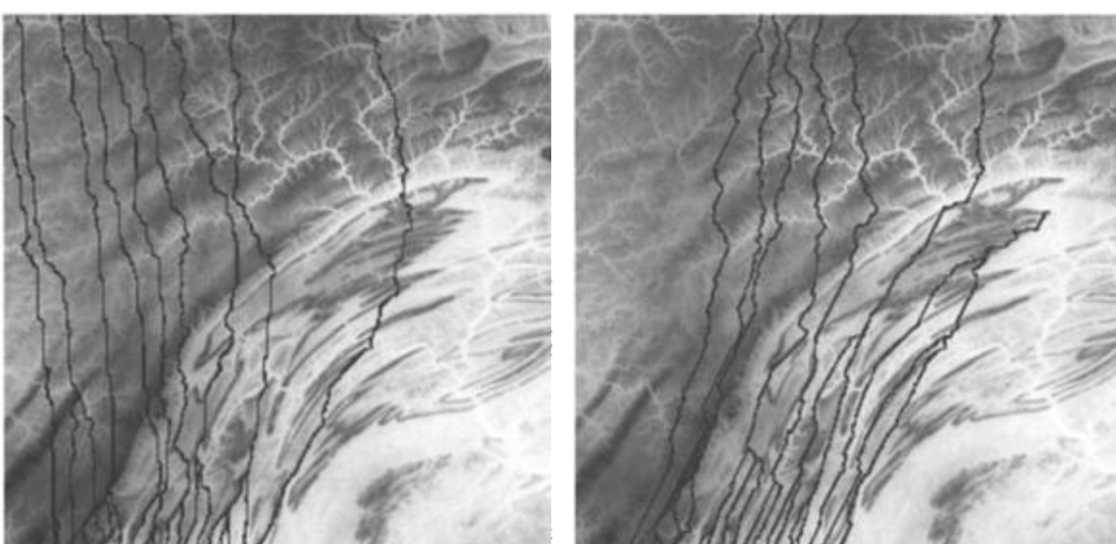

Figure 7. Simulated migration tracks through central Pennsylvania for east/northeast winds. Left image for principal axis of migration (PAM) = 0°, right image for PAM = 30°.

slower than those that enter within the ridge-and-valley region. Three particular entry areas produce the highest velocity tracks: columns 500–700, columns 850–950, and column 1100. Each of these corresponds to the locations of long parallel ridges (Fig. 1).

DISCUSSION

Simulated Migration Tracks. The model results indicated that migration patterns of raptors using terrain updrafts for lift can be simulated using digital-elevation model data and the fluid flow analogy. The particular pathways are dependent on the structure and orientation of the terrain, the wind direction, and choice of PAM. The convergence of pathways as the migration progresses is present to varying degrees in all simulations, and is the natural result of the requirement of minimum energy consumption in traversing a network of conductive pathways. This convergence effect, coupled with spatial differences in terrain conductivity, is at least partially responsible for the difference in migration counts between sites.

For the application to spring migration of Golden Eagles through central Pennsylvania, the model suggests that under south/southeast or north/northwest winds, Golden Eagles migrate through the ridge-and-valley region, and then north or northeast across the Allegheny Plateau, with convergence of pathways as migration progresses northward. Under west/southwest and east/northeast winds, the orientation of the topographic features is such that high conductivity zones are less well connected across the region, and thus the pattern is less influenced by the ridge network and less subject to pathway convergence. Furthermore, these winds result in poor lift conditions with lower mean track velocities through the study area (Table 2). This is qualitatively consistent with our experience at Tussey Mountain, where 230 of 285 Golden Eagles counted during full-time coverage in spring 2001 and 2002 were on south/southeast or north/northwest winds, and all large Golden Eagle flights (>10/d) have occurred on south/southeast or north/northwest winds (D. Ombalski, D Brandes, and M. Lanzone unpubl. data). At Tussey Mountain, south/southeast winds in early spring are usually associated with rapidly warming temperatures, and east/northeast winds are often accompanied by low pressure and rain, which may account for some of these observed differences.

The entry locations producing the highest velocity tracks (columns 500–700, columns 850–950, and column 1100) are in qualitative agreement with available count data. The first location includes two parallel ridges that converge to Tussey Mountain, the second includes two parallel ridges that converge to Sideling Hill, and the third is near the end of Tuscarora Mountain. Tussey and Sideling are both known for spring Golden Eagle migration (Table 1). Golden Eagles are uncommon migrants at Tuscarora Mountain, which is the easternmost ridge that consistently records Golden Eagles in spring (Table 1).

In no cases do simulated migration tracks follow the Kittatinny Ridge to the northeast. However, this is a direct result of the location of the chosen entry points, not a lack of updrafts along that particular ridge. Nonetheless, the simulations are consistent with field data: mean of one Golden Eagle per year is seen during the spring count at Hawk Mountain (L. Goodrich pers. comm.), and other part-time counts that have been conducted along the Kittatinny Ridge have rarely reported Golden Eagles. Thus, the model provides indirect evidence that Golden Eagles are not entering Pennsylvania to the east of Tuscarora Mountain.

The lack of Golden Eagles in spring on the southern shore of Lake Erie and the southwestern shore of Lake Ontario (Table 1) is also predicted by the model. Only two cases simulated (west/southwest winds with PAM = 0 and east/northeast winds with PAM = 0) showed migration tracks toward these areas, and these are low-velocity tracks, indicating poor lift conditions.

Although the simulated migration pattern is consistent with available data, we suspect that the model tends to overpredict convergence of flight tracks due to the deterministic tracking algorithm. Once two tracks converge, they cannot branch off because there is no stochastic or random component to the tracking algorithm. In reality, birds may leave a flight path for a variety of reasons during migration (e.g., foraging, habitat preference, to interact with other birds). Such behavior undoubtedly occurs more than the model results indicate. We chose not to include wind drift effects, although these could easily be incorporated into the tracking algorithm. Satellite tracking data across the relatively flat terrain of southern Quebec and Ontario showed that Golden Eagles can maintain a consistent heading against prevailing winds (Brodeur et al. 1996). Our observations (pers. obs.) of Golden Eagles migrating along central Pennsylva-

Table 2. Summary of mean velocities for simulated migration tracks across central Pennsylvania. The values shown have been normalized by the mean velocity of all simulated tracks.

Starting Column	PAM = 0					PAM = 30				
	SSE	NNW	WSW	ENE	Mean[a]	SSE	NNW	WSW	ENE	Mean[a]
200	0.33	0.63	0.37	0.28	0.40	0.76	1.24	0.28	0.26	0.64
250	1.10	0.61	0.38	0.34	0.61	1.18	1.18	0.40	0.28	0.76
300	1.08	0.57	0.37	0.48	0.63	0.78	Dead-end	0.37	0.50	0.55
350	1.07	0.63	0.32	0.53	0.64	0.81	1.44	0.30	0.50	0.76
400	0.85	0.55	0.30	0.47	0.54	0.82	1.39	0.32	0.60	0.78
450	1.00	0.54	0.33	0.43	0.58	0.84	1.31	0.32	0.74	0.80
500	0.91	2.12	1.04	0.40	1.12	1.16	1.82	1.10	1.14	1.31
550	1.12	1.64	0.67	1.02	1.11	0.96	1.64	0.53	1.12	1.06
600	1.52	1.77	1.44	0.98	1.43	1.96	1.53	0.65	0.97	1.28
650	1.93	1.77	1.46	0.60	1.44	2.01	1.34	0.73	1.08	1.29
700	1.42	1.19	1.00	1.58	1.30	1.15	1.12	0.60	0.75	0.91
750	0.86	1.20	1.06	1.15	1.07	1.02	1.15	0.67	0.75	0.90
800	0.81	1.23	0.86	1.02	0.98	1.05	1.60	0.71	0.55	0.98
850	1.56	1.26	1.66	0.92	1.35	1.34	1.45	0.99	0.77	1.14
900	1.39	1.26	1.27	1.06	1.25	1.44	1.54	1.01	1.29	1.32
950	1.52	1.15	1.20	1.22	1.27	1.68	0.57	0.36	1.17	0.94
1000	1.59	1.11	1.03	1.07	1.20	1.57	0.72	0.35	0.50	0.79
1050	1.51	1.08	1.01	0.82	1.11	0.70	1.90	0.60	0.57	0.94
1100	1.28	1.95	1.03	1.48	1.44	1.20	2.57	0.35	1.09	1.30
Mean[b]	1.20	1.17	0.88	0.83		1.18	1.42	0.56	0.77	

[a] Mean velocity for a particular track across all four directions.
[b] Mean velocity for a particular direction across all tracks.

nia ridges under high-wind conditions (>50 km/hr) following passage of late fall cold fronts further argues against a wind drift effect on Golden Eagle migration.

Overall, the model results demonstrate that the fluid-flow analogy and digital-elevation-model-based approach is useful for simulating raptor migration. The model yields quantitative insight into observed migration patterns through a ridge system, and helps explain why some count sites yield greater numbers than others. The model can also be used to predict sites of concentrated raptor passage, given known locations for the origin and destination of the flight.

Limitations. The ability to quantify the model results more precisely, or to test and calibrate the model, is dependent on accurate boundary conditions, that is, data on the distribution of raptors entering the modeled region. In our application, we showed migration tracks initiating from equally spaced starting points along a portion of the southern boundary, but do not have the necessary data to assign numbers of Golden Eagles to each point. With such data, one could use the model to predict numbers of migrants at different locations within the region, which could be tested by field observation. Future simulations and model calibration will explore the effects of different raptor distributions at the model boundary.

It is clear that there are limitations to the fluid-flow analogy. Choices of migration direction are assumed to occur based on an energetic response to local conditions encountered during migration, which does not reflect the behavioral flexibility of migrating raptors. The model cannot account for the fact that a migrating eagle can see several kilometers ahead and choose its flight path based on distant landscape features; this is particularly evident in simulations where tracks go up valleys despite a nearby parallel ridge of high conductivity (especially in the case of PAM = 30°), or fail to cross a several-kilometer gap in a ridge. Klem et al. (1985) showed that >95% of migrating raptors proceeded across a 1.3-km water gap (Lehigh River) in the Kittatinny Ridge without leaving the ridge, so it is clear that a raptor's decision process is not based strictly on local energy conditions. However, a modified tracking algorithm is under development that will search beyond adjacent gridpoints to choose the direction toward the location of highest conductivity within a specified distance.

Finally, the model also does not take into account "learned" behavior. Long-lived species like Golden Eagles may develop a preferred migration route over many seasons of experience that is only partially dependent on energy minimization. Other factors may determine migration route choices, such as selection based on preferred or habitually-used habitat, prey availability, avoidance of humans, or visual cues from other migrants. In the case of Golden Eagles, the Pennsylvania ridges constitute some of the most extensive and remote woodland corridors in the region, so these high conductivity pathways may also be preferred migration routes for other such reasons. One could conceivably use habitat overlays based on geographical information system datasets as weighting or adjustment factors for the conductivity field, thus incorporating habitat considerations into the model.

Possible Applications and Extensions to the Model. The model as described here is capable of simulating the migration of a variety of diurnal raptors, so long as the basic premise of the model is met—that updrafts resulting from horizontal surface winds deflecting off sloping terrain are the dominant source of lift. This would include other late fall and early spring migrants besides Golden Eagles, or migration during overcast conditions. For smaller species, it may be necessary to incorporate a wind-drift algorithm when crossing low conductivity (flat) terrain.

Application of the model over larger spatial domains (e.g., the entire Appalachian Mountain range) is possible; however, several problems must be overcome. First, computer memory is a significant limitation, because even at much larger scales, the digital-elevation model must be of sufficient resolution to accurately represent the landscape features that affect migration. Simulation of migration over a 2000 × 1000 km region using the 100-m resolution data would require the processing of ca. 1.5-gigabyte computer files. Secondly, the larger the spatial scale, the more time required for migration through the model domain. This means that a realistic large-scale simulation must take into account changing wind conditions, and thus a time-varying conductivity field. However, dynamic models of thermal uplift in the atmospheric boundary layer already exist, and could be coupled with our terrain-based updraft model and habitat data to create a raptor migration model capable of large-scale dynamic simulations. Such a model would be a valuable tool in identifying conservation priorities at the continental scale, or planning field studies in likely concentration areas where data are lacking. In addition, this type of model for a local region could be used as a predictive tool to estimate times, conditions, and locations when migrating birds present a high risk of collision with aircraft.

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