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Roost- and perch-site selection by Golden Eagles (*Aquila chrysaetos*) in eastern North America

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ABSTRACT—Birds select critical resources to meet needs that vary in response to spatial, temporal, and individual variation. As an example, perch or roost sites may be at locations that provide protection from predators, mobbing, or inclement weather. Applied to large, soaring predators, this theory suggests that they may select perch and roost sites near food resources or at sites where environmental updrafts develop. To test these theories, we characterized selection of non-flight locations throughout the annual cycle for Golden Eagles (*Aquila chrysaetos*) in eastern North America. We determined factors associated with selection of perching (daytime) and roosting (nighttime) sites by eagles by comparing land cover and topographic characteristics of GPS telemetry locations for eagles (used) with random (available) locations. We separately assessed selection for perch and roost sites during each of 4 seasons (winter, summer, and spring and fall migration). Golden Eagles showed different selection patterns for perching by season and age. Throughout the year, eagles selected perch sites on steep slopes. The direction these slopes faced differed among seasons, with eagles selecting south-facing slopes in summer and east-facing slopes during migration. Adults showed greater preferences for broadleaf forests in summer and for ridges in fall. Patterns of perch-site use were consistent with selection for sites that provide thermal protection and access to thermal updrafts. We found few patterns of selection for roosting sites. Our analysis provides insight into decision-making by a long-distance migrant across its annual cycle and throughout its geographic range, and thus into how resource selection changes seasonally. *Received 28 November 2017. Accepted 5 December 2018.*

Key words: *Aquila chrysaetos*, Golden Eagle, habitat selection, land cover, resource selection, topography

Selección de sitios de percha y dormidero por águilas reales (*Aquila chrysaetos*) en el este de Norteamérica

RESUMEN (Spanish)—Las aves seleccionan recursos críticos que satisfacen sus necesidades en respuesta a variación espacial, temporal e individual. Por ejemplo, los sitios de percha o dormideros pueden encontrarse en localidades que les proveen de protección ante depredadores, acoso o inclemencias del tiempo. Aplicada a depredadores planeadores grandes, esta teoría sugiere que podrían seleccionar perchas y dormideros cerca de recursos alimenticios o en sitios donde se desarrollan corrientes de aire ascendentes. Para someter a prueba esta teoría, caracterizamos la selección de localidades de no-vuelo a lo largo del ciclo anual para águilas reales (*Aquila chrysaetos*) en el este de Norteamérica. Determinamos los factores asociados con la selección de sitios de percha (durante el día) y dormideros (durante la noche) de las águilas, comparando las características de cobertura del suelo y topografía de posiciones de telemetría GPS usadas por águilas con localidades aleatorias (disponibles). Por separado, determinamos la selección de perchas y dormideros durante cada una de las cuatro estaciones (invierno, verano, y migraciones de primavera y otoño). Las águilas reales mostraron diferentes patrones de selección de perchas por temporada y edad. A lo largo del año, las águilas seleccionaron sitios de percha en laderas escarpadas. La orientación de esas laderas difirió entre estaciones, donde las águilas seleccionan laderas con dirección al sur en el verano y con dirección al este durante la migración. Los adultos mostraron mayor preferencia por bosques latifoliados en el verano y por crestas de cordillera en el otoño. Los patrones de uso de sitios percha fueron consistentes con la selección de sitios que proveen protección termal y acceso a corrientes de aire ascendente. Encontramos pocos patrones de selección de sitios dormidero. Nuestro análisis hace aportes al entendimiento de la toma de decisiones por una especie migratoria de grandes distancias a lo largo de su ciclo anual y su rango geográfico, y con ello a cómo la selección de recursos cambia estacionalmente.

Palabras clave: águila real, *Aquila chrysaetos*, cobertura del suelo, selección de hábitat, selección de recursos, topografía

Resource selection varies in response to spatial, temporal, and individual variation (Newton 2010, Jirinec et al. 2015). When choosing breeding sites, animals select locations that provide not only access to resources required to survive or raise young, but also to features that provide protection (Newton 2010). As young mature and disperse, they may select habitats for those same reasons and also to avoid intraspecific competition (Forsman et al. 1984). The factors that influence resource selection are even more diverse for migratory animals, which must select routes and time seasonal movements so that critical resources are available at all times and places (van Wijk et al.

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2012). Furthermore, resource selection by these animals has an added layer of complexity because they often occupy different habitat types during breeding and nonbreeding seasons (Marzluff et al. 1997, Lausen and Barclay 2002, Newton 2010, Braham et al. 2015, Markham et al. 2016).

Perch sites are important resources for animals and the habitats that they use for perching should be specific to an individual's needs. For example, animals may select perch locations that provide protection from inclement weather (Forsman et al. 1984, Walsberg 1986, Atkinson 1993, Lewis 1996, Yackel Adams et al. 2000, Kerth 2008), parasites (Lewis 1996, Rohner et al. 2000, Markham et al. 2016), predators (Atkinson 1993, Kerth 2008), or, in some cases, mobbing (Hendrichsen et al. 2006). They may also select perch sites close to breeding areas (Coleman and Fraser 1989, Jirinec et al. 2015) or food resources (Gess et al. 2013, Markham et al. 2016), or sites that provide information about foraging locations provided by other animals (Ward and Zahavi 1973, Buckley 1996).

Birds, despite their movement capacity, are known to select perch sites in close proximity to environmental resources. Scavengers often perch near food resources (Coleman and Fraser 1989) and predators perch near their prey, especially during the nonbreeding season (Anthony et al. 1982, Keister and Anthony 1983). For some species, females roost on their nest over eggs or nestlings, although males select cover that can be far from the nest (Jirinec et al. 2015). Additionally, soaring birds use weather and topographic conditions that promote environmentally generated updraft (Chevallier et al. 2010, Mellone et al. 2011, Katzner et al. 2012a, Lanzone et al. 2012, Miller et al. 2014, Panuccio et al. 2016) and therefore may select perch sites where updrafts form (Thompson et al. 1990).

We studied the drivers of perch (diurnal) and roost (nocturnal) site selection by a large, migratory, soaring, apex predator, the Golden Eagle (*Aquila chrysaetos*) in eastern North America. Golden Eagles in this region occupy more forested habitats than eagles in western North America, they are of conservation concern, and there have been studies dedicated to understanding their numbers (Dennhardt et al. 2015, 2017) and use of resources while in flight (Katzner et al. 2012a, Lanzone et al. 2012, Duerr et al. 2015) and at the scale of their home ranges (Miller et al. 2017). However, few details are known about habitat selection at smaller scales within their home ranges, despite the fact that there is substantial ecological change occurring throughout their range (Katzner et al. 2012b). Our objective in this study was to characterize selection of non-flight locations, termed perch and roost sites, by eagles throughout their annual cycle (spring migration, summer, fall migration, and winter). We focused on selection for 4 types of habitat variables: (1) aspect, (2) slope, (3) topographic position, and (4) land cover type, and we evaluated how eagle age influenced selection.

Methods

Study species and area

The distribution of Golden Eagles in eastern North America extends from the southern extent of the Appalachian Mountains north to the Hudson Bay and Strait (Fig. 1; Katzner et al. 2012b). Breeding grounds occur on northern forests, taiga, tundra, and Arctic cordillera ecoregions in Canada (Level 1 Ecoregions; CEC 1997). Wintering areas include northern and eastern temperate forest ecoregions (Duerr et al. 2015). Topography throughout this range varies from mountains, large plateaus, ridge and valley systems, and coastal plains in the south to hilly and rolling terrain in the north (CEC 1997). Eagles usually build nests on cliffs, although they build some in trees, and in a wide range of settings (Lumsden 1964, Morneau et al. 1994, Brodeur and Morneau 1999).

Eagle data collection and processing

We used cannon or rocket nets to capture 55 Golden Eagles during winters 2009–2014 in Alabama, Maryland, New York, North Carolina, Pennsylvania, Tennessee, Virginia, and West Virginia, USA, primarily along the Appalachian Mountain Range. We aged eagles based on plumage and molt characteristics (Jollie 1947, Bloom and Clark 2001) and classified them as either adult (5th year of life or older) or subadult (4th year of life or younger). We telemetered no eagles before their first fall migration. Eagles were outfitted with 95 g Cellular Tracking Technologies (CTT, Rio Grande, New Jersey, USA) CTT-1100 global positioning system (GPS) Global System

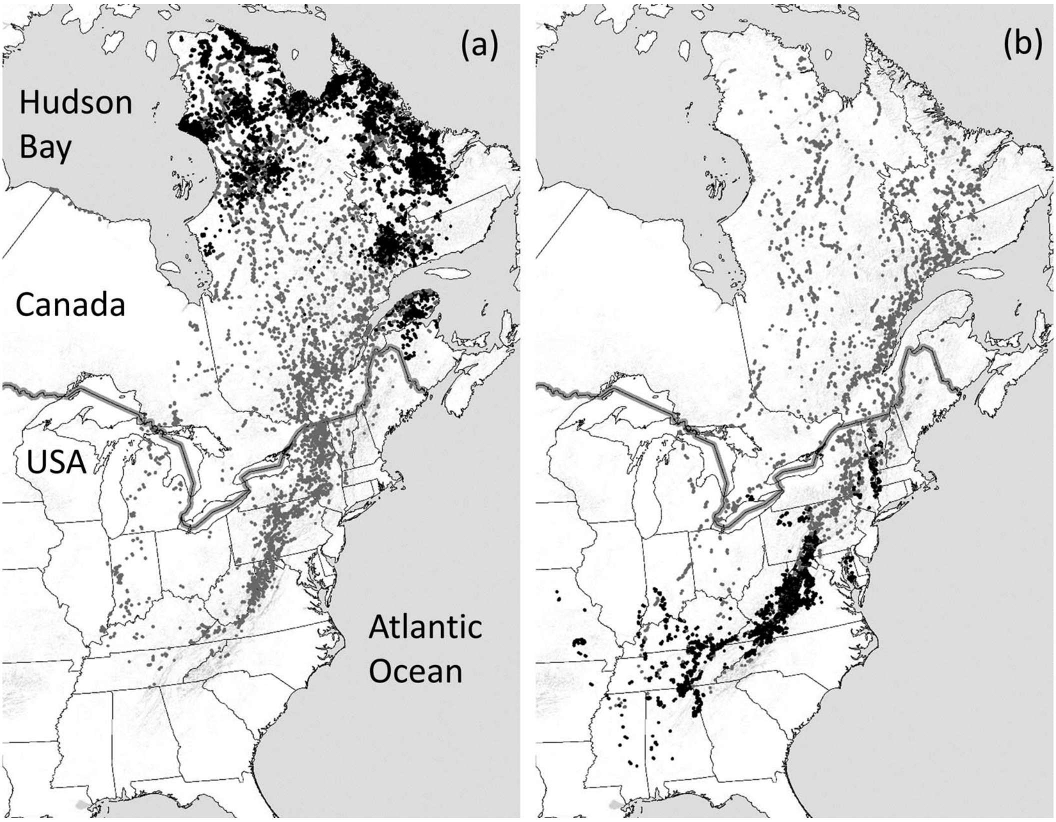


Figure 1. Area of eastern North America where perching-site selection of Golden Eagles occurred from 2009 to 2015. (a) Combined perch and roost locations in spring (gray dots) and summer (black dots). (b) Fall (gray dots) and winter (black dots) perch and roost locations.

for Mobile Communication (GSM) telemetry systems attached as backpacks with Teflon ribbon (Bird and Bildstein 2007) and released. CTT-1100s collected a suite of data including latitude, longitude, altitude above mean sea level (above the geoid), and movement speed. These devices were programmed to collect data between sunrise and sunset at intervals of 15 min (Lanzone et al. 2012). However, when they were located between latitudes 39.5° and 42.5° north and were in flight (movement speed $>$5 knots), transmitters collected data at 30 sec intervals; this was to satisfy goals of a separate, parallel study. Twelve units did not cease data collection during nighttime and collected roost locations at these same intervals.

Data were stored on the telemetry device and then transmitted, on a daily basis, through the GSM network. When out of coverage, stored data were transmitted when a GSM connection was next available. GPS accuracy was $\leq$2.5 m (Lanzone et al. 2012). We removed 2D locations and locations with horizontal dilution of precision (HDOP) $>$10. HDOP describes the factor by which each location differs from GPS accuracy, thus a HDOP of 10 describes GPS error of 25 m (D'eon and Delparte 2005).

We identified stationary locations (i.e., places where eagles were perching or roosting) based on altitude above ground level (AGL) and movement speed reported by the telemetry device. Because of a known issue with speed measurements collected at 30 sec intervals from some CTT firmware (Poessel et al. 2017), we only used data collected at 15 min intervals for analyses. We estimated ground elevation at each GPS location from a 30 m digital elevation model (DEM; US NASA and METI 2011). AGL was then calculated by subtracting ground elevation at GPS locations from eagle altitude above mean sea level. We classified eagles as stationary when eagle AGL was both within 50 m of the earth's surface and movement speed was 0 knots (Poessel et al. 2018).

We characterized all stationary locations as being either perches or roosts based on solar elevation angle for each location (http://www.esrl.noaa.gov/gmd/grad/solcalc/, accessed 19 Mar 2015). We defined perches as those sites where eagles were stationary during the day, between dawn and dusk, as defined by civil twilight (sun at 6° below the horizon; http://aa.usno.navy.mil/faq/docs/RST_defs.php, accessed 19 Mar 2015). We defined roosts as those sites where eagles were stationary at night, between dusk and dawn. To ensure there were no duplicate points, we removed eagle locations subsequently recorded within 0.01° latitude or longitude (~850–1,200 m) of another stationary location.

We paired each roost and perch location with a random point for analysis of resource selection (Manly et al. 2002). To assess conditions that were available to eagles, we used a uniform distribution to randomly place a point within a circular buffer that began 30 m away from each eagle location and extended to 500 m from that eagle location (gencondrandompnts, Geospatial Modeling Environment, Spatial Ecology LLC, www.spatialecology.com/gme, accessed 24 Sep 2015; R 3.2.1, R Core Team 2012). This framework allowed us to determine which features eagles either selected (occurred more often at eagle locations than random locations) or avoided (occurred less often at eagle locations than random locations) at the home-range scale (third-order selection sensu Johnson 1980). We used ArcGIS 10.3.1 (ESRI, Redlands, California, USA) for all spatial analyses.

We categorized all locations by season in the annual cycle (summer, fall migration, winter, spring migration). Because each individual starts migration independent of other eagles, the date of the start and end of each season was unique for each eagle in each year. Eastern Golden Eagles have distinct breeding and wintering areas and show clear directional movements when migrating between those areas (Miller 2012). We used these directional movements to identify year- and eagle-specific start and end dates of each migration and thus start and end dates of winter and summer seasons for each eagle (Miller et al. 2016).

Data associations

We associated each eagle and random location with measurements of slope, aspect, and topographic position. We used Spatial Analyst in ArcGIS to calculate slope and aspect from the 30 m DEM (US NASA and METI 2011). We converted circular (i.e., 1–360°) measures of aspect into Euclidean vectors (ranging in value from –1 to 1) for analysis, termed eastness (positive values face east, negative values face west) and northness (positive values face north, negative values face south; Roberts 1986). We calculated a standardized topographic position index (TPI) based on an annulus neighborhood of 300–2,000 m surrounding each 30 m grid cell (Jenness et al. 2013). We then categorized TPI as valleys, hillsides, ridges, and mountain tops (i.e., the highest ridges).

The range of eastern Golden Eagles encompasses 14 of the land cover classes defined by the Commission for Environmental Cooperation (CEC 2010). We combined similar land cover types to define 6 general classes (needleleaf forest, broadleaf forest, mixed forest, lichen-moss, wetland, and "other"; Appendix Table A1).

Data analysis

We used a total of 8 statistical models to identify factors that were associated with Golden Eagle selection of perches and roosts during each of the 4 seasons in the annual cycle (resource selection functions; Manly et al. 2002, Keating and Cherry 2004). We used case–control logistic regression (PHREG procedure; SAS 9.4, Cary, North Carolina, USA) to determine differences between pairs of eagle use and random locations. We included eagle ID as a random factor to account for autocorrelation among locations collected from the same individuals. We also included a date–time field, which was unique to and identified each pair of use (case) and random (control) locations. For each analysis, the response variable was use or availability of resources at a location defined by eagle and random locations, respectively. The explanatory variables we used included aspect (northness and eastness), slope, eagle age (adult or subadult), land cover, topographic position, and interactions between age and land cover, age and topographic position, and land cover and topographic position. Results from the PHREG procedure do not include intercept terms.

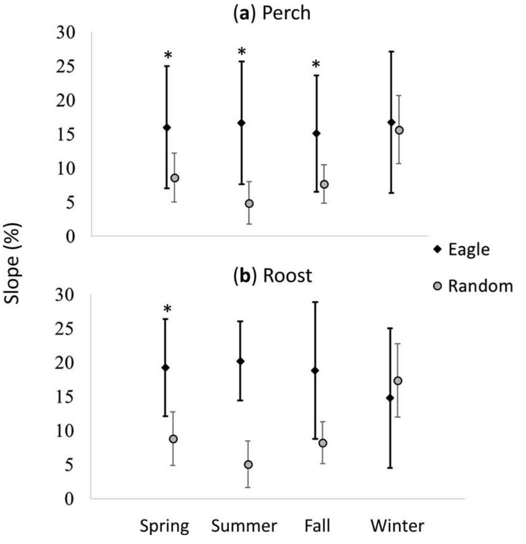


Figure 2. Percent slope for Golden Eagle and random locations in each season for perch (a) and roost (b) sites in eastern North America 2009–2015. Eagle locations are black diamonds with black error bars (1 SE), random locations are gray circles with gray error bars (1 SE). Measures are empirically based grand means from individual eagles and do not account for variation accounted for in case–control logistic regression models. *Values differed between eagle and random locations based on analyses (See Appendix 2).

We present 2 types of results from analyses: (1) Type III fixed effects and (2) slope estimates from linear models. Statistics from Type III fixed effects identify factors that occur more or less often at eagle perch or roost sites compared to random sites. Interpretation of slope estimates is different for categorical and continuous variables. In the case of categorical variables (age, land cover, topographic position, and their interactions), the slope estimates of the regression line ($\pm$SE) identify the log odds of eagles using a site with that particular characteristic (Keating and Cherry 2004). In the case of the continuous variables, the slope estimates of the regression line ($\pm$SE) provide the change in log odds of an eagle using a site when the variable value increased by 1 unit.

Results

Location classification

The 55 Golden Eagles we studied were tracked for a mean of 398 d (SD 458). We tracked most eagles for more than 1 yr and over more than 1 age (14 tagged in their 1st year of life, 11 in their 2nd year, 5 in their 3rd year, 10 in their 4th year, and 15 in their 5th year or older). The database started with 999,806 eagle locations, of which 542,955 were collected at 15 min intervals. A total of 48,685 stationary locations were at least 0.01° latitude or longitude from any other eagle location. The mean HDOP of the locations that were used in the analysis was 1.6 (SD 0.8, range 0.6–4.0), which corresponds to GPS error of 4.0 m (SD 2.0, range 1.5–10 m).

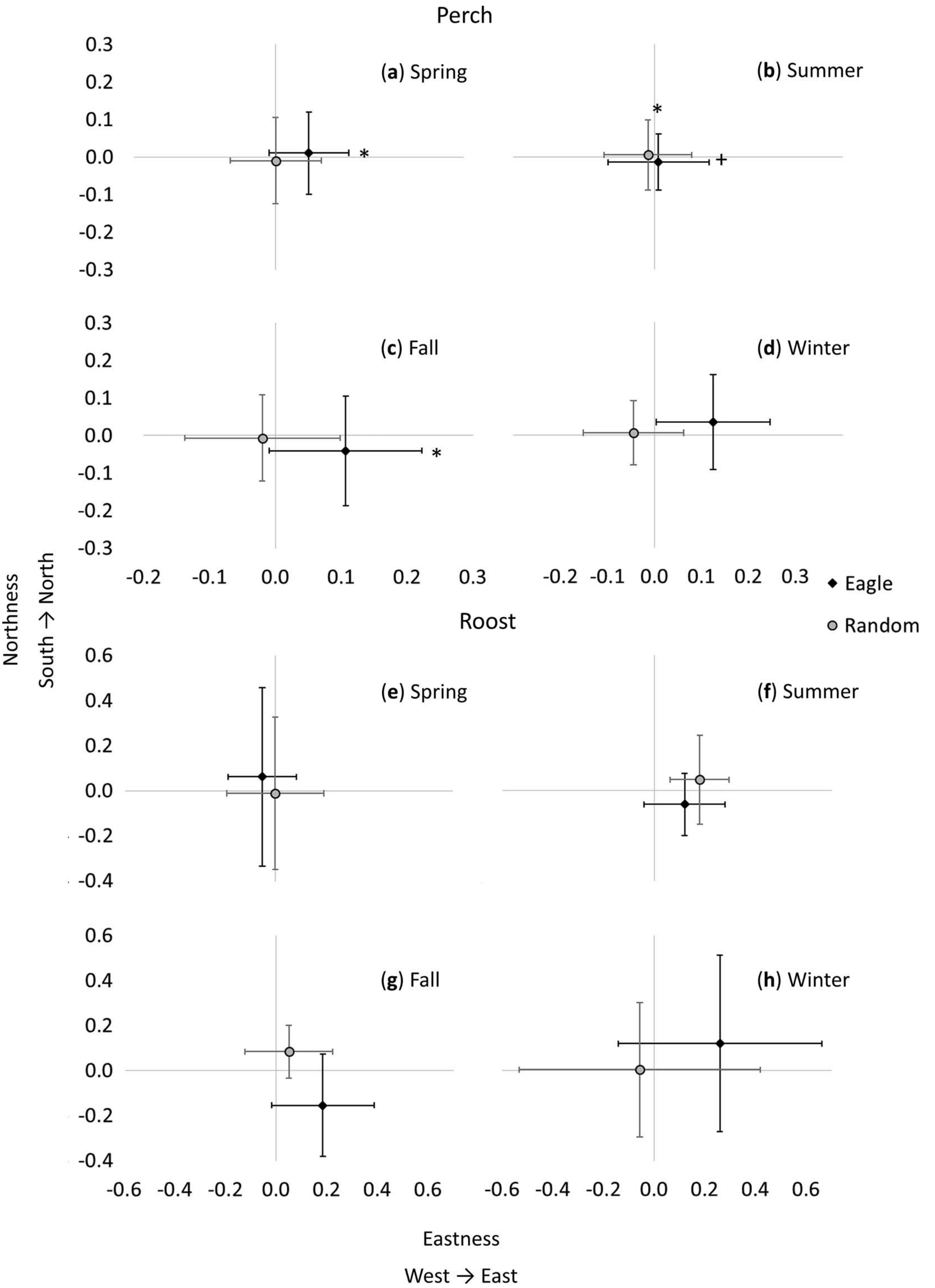
We identified 47,067 perch locations collected between February 2009 and March 2015 (Fig. 1). Of these perch locations, 52% were from adults, and 21% from spring, 49% from summer, 13% from fall, and 17% from winter. We recorded 855 (SD 1,017, range 9–3,968) perch locations for each eagle, or ~2.1 perch locations per eagle-day.

We also identified 1,618 roost locations from the 12 eagles whose transmitters functioned at night. Most roost locations (75%) were from subadult eagles, and 22% were from spring, 43% from summer, 8% from fall, and 27% from winter. On average, we recorded 134 (SD 165, range 1–448) roost locations per eagle, or ~1 roost location every 5 d.

When perching, Golden Eagles (adults and subadults combined) used steep slopes (grand mean of the slope variable $>$15%; Fig. 2a) that faced eastward in spring, fall, and winter (Fig. 3a–3d). Eagles used broadleaf forests (grand mean $>$35% of locations; Fig. 4a, 4c, 4d) more than other land cover types in spring, fall, and winter, and lichen-moss most in summer (grand mean $>$70% of locations; Fig. 4b). They also used the topographic position of hillsides more than other positions throughout the year (grand mean $>$43% of locations; Fig. 5a–d).

→

Figure 3. Measures of aspect (northness and eastness) for perch (a–d) and roost (e–h) locations of Golden Eagles and random locations in spring (a and e), summer (b and f), fall (c and g), and winter (d and h) in eastern North America 2009–2015. Eagle locations are black diamonds with black error bars (1 SE), random locations are gray circles with gray error bars (1 SE), and units are radians. Measures are empirically based grand means from individual eagles and do not account for variation accounted for in case–control logistic models. Values differed between eagle and random locations (* $P < 0.05$, + $P < 0.10$) based on analyses (see Appendix 2).


Perch
(a) Spring
(b) Summer
(c) Fall
(d) Winter
Roost
(e) Spring
(f) Summer
(g) Fall
(h) Winter
Northness
South → North
Eastness
West → East
Eagle
Random
0.3
0.2
0.1
0.0
-0.1
-0.2
-0.3
0.6
0.4
-0.4
-0.6
*
+

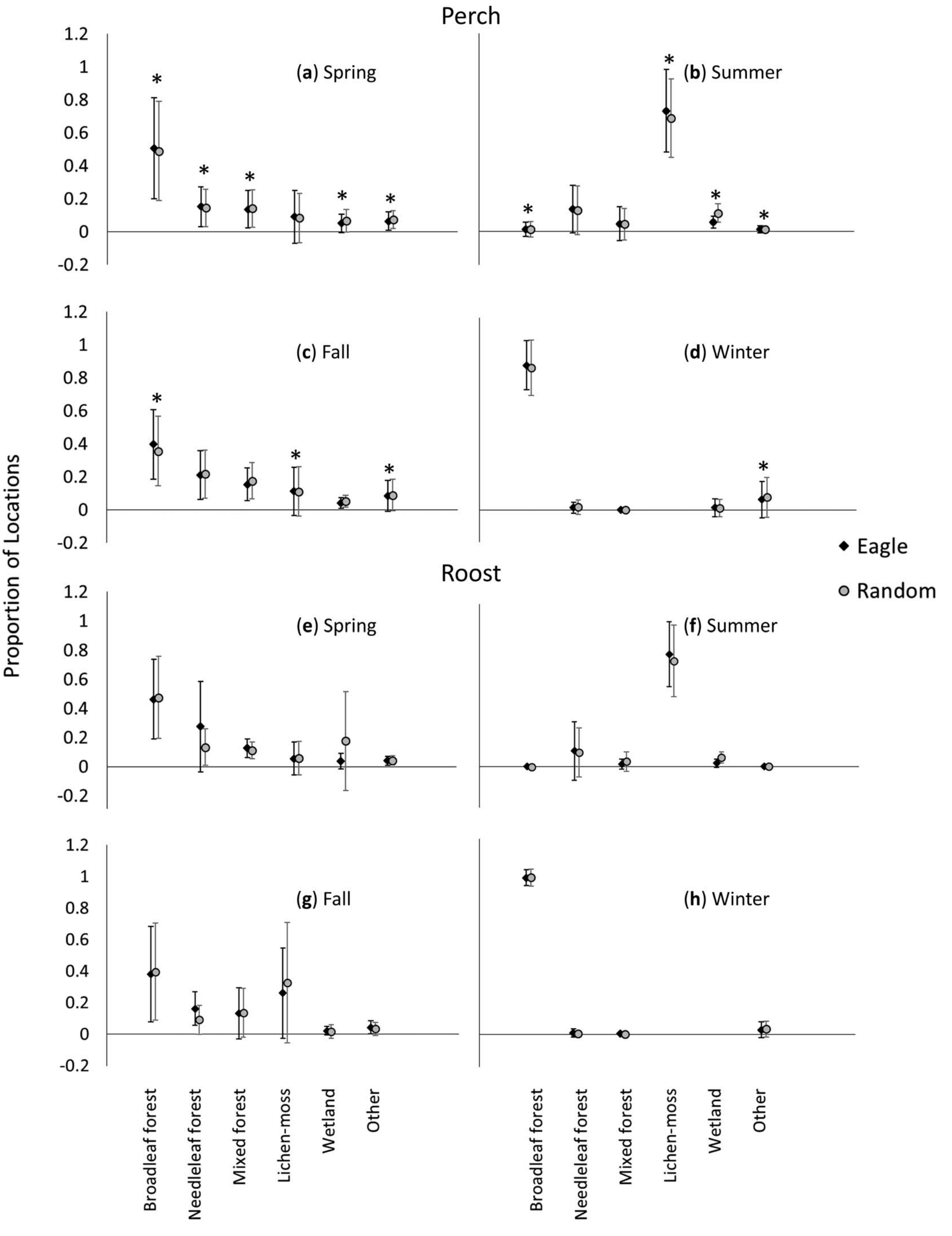


Figure 4. Proportion of land cover types where perch (a–d) and roost (e–h) sites were located for Golden Eagles and random locations in spring (a and e), summer (b and f), fall (c and g), and winter (d and h) in eastern North America 2009–2015. Eagle locations are black diamonds with black error bars (1 SE), random locations are gray circles with gray error bars (1 SE). Measures are empirically based grand means from individual eagles and do not account for variation accounted for in generalized linear mixed models. *Proportion of land cover measured at any topographic position differed between eagle and random locations based on case–control logistic regression analyses (see Appendix 2).

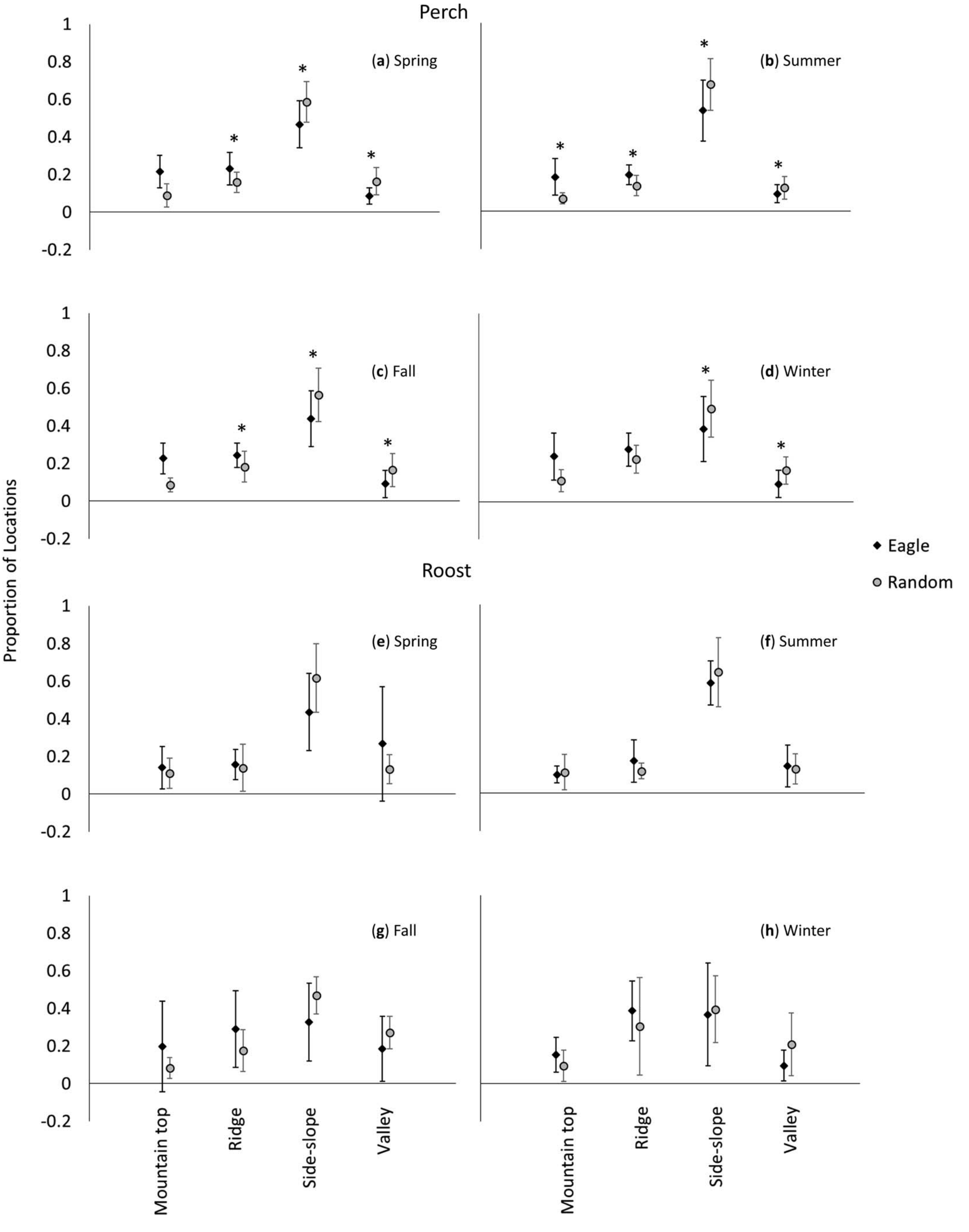


Figure 5. Proportion of topographic positions where perch (a–d) and roost (e–h) sites were located for Golden Eagles and random sites in spring (a and e), summer (b and f), fall (c and g), and winter (d and h) in eastern North America 2009–2015. Eagle locations are black diamonds with black error bars (1 SE), random locations are gray circles with gray error bars (1 SE). Measures are empirically based grand means from individual eagles and do not account for variation accounted for in case–control logistic regression models. *Proportion of topographic position measured at any land cover differed between eagle and random locations analyses (see Appendix 2).

When roosting, Golden Eagles (adults and subadults combined) used steep slopes (grand mean of the slope variable >14%; Fig. 2b) that faced eastward in summer, fall, and winter (Fig. 3e–h). Eagles used broadleaf forests (grand mean >38% of locations; Fig. 4a, 4c, 4d) more than other land cover types in spring, fall, and winter and lichen-moss most in summer (grand mean >83% of locations; Fig. 4b). They also used the topographic position of hillsides more than other positions throughout the year (grand mean >33% of locations; Fig. 5e–h).

Perch-site selection

Most characteristics of perch sites that Golden Eagles selected differed among the 4 seasons. Common factors that eagles selected for perch sites included eastness, slope, topographic position, and the interactions of land cover and topographic position (Table 1). In most seasons, the odds of eagles using a site increased the steeper it was (slope; Fig. 2) and the more it faced toward the east (eastness; Fig. 3), and decreased for the land cover type identified as "other" (Fig. 4). Eagle selection for perches associated with the other explanatory variables we evaluated was not consistent among seasons.

Odds of eagles using perch sites in spring increased as slopes became steeper (log odds = 0.096), the more they faced eastward (0.14), and if they were located in lichen-moss on hillsides (0.622; Table 1, Fig. 2a, 3a, 4a, 5a, Appendix Table A2). Odds of use decreased for 4 land-cover types located in valleys: needleleaf forests (–0.725), broadleaf forests (–1.073), mixed forests (–1.134), and the other land cover type (–0.960). Odds of use also decreased for "other" areas, both on hillsides (–1.618) on ridges (–1.061).

Odds of Golden Eagles using summer perch sites increased as slopes became steeper (0.100), the more they faced south (–0.086, northness) and in wetlands located on ridges (1.171; Table 1, Fig. 2a, 3b, 4b, 5b, Appendix Table A3). Odds of use also increased for valleys, hillsides, and ridges both in broadleaf forests (1.445–1.838) and in lichen-moss (0.733–1.164), but decreased on mountain tops located in both broadleaf forests (–1.925) and lichen-moss (–1.002). Odds of an adult using a site for perching increased in broadleaf forests (0.945) and decreased in valleys (–0.627), on hillsides (–0.474), and on ridges (–0.274) relative to odds of subadult use.

During fall migration, odds of eagles using a site for perching increased as slopes became steeper (0.085), as they faced more eastward (0.228), and for lichen-moss areas located on hillsides (0.752; Table 1, Fig. 2a, 3c, 4c, 5c, Appendix Table A4). Odds of an eagle perching decreased in broadleaf forests in valleys (–1.316) and in other land cover types in both valleys (–1.182) and hillsides (–1.983). Adult eagles had greater odds of perching on ridges (0.437) than did subadult eagles.

The only evidence that Golden Eagle selection of perches during winter responded to any of the factors that we examined was that odds of use decreased for "other" land-cover types in both valleys (–1.251) and hillsides (–1.699; Table 1, Fig. 2a, 3d, 4d, 5d, Appendix Table A5).

Roost-site selection

There was only one characteristic that we identified that influenced odds of use of roost sites by Golden Eagles (Table 1, Fig. 2–5, Appendix Tables A6–A9). Odds of roosting at a site increased as slope increased during spring (log odds = 0.113). That said, patterns in the comparison between roost-sites used by eagles and random locations were similar to patterns for perch locations.

Discussion

Analyses of habitat selection are often season- and region-specific and typically behavior-agnostic. Here, by following individuals across seasons and regions, and by separately characterizing selection for perch and roost sites, we were able to provide unusual insight into the behavior of a conservation-dependent species. These analyses have particular value because eastern Golden Eagles occupy a heavily impacted region where the population appears to be stable or growing.

There are numerous potential drivers and associated behaviors for both perch and roost selection for birds. For example, prey availability and energy demands are likely drivers of hunting and feeding behaviors and protection from predators, conspecifics, or weather are possible drivers of site selection for preening, resting, sleeping, or

Table 1. Chi-square tests for Type III fixed effects from generalized linear mixed models used to determine factors associated with selection of perch or roost sites by Golden Eagles in eastern North America, 2009–2015. $P < 0.05$ are in **bold**, $P < 0.10$ are underlined.

Season	Behavior	Statistic	Northness	Eastness	Slope	Age	Land cover	Topographic position	Age × land cover	Age × topographic position	Land cover × topographic position
Perch	Spring	χ^2	2.7161	25.5745	2032.08	1.4471	8.9477	50.1985	2.9206	3.4831	62.8081
		df	1	1	1	1	5	3	5	3	15
		P	0.099	**<0.001**	**<0.001**	0.229	0.111	**<0.001**	0.712	0.323	**<0.001**
	Summer	χ^2	25.5899	2.8839	4302.78	0.0008	26.86	37.6744	6.9967	41.1233	88.4148
		df	1	1	1	1	5	3	5	3	15
		P	**<0.001**	0.090	**<0.001**	0.977	**<0.001**	**<0.001**	0.221	**<0.001**	**<0.001**
	Fall	χ^2	2.2884	43.4688	1046.88	2.2443	8.8013	53.6518	13.0134	7.4589	42.914
		df	1	1	1	1	5	3	5	3	15
		P	0.130	**<0.001**	**<0.001**	0.134	0.117	**<0.001**	**0.023**	0.059	**<0.001**
	Winter	χ^2	0	0	0	0.1797	2.5144	33.8658	0.4806	0.1443	16.0418
		df	0	0	0	1	4	3	4	1	12
		P	–	–	–	0.672	0.642	**<0.001**	0.975	0.704	0.189
Roost	Spring	χ^2	0.4069	1.7731	82.8908	0	1.2697	1.1502	7.4462	3.3499	8.9699
		df	1	1	1	0	5	3	4	3	14
		P	0.524	0.183	**<0.001**	–	0.938	0.765	0.114	0.341	0.833
	Summer	χ^2	0	0	0	0	0.0001	0.0004	1.0033	4.5273	1.1599
		df	0	0	0	0	3	1	5	3	6
		P	–	–	–	–	1.000	0.984	0.962	0.210	0.979
	Fall	χ^2	0	0	0	0	1.0439	1.5767	0.4618	0	0.6669
		df	0	0	0	1	3	2	1	0	5
		P	–	–	–	0.999	0.791	0.455	0.497	–	0.985
	Winter	χ^2	0	0	0	0	1.0439	1.5767	0.4618	0	0.6669
		df	0	0	0	1	3	2	1	0	5
		P	–	–	–	0.999	0.791	0.455	0.497	–	0.985

nesting behaviors. Our insight was limited to potential drivers for use of stationary locations and not associated behaviors. Further, data were not available to assess drivers such as prey availability or other measures that would describe fourth-order selection. Despite these limitations, the patterns that we did detect provide important insight into the drivers of perch- and roost-site selection.

Perch-site selection

During both spring and fall migration, Golden Eagles selected perch sites that likely provided both protection from prevailing winds and access to thermal updrafts. Evidence for these patterns comes from selection of steep slopes with east-facing aspects. East-facing slopes would be well protected from prevailing winds that come from the southwest in fall and northwest in spring (Duerr et al. 2015). Likewise, east-facing slopes are exposed to solar radiation earlier in the day and thermals could develop earlier there than anywhere else. In contrast, eagles did not select perch locations along the windward side of hills where orographic updrafts form and they avoided areas where updraft development was less likely to occur (forested valleys; Reichmann 1978). Selection for these characteristics indicates that eagles are seeking both protection from thermal extremes and minimization of energetic expenditures associated with takeoff (the most energetically demanding part of flight; Dial and Biewener 1993, Rayner and Swaddle 2000).

Golden Eagles establish seasonal home ranges during summer and winter (Miller et al. 2017) and their perching behavior during these periods was distinct from that during migratory seasons. During summer, Golden Eagles selected steep slopes that faced southward. These slopes both face prevailing winds (from the southwest) and are exposed to solar radiation throughout the day. Therefore, instead of seeking shelter from wind as they do during migration, during summer eagles appeared to have selected perch sites where both thermal and orographic updrafts could form. Such selection suggests that during the breeding season the birds are placing a priority on reducing the energetic demands of taking flight.

In contrast to summer, during winter eagles selected perch sites on steep slopes that faced eastward and away from prevailing southwest winds. As such, selection of these perch sites should provide eagles with the greatest possible thermal protection. This suggests that during the coldest part of the year, these birds are making perching decisions primarily based on thermal constraints and somewhat less on the energetics associated with flight. However, even under thermal constraints, flight energetics are not completely ignored. In addition to proximity to thermal development, the consistent use of steep slopes would allow these birds to get airborne more easily than under similar weather conditions over flatter terrain.

Roost-site selection

Although we were able to detect patterns in perch-site selection, our analyses of roost-site selection by Golden Eagles detected selection for relatively few characteristics. In fact, selection for steep slopes during spring migration was the only roost-site selection we detected. Although it is difficult to interpret this single statistical pattern, the trend implies a motivation to reduce the energetic costs of takeoff, as was the case for perch-site selection during several seasons.

We interpret the general lack of statically relevant patterns in the roost-site data in 2 ways. Most likely, our results suggest that the drivers for selection of roosting sites are different from those at perching sites and that the specific fixed effects we modeled, or their spatial scale, failed to capture the nuance of this selection. Diurnal animals likely require greater protection from predators or inclement weather at night than they do during daytime. Such protection could come from vegetation, terrain, or other characteristics that either we did not measure or would have to be measured at finer scales (e.g., fourth-order selection described below). For example, determining which roosting-site characteristics eagles select likely would require comparing habitat features measured directly at roost and random sites by visiting specific roost trees.

It is possible that our sample size for analysis of roost-site selection ($n = 12$ birds and 1,618 roost locations) and uneven sampling by age (75% of locations from subadults) reduced our ability to detect patterns in these data. This is especially possible given the massive extent of our study area and the immense topographic and landscape variation it contains. The smaller sample of roosting sites certainly contained more bias and less consistent sampling across ecotypes than did the larger perch dataset ($n = 55$ birds and 47,067 perch locations) for which we were able to detect strong patterns. Thus, our analysis is only a first step in characterizing roost-site selection for this species.

Influences on perch- and roost-site selection

Habitat selection by animals is evaluated as a hierarchical process (Johnson 1980), with first-order selection of a geographic range or landscape, second-order selection of a home range within the landscape, third-order selection of conditions within the home range (e.g., stand of trees used for roosting), and fourth-order selection within the stand (e.g., specific tree or tree branch). We focused our analyses at the third-order of selection within the larger home range that the animals select (recognizing that migrating eagles do not have a "home range," sensu stricto). Selection of perch and roost sites occurs after home ranges are selected (the third-order selection is conditional upon second-order selection) and before a specific tree branch or landing spot is occupied (fourth-order selection). At the third-order scale, we were able to detect biologically relevant patterns in perch-site selection.

Golden Eagles perched and roosted predominantly in forested areas in fall (76% of perch and 68% of roost sites), winter (92% and 97%), and spring (79% and 86%). That said, Golden Eagles also showed some preferences for certain open cover types. In particular, eagles selected perch sites in the lichen-moss cover type in spring (9% of perch sites), summer (73%), and fall (11%). These patterns generally agree with prior work (e.g., Miller et al. 2017) that suggested Golden Eagles in eastern North America respond to an interplay of open and forested land cover types. This is relevant because throughout other parts of their circumpolar distribution, Golden Eagles are thought to use predominantly open environments without extensive forest cover (Marzluff et al. 1997, Watson 2010, Braham et al. 2015; but see Singh et al. 2016). Open areas probably provide eagles with food, updrafts, and winds that drive away biting insects (Rohner et al. 2000). In eastern North America, the Golden Eagles we studied were reliably catholic in their selection of particular types of open areas, avoidance of others (cover type "other"), and use of forested cover as an important perching resource.

Age also influenced perch-site selection by eagles. In particular, in fall, adult eagles showed a relatively greater preference for perching on ridgelines where orographic updrafts occur. Orographic updraft is an important resource for eagles that is especially used early and late in the day (Katzner et al. 2015, Murgatroyd et al. 2018). As such, perching close to this resource means eagles can use it more readily, and this pattern is consistent with past evidence suggesting that, in fall, adults migrate more efficiently and more frequently with orographic updraft than do subadults (Duerr et al. 2015, Rus et al. 2017). Finally, as compared to subadults, adults also showed preference for perching in broadleaf forests in summer. Adult Golden Eagles use smaller home ranges with more open areas during the summer than do subadults (Miller et al. 2017); therefore, they likely were limited to perch sites in the broadleaf forests that occurred within their home ranges. Subadults, in contrast, range over larger areas and were likely less constrained in their choice of perch site.

We did not find differences in perch- or roost-site selection that reflected age-specific migration strategies in spring. This is despite the fact that past work has shown that, during both spring and fall migration, adult Golden Eagles in eastern North America use different environmental resources (weather conditions and updrafts) than do subadults (Duerr et al. 2015, Rus et al. 2017). This suggests that, despite using different flight strategies, selection of perch sites that promote access to thermal updrafts likely is an optimal strategy regardless of season. This makes sense because we know that thermal soaring and gliding is more efficient than orographic soaring (Duerr et al. 2012) and thus it may benefit a bird to be near thermal updraft whenever possible.

Conclusions

By focusing on 2 distinct but related behaviors, we have shown the degree to which perch- and roost-site selection by Golden Eagles differed across spatial and temporal scales. Tracking these patterns across variation at such large scales allowed us to identify some behaviors that were consistent across space and time (use of steep slopes, for example) and others that varied seasonally (access to thermal protection and updraft). These patterns are relevant because the landscape used by Golden Eagles in eastern North America is undergoing change, with afforestation occurring through the northern portion of their range and infrastructure (wind and gas pipeline) development occurring through the southern portion (Katzner et al. 2012a). This population of eastern Golden Eagles is small (Katzner et al. 2012a; Dennhardt et al. 2015, 2017) and its conservation is likely to be improved if characteristics of perch and roost sites are considered in habitat conservation planning.

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Appendix 1.

Table A1. Land-cover classes within the range of Golden Eagles in eastern North America defined by the North American Land Cover Database (CEC 2010). We used combined classes for analysis of resource selection functions for perching and roosting sites of Golden Eagles.

North American land-cover classes	Combined classes
Temperate or sub-polar needleleaf forest[a]	Needleleaf forest
Sub-polar taiga needleleaf forest	Needleleaf forest
Temperate or sub-polar broadleaf deciduous forest	Broadleaf forest
Mixed forest	Mixed forest
Temperate or sub-polar shrubland	Other
Temperate or sub-polar grassland	Other
Sub-polar or polar shrubland-lichen-moss[b]	Lichen-moss
Sub-polar or polar grassland-lichen-moss	Lichen-moss
Sub-polar or polar barren-lichen-moss	Lichen-moss
Wetland[c]	Wetland
Cropland	Other
Barren land	Lichen-moss
Urban and built up	Other
Water	Wetland

[a] Forests are dominated by tree cover taller than 3 m. For each forest type (evergreen, broadleaf, and mixed), crown cover includes at least 75% of the respective tree types.
[b] Lichen-moss vegetation types include at least 20% vegetation cover by lichen and moss, with remaining vegetation including shrubs, grasses, or barren areas.
[c] Wetlands include areas dominated by perennial vegetation that is influenced by the presence of water and areas of open water in northern forests, taiga, and tundra.

Appendix 2.

Tables A2–A9. Solutions for fixed effects from season- and behavior-specific models of habitat selection of Golden Eagles in eastern North America, 2009–2015. The response variable for each logistic model was use or availability of resources at a location defined by eagle and random locations, respectively. Effects of continuous and categorical variables are given in log odds (SE). Categorical variables included age (adult and subadult), topographic position (valley, hillside, ridge, and mountain top), and land cover (needleleaf forest, broadleaf forest, mixed forest, lichen-moss area, wetland, and other area). Reference categories were subadult age, mountain top, and other land cover type. Values differed between eagle and random locations (* $P < 0.05$, + $P < 0.10$) as identified in global tests (Table A2).

We have arranged results in a way that combines main effects and interaction effects from each model to improve clarity. When a factor was included without any interactions, it is listed as a single effect (except age, below). If a factor was included in an interaction term, it is listed under combined effects. The combined effects for the reference category of land cover type are the main effects for the reference topographic position of mountain top (i.e., main effects for valley, hillside, and ridge) and vice versa. Age was included as an interaction with both land cover and topographic position, so the effect is for the adult age. The main effect of age represents adults on mountain tops and in other areas, thus the main effect for adult age represents adult age at both the reference categories of mountain top and the other land cover type. We mark cells that were never estimated as N/A (not applicable) to differentiate them from other factors that were not estimable due to lack of degrees of freedom (blank).

Table A2. Spring perch.

Single effects							
Adult age	−0.454 (0.377)[a]						
Northness	−0.045 (0.027)						
Eastness	0.140 (0.028)*						
Slope	0.096 (0.002)*						
Combined effects	Adult age	Needleleaf forest	Broadleaf forest	Mixed forest	Lichen-moss	Wetland	Main effect[b]
Adult age	N/A	0.308 (0.243)	0.376 (0.237)	0.251 (0.246)	0.322 (0.295)	0.245 (0.278)	N/A
Valley	−0.001 (0.157)	−0.725 (0.325)*	−1.073 (0.311)*	−1.134 (0.340)*	0.039 (0.325)	−1.254 (0.661)	−0.960 (0.288)*
Hillside	0.181 (0.131)	0.056 (0.259)	−0.045 (0.244)	−0.385 (0.269)	0.622 (0.258)*	−0.770 (0.601)	−1.618 (0.230)*
Ridge	0.181 (0.137)	0.233 (0.285)	0.159 (0.264)	−0.293 (0.295)	0.489 (0.281)	0.103 (0.690)	−1.061 (0.249)*
Main effect[c]	N/A	0.048 (0.268)	0.050 (0.259)	0.405 (0.275)	−0.230 (0.285)	0.744 (0.606)	N/A

[a] Main effect for adult age—represents the effect of adult age for reference categories of land cover and topographic position.
[b] Main effect for topographic position—represents effects for the reference land cover category (other).
[c] Main effect for land cover—represents effects for the reference topographic position (mountain top).
* $P < 0.05$.
+ $P < 0.10$

Table A3. Summer perch.

Single effects							
Adult age	−0.010 (0.360)[a]						
Northness	−0.086 (0.017)*						
Eastness	0.032 (0.019)[+]						
Slope	0.100 (0.002)*						
Combined effects	Adult age	Needleleaf forest	Broadleaf forest	Mixed forest	Lichen-moss	Wetland	Main effect[b]
Adult age	N/A	0.574 (0.298)	0.945 (0.416)*	0.401 (0.326)	0.514 (0.297)	0.515 (0.309)	N/A
Valley	−0.627 (0.108)*	0.658 (0.414)	1.838 (0.580)*	0.451 (0.448)	1.164 (0.405)*	0.536 (0.540)	−1.897 (0.408)*
Hillside	−0.474 (0.090)*	0.366 (0.291)	1.623 (0.419)*	0.475 (0.320)	0.862 (0.281)*	0.037 (0.444)	−1.622 (0.283)*
Ridge	−0.274 (0.096)*	0.339 (0.313)	1.445 (0.456)*	0.265 (0.349)	0.733 (0.302)*	1.171 (0.492)*	−1.055 (0.306)*
Main effect[c]	N/A	−0.653 (0.350)	−1.925 (0.471)*	−0.537 (0.383)	−1.002 (0.341)*	−0.840 (0.483)	N/A

[a] Main effect for adult age—represents the effect of adult age for reference categories of land cover and topographic position.
[b] Main effect for topographic position—represents effects for the reference land cover category (other).
[c] Main effect for land cover—represents effects for the reference topographic position (mountain top).
* $P < 0.05$.
+ $P < 0.10$.

Table A4. Fall perch.

Single effects	
Adult age	−0.592 (0.395)[a]
Northness	−0.052 (0.035)
Eastness	0.228 (0.035)*
Slope	0.085 (0.003)*

Combined effects	Adult age	Needleleaf forest	Broadleaf forest	Mixed forest	Lichen-moss	Wetland	Main effect[b]
Adult age	N/A	0.379 (0.300)	0.408 (0.314)	0.112 (0.310)	0.516 (0.454)	−0.390 (0.364)	N/A
Valley	0.188 (0.189)	−0.548 (0.400)	−1.316 (0.395)*	−0.787 (0.420)	−0.254 (0.487)	−1.822 (0.995)	−1.182 (0.379)*
Hillside	0.271 (0.161)+	0.399 (0.323)	−0.207 (0.317)	0.234 (0.335)	0.752 (0.379)*	−1.105 (0.936)	−1.983 (0.308)*
Ridge	0.437 (0.164)*	−0.308 (0.361)	−0.423 (0.349)	−0.323 (0.381)	−0.158 (0.412)	−1.855 (1.030)	−0.637 (0.341)
Main effect[c]	N/A	−0.278 (0.355)	0.172 (0.356)	−0.136 (0.360)	−0.631 (0.465)	1.593 (0.942)	N/A

[a] Main effect for adult age—represents the effect of adult age for reference categories of land cover and topographic position.
[b] Main effect for topographic position—represents effects for the reference land cover category (other).
[c] Main effect for land cover—represents effects for the reference topographic position (mountain top).
* $P < 0.05$.
+ $P < 0.10$.

Table A5. Winter perch.

Single effects	
Adult age	0.138 (0.326)[a]
Northness	0.134 (0)
Eastness	0.353 (0)
Slope	−0.001 (0)

Combined effects	Adult age	Needleleaf forest	Broadleaf forest	Mixed forest	Wetland	Main effect[b]
Adult age	N/A	0.268 (0.493)	−0.038 (0.209)	13.259 (751.848)	−12.594 (266.176)	N/A
Valley	−0.050 (0.131)	−1.296 (0.918)	−0.339 (0.526)	−4.888 (58.174)	−0.700 (1.195)	−1.251 (0.524)*
Hillside	−0.232 (0)	−0.518 (0.767)	0.490 (0.465)	2.774 (1.929)	0.200 (1.043)	−1.699 (0.465)*
Ridge	−0.144 (0)	−0.499 (0.813)	0.013 (0.507)	1.438 (1.772)	14.633 (1158)	−0.559 (0.507)
Main effect[c]	N/A	0.588 (0.763)	0.073 (0.467)	−1.658 (1.470)	0.332 (1.009)	N/A

[a] Main effect for adult age—represents the effect of adult age for reference categories of land cover and topographic position.
[b] Main effect for topographic position—represents effects for the reference land cover category (other).
[c] Main effect for land cover—represents effects for the reference topographic position (mountain top).
* $P < 0.05$.
+ $P < 0.10$.

Table A6. Spring roost.

Single effects	
Adult age	
Northness	−0.098 (0.153)[a]
Eastness	0.205 (0.154)
Slope	0.113 (0.012)*

Combined effects	Adult age	Needleleaf forest	Broadleaf forest	Mixed forest	Lichen-moss	Wetland	Main effect[b]
Adult age	N/A	3.130 (3.861)	2.150 (3.839)	0.146 (3.786)		2.831 (4.075)	N/A
Valley	−1.509 (0.947)	−2.181 (2.978)	−1.945 (2.983)	−0.866 (3.133)	−3.019 (3.304)		1.330 (2.948)
Hillside	−1.044 (0.833)	0.550 (2.022)	0.262 (2.035)	1.629 (2.155)	−1.177 (2.369)	1.527 (2.711)	−0.959 (2.001)
Ridge	−0.136 (0.881)	1.322 (2.394)	1.583 (2.353)	1.254 (2.562)	0.051 (2.757)	1.731 (3.086)	−1.102 (2.310)
Main effect[c]	N/A	−0.775 (1.727)	−0.533 (1.808)	−0.681 (1.854)	0.155 (2.300)	−2.266 (2.648)	N/A

[a] Main effect for adult age—represents the effect of adult age for reference categories of land cover and topographic position.
[b] Main effect for topographic position—represents effects for the reference land cover category (other).
[c] Main effect for land cover—represents effects for the reference topographic position (mountain top).
* $P < 0.05$.
+ $P < 0.10$.

Table A7. Summer roost.

Single effects	
Adult age	
Northness	−0.264 (0)[a]
Eastness	0.250 (0)
Slope	0.050 (0)

Combined effects	Adult age	Needleleaf forest	Broadleaf forest	Mixed forest	Lichen-moss	Wetland	Main effect[b]
Adult age	N/A	48.314 (2,937.000)	80.888 (3,996.000)	63.023 (2,539)	48.189 (5,257)	2.508 (3,402)	N/A
Valley	−0.115 (1.510)	−17.685 (754.968)	−1.495 (69.368)	−2.952 (69.349)	−1.311 (69.369)	−4.514 (1,488)	1.396 (69.361)
Hillside	−1.007 (1.475)	−1.141 (671.697)	16.878 (0)	14.158 (0)	16.099 (0)	−0.967 (1,018)	−16.704 (0)
Ridge	−2.766 (1.555)	16.836 (2,616.000)	19.499 (0)	19.545 (0)	17.051 (0)		−16.269 (0)
Main effect[c]	N/A	1.273 (671.695)	−15.504 (0)	−15.187 (0)	−32.695 (3,681)	0.182 (1,018)	N/A

[a] Main effect for adult age—represents the effect of adult age for reference categories of land cover and topographic position.
[b] Main effect for topographic position—represents effects for the reference land cover category (other).
[c] Main effect for land cover—represents effects for the reference topographic position (mountain top).
* $P < 0.05$.
+ $P < 0.10$.

Table A8. Fall roost.

Single effects	
Adult age	−17.04 (8,998)[a]
Northness	0.476 (0)
Eastness	0.767 (0)
Slope	0.008 (0)

Combined effects

	Adult age	Needleleaf forest	Broadleaf forest	Mixed forest	Lichen-moss	Wetland	Main effect[b]
Adult age	N/A		17.636 (8,998)		0 (0)	0 (0)	N/A
Valley	0.064 (0)				0 (0)	0 (0)	−0.908 (0)
Hillside	−0.181 (0)	18.135 (9,012.000)	1.080 (1.467)	17.704 (9,016)	0 (0)	0 (0)	−1.852 (1.475)
Ridge	−0.444 (0)	0.071 (12,709.000)	18.238 (8,991.000)		0 (0)	0 (0)	−18.135 (8,991.000)
Main effect[c]	N/A	−0.682 (2.243)	−0.862 (1.406)	0.389 (2.037)	0 (0)	0 (0)	N/A

[a] Main effect for adult age—represents the effect of adult age for reference categories of land cover and topographic position.
[b] Main effect for topographic position—represents effects for the reference land cover category (other).
[c] Main effect for land cover—represents effects for the reference topographic position (mountain top).
* $P < 0.05$.
+ $P < 0.10$.

Table A9. Winter roost.

Single effects	
Adult age	−17.04 (8,998.000)[a]
Northness	0.476 (0)
Eastness	0.767 (0)
Slope	0.008 (0)

Combined effects

	Adult age	Needleleaf forest	Broadleaf forest	Mixed forest	Wetland	Main effect[b]
Adult age	N/A		17.636 (8,998.000)		0 (0)	N/A
Valley	0.064 (0)				0 (0)	−0.908 (0)
Hillside	−0.181 (0)	18.135 (9,012.000)	1.08 (1.467)	17.704 (9,016)	0 (0)	−1.852 (1.475)
Ridge	−0.444 (0)	0.071 (12,709.000)	18.238 (8,991.000)		0 (0)	−18.135 (8,991)
Main effect[c]	N/A	−0.682 (2.243)	−0.862 (1.406)	0.389 (2.037)	0 (0)	N/A

[a] Main effect for adult age—represents the effect of adult age for reference categories of land cover and topographic position.
[b] Main effect for topographic position—represents effects for the reference land cover category (other).
[c] Main effect for land cover—represents effects for the reference topographic position (mountain top).
* $P < 0.05$.
+ $P < 0.1$.