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SATELLITE TRACKING OF BALD EAGLES IN THE UPPER MIDWEST

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ABSTRACT.—We investigated the movement ecology of Bald Eagles *(Haliaeetus leucocephalus)* that winter along the Upper Mississippi River Valley. During late autumn and winter from March 1999 through February 2006, we outfitted with satellite transmitters 14 wild-caught Bald Eagles (12 adults, 2 subadults) on a winter range or migration stopover point in southwestern Wisconsin. These birds wintered as far south as the Mississippi and Illinois rivers, northwest of St. Louis, Missouri. Summer ranges extended out from the Upper Mississippi River Valley migration corridor as far north as Arviat, Nunavut, Canada, on the western shore of Hudson Bay. Migration route fidelity was apparent, with two notable exceptions. Fidelity to summer and winter ranges also was apparent, but variable. Some eagles remained on a small range the entire season; others traveled extensively, often to the same areas in successive years. Spring migration mean start and end dates for adults were 24 February ± 23 (SD) d and 27 April ± 40 d, respectively. Eagles took from 6–151 d to reach their summer ranges (mean: 67 ± 48 d). Mean start and end dates for autumn migration were 21 October ± 28 d and 11 December ± 16 d, respectively; travel duration ranged from 15–77 d (mean: 51 ± 20 d). Individual mean straight-line distances between core winter and summer ranges ranged from 611–2222 km (mean: 1655 ± 526 km). Our study provided new information on Bald Eagle movement ecology in a vast region where such knowledge was previously lacking. Compared to other tracking studies of Bald Eagles, our study documented greater variation in migration timing and duration, but similar range and route fidelity and distances traveled.

KEY WORDS: *Bald Eagle*; Haliaeetus leucocephalus; *satellite telemetry*; *migration*; *Mississippi River*; *summer range*; *winter range*.

RASTREO SATELITAL DE *HALIAEETUS LEUCOCEPHALUS* EN EL MEDIO OESTE SUPERIOR

RESUMEN.—Investigamos la ecología de movimiento de individuos de *Haliaeetus leucocephalus* que invernan a lo largo del Valle Superior del Río Mississippi. Durante el otoño tardío y el invierno de marzo de 1999 hasta febrero de 2006, equipamos con transmisores satelitales a 14 individuos silvestres de *H. leucocephalus* atrapados (12 adultos, 2 subadultos) en un área de invernada o en puntos de parada de migración en el sudoeste de Wisconsin. Estas aves invernaron hacia el sur hasta los ríos Mississippi e Illinois, al noroeste de St. Louis, Missouri. La distribución durante el verano se extendió desde el corredor migratorio del Valle Superior del Río Mississippi hacia el norte hasta Arviat, Nunavut, Canadá, en la costa oeste de la Bahía de Hudson. La fidelidad a la ruta de migración fue evidente, con dos excepciones notables. La fidelidad a las distribuciones de verano e invierno también fue evidente, pero variable. Algunas águilas permanecieron en un área pequeña durante toda la estación; otras viajaron considerablemente, a menudo a las mismas áreas en años consecutivos. Las fechas medias de comienzo y finalización de la migración de primavera fueron 24 de febrero ± 23 (DE) días y 27 de abril ± 40 días, respectivamente. A las águilas les tomó 6–151 días llegar a

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sus áreas de verano (media: 67 ± 48 días). Las fechas medias para el comienzo y finalización de la migración de otoño fueron 21 de octubre ± 28 días y 11 de diciembre ± 16 días, respectivamente. La duración del viaje varió entre 15–77 días (media: 51 ± 20 días). Las distancias medias en línea recta individuales entre las áreas núcleo de invierno y verano oscilaron entre 611–2222 km (media: 1655 ± 526 km). Nuestro estudio brindó nueva información acerca de la ecología de movimiento de *H. leucocephalus* en una vasta región para la que faltaba este conocimiento. Comparado con otros estudios de rastreo de *H. leucochephalus*, el nuestro documentó una mayor variación en el tiempo y duración de la migración, pero una similitud con respecto a áreas, fidelidad de rutas y distancias recorridas.

[Traducción del equipo editorial]

The Mississippi River serves as a major migration corridor for numerous avian species, including Bald Eagles (*Haliaeetus leucocephalus*), which use the upper reach of the river corridor for breeding, migration, and wintering. In autumn and early winter, several thousand Bald Eagles migrate south through geographical concentration points such as Eagle Valley Nature Preserve (EV) along the Mississippi River in southwestern Wisconsin (Mandernack and McKay 1997, Mandernack et al. 2011) and Hawk Ridge near Duluth, Minnesota, at the western tip of Lake Superior. Standardized autumn migration counts at these two sites consistently have recorded the highest numbers of Bald Eagles in North America (see annual flyway reports in *Hawk Migration Studies* 1992–2010). Wintering eagles concentrate from St. Paul, Minnesota, south to St. Louis, Missouri, along the Upper Mississippi River where food and protected winter roost sites are available, such as at EV. In this region, northward migration back to summer ranges occurs from late January into April. Early studies in North America used band returns, color marking, and conventional VHF radio transmitters to document Bald Eagle migration in Illinois (Southern 1964), Saskatchewan (Gerrard et al. 1978), Maryland (Buehler et al. 1991), Colorado (Harmata and Stahlecker 1993, Harmata 2002), Texas (Mabie et al. 1994), Montana (McClelland et al. 1994), and more recently in south-central Wisconsin along the Wisconsin River (Hall 2005).

With the advent of satellite-received tracking devices, information on Bald Eagle movements proliferated rapidly. Studies have focused on tracking juveniles dispersing from natal areas in Labrador and southern Ontario, Canada (Laing et al. 2005, Allair 2010), and on the Channel Islands of California (Dooley et al. 2005). Other researchers tracked eagles of various ages in New York (P. Nye pers. comm.) and from wintering areas in central California (Linthicum 2003, Linthicum et al. 2007), and adults from a winter range in Washington (Watson and Pierce 1998, 2001). Grubb et al. (1994) tracked one third-year female from Michigan for 4 mo.

In this study, we used satellite transmitters primarily on adult eagles to learn more about migration routes and summer areas selected by potential breeders wintering in this region. Our objectives were to identify summer and winter ranges and migration routes between those ranges. We also examined fidelity and mobility on ranges, duration and distance of spring and autumn migration, and route use on northbound versus southbound migration.

METHODS

Eagle Valley Nature Preserve is a private preserve with a 100-m deep, protected valley used by Bald Eagles during winter as a traditional, communal night-roost site. The site provides overwintering eagles with old-growth roost trees, shelter from harsh weather, solitude, and protection from disturbance. Food sources are available at ice-free areas on the adjacent Mississippi River, as well as at numerous inland sites where various forms of carrion typically are available (e.g., from livestock production, hunting, and trapping).

From November through March of 1999–2002 and 2004–06, we trapped Bald Eagles using a rocket net (Grubb 1988, 1991) or snare (Hertog 1987) baited with mammal carcasses (hog, road-killed deer, and/or trapped beaver) in an agricultural field 4 km east of EV, where eagles traditionally feed on carrion. After we caught an eagle, an experienced handler secured the bird and placed a falconry hood over the bird's head. We took a blood sample from the brachial vein of some birds for use in a concurrent study of lead contamination. We attached a standard U.S. Geological Survey aluminum leg band and measured wing chord, tail length, tarsus width, and bill depth to determine sex (Garcelon et al. 1985).

We fitted eagles with PTTs (10 manufactured by Microwave Telemetry [Columbia, Maryland], and four by North Star Science and Technology [Baltimore, Maryland]) attached using a backpack-style

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Table 1. Types of satellite transmitters used and the tracking periods and durations (mo) for Bald Eagles tracked between 1999 and 2007 from Eagle Valley, Wisconsin, U.S.A.

PTT #; AGE/SEX	CAPTURE DATE; END DATE	DURATION	PTT TYPE
838; Subadult/♂	2 March 1999; November 2000	21	Battery
832; Adult/♀	16 November 1999; June 2000	7	Battery
221; Adult/♂	17 November 1999; February 2003	39.5[1]	Battery
216; Adult/♂	8 December 1999; April 2001	16.5	Solar + VHF
217; Adult/♂	8 December 1999; 25 November 2006	83.5	Solar + VHF
219; Adult/♀	9 December 1999; October 2000	11	Solar + VHF
220; Adult/♀	10 December 1999; January 2000	2	Solar + VHF
365; Adult/♀	13 December 2000; June 2004	42.5	Battery
288; Adult/♂	11 January 2001; July 2003	30.5	Battery
687; Adult/♀	28 February 2002; April 2002	1.5	Solar GPS
614; Adult/♀	29 December 2004; August 2006	20	Solar + VHF
615; Adult/♀	11 January 2005; 14 August 2005	7	Solar + VHF
	Restarted 9 January 2007; 19 April 2007	3.5	
945; Subadult/♂	9 February 2006; 6 April 2006	2	Solar GPS
944; Adult/♀	26 February 2006; 19 April 2006	2	Solar GPS

[1] No data received between 23 March and 12 July 2002.

harness (Kenward 1987) with Teflon ribbon (Bally Ribbon Mills, Bally, Pennsylvania) or neoprene straps (Table 1). Over the 8-yr course of the study, changes in technology allowed us to use increasingly sophisticated PTTs. Lithium-cell batteries powered five PTTs with duty cycles of 8 hr on and 2.3–11 d off. To prolong battery life, we preset multi-season duty cycles to receive more locations during migration periods and fewer during nesting and wintering periods. Duty-cycle timing was contingent on predicting capture dates and migration activity; neither was as predictable as anticipated, which led to occasional data gaps. The other nine PTTs were solar powered, which enabled year-round daily or near-daily transmissions (8–10 hr on and 18–20 hr off for six Doppler units; one GPS location every 12 hr for three GPS units). To facilitate local tracking, we coupled six of the Doppler PTTs with VHF transmitters (Table 1). The GPS units yielded locations typically accurate to within 25 m.

We received all PTT location data using the Argos (2008) data collection and processing system through CLS America (Lanham, Maryland). We sorted the data by Argos location classes and generally selected the highest quality point per duty cycle; however, we also used some lower quality locations because they provided sufficient accuracy to help define a geographic location or interpretation of movement at a regional scale. In a few cases, where multiple locations indicated obvious travel within a duty cycle, we selected more than one point to better reflect the travel pattern. We plotted the selected data and measured distances from winter to summer ranges using ArcGIS 9 (ESRI, Redlands, California). We defined the start of migration as the initiation of steady northbound (spring) or southbound (autumn) movement preceded by concentrated localized movement that delineated a winter or summer range. We considered limited movement for extended periods during migration as indicative of stopover behavior. Because much of our location data were not high-accuracy GPS quality, we did not address habitat use or home range analysis.

To remove bias of birds tracked in multiple years, we calculated median and mean values for each individual to determine overall migration timing and duration. We excluded from analyses potential winter-range arrival dates from the first year of tracking, because an eagle might have already been on its winter range prior to capture. Because our focus was tracking adult Bald Eagles, we present migration data for subadult eagles separately to render a clearer picture of adult eagle movements. We present all data as means ± SD, and frequently include median values for comparison. Where appropriate, we used *t*-tests to compare sex-specific means for timing and duration metrics; however, small sex-specific samples sizes often precluded effective statistical comparisons.

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RESULTS

Between 1999 and 2006, we trapped 72 Bald Eagles and fitted 12 adults (eight females, four males) and two subadult males (a two- and a three-year-old, as determined by plumage) with PTTs. We outfitted the subadult birds with the expectation of multiyear tracking and the possibility of assessing changes in migration behavior with age; however, neither PTT was active long enough to provide this information. The tracking periods for individual eagles ranged from 2–83.5 mo (Table 1). The overall, multiyear winter range for the 14 eagles extended along the Mississippi River Valley and its tributaries from 39°18.2′N latitude, just northwest of St. Louis, Missouri, to 44°23.7′N latitude in southeastern Minnesota/west-central Wisconsin (Fig. 1). The collective summer range expanded out from the Upper Mississippi River Valley migration corridor from 46°13.2′N latitude in northern Minnesota to 61°30.7′N latitude near the western shore of Hudson Bay in Nunavut, east into western Ontario, and west into eastern Saskatchewan (Fig. 1). The southern end of the migration corridor was relatively constricted and concentrated over the Mississippi River valley north to Minneapolis/St. Paul in Minnesota (Fig. 1). The corridor widened eastward to the western tip of Lake Superior and westward to central Minnesota, and continued to broaden as eagles spread out across summer ranges farther north.

Fidelity and Mobility. *Winter ranges.* We tracked seven adult eagles (four males, three females) for 1–6 complete winter seasons each ($n = 16$ total winter seasons) and one subadult male for one complete winter. Adults spent from 10–120 d (mean: 70 ± 36 d) on winter ranges. Females averaged 10 d longer on their winter ranges than males, but small sample sizes likely precluded demonstration of statistical significance (males: 66 ± 39 d; females: 76 ± 39 d; $t = 2.8$, df = 4, $P = 0.76$). Subadult male #838 spent 55 d on his winter range. Three eagles (females #365 and #614 and male #288) showed strong winter range fidelity and low mobility, remaining in the EV vicinity for the majority of their winter stay (Figs. 2, 3). Female #615 yielded just six winter data points in 2007, but these suggested fidelity to the same winter range used in 2005. Two other males (#216 and #217) showed some range overlap in successive winters, but their degree of mobility varied greatly among years (Fig. 4). The subadult male exhibited similar behavior. In contrast, adult male #221 used a different range during each of four winters (Fig. 5).

Summer ranges. We collected summer range data for 10 adults and one subadult eagle. We tracked five adults for at least two summers each ($n = 19$ total summer seasons). All five showed strong fidelity to summer ranges; however, mobility on summer ranges varied greatly both among eagles and sometimes among years for the same eagle. Adult male #221 restricted his activities to a small summer range each year (Fig. 5), indicating possible breeding or at least attachment to a specific summer territory. Adult male #288 (Fig. 3) and adult female #614 exhibited fidelity to a particular core area; however, interannual variation in the degree of movement to and from their core areas was high, suggesting a failed pair bond or nest attempt in the years when they were more mobile. We believe that adult male #217 (Fig. 4) and adult female #365 (Fig. 2) were not successful breeders and would have been unavailable to raise young, based on their highly mobile behavior, moving often and/or long distances over the summer months every year tracked ($n = 7$ yr for #217 and $n = 4$ yr for #365). Nevertheless, both eagles routinely used the same or similar areas at similar times in successive years. The one subadult male also demonstrated fidelity to a particular area, but made lengthy trips to and from his core summer range (Fig. 1). For adult eagles, no consistent sex-specific differences in summer-range fidelity or mobility were apparent.

Migration Timing, Duration, and Distance. *Spring.* Based on 27 spring migration records for 11 adult eagles (four males, seven females), migration began between 12 January and 30 March (median: 4 March; mean: 24 February; Table 2). The start dates for females averaged 4 d later than that for males (Table 3). The two subadult males began their spring migrations between 6 and 10 March (Table 2). Based on 23 complete spring migration records for 10 adult eagles (four males, six females), arrival dates on summer ranges varied from 18 February to 17 June (median: 10 April; mean: 27 April; Table 2). Females arrived on average 7 d earlier than males (Table 3). One subadult male arrived on his summer range on 9 and 20 March in two consecutive years (Table 2). Adults took 6–151 d to complete their spring migrations (median: 68 d; mean: 67 d; Table 4). Migration duration averaged 13 fewer days for females than for males (Table 3). For adult eagles, straight-line distances between winter and northernmost summer ranges ranged from 611–2222 km (median: 1820 km; mean: 1655 km; Table 4). Travel distances for one subadult male averaged 599 km on two migrations (Table 4).

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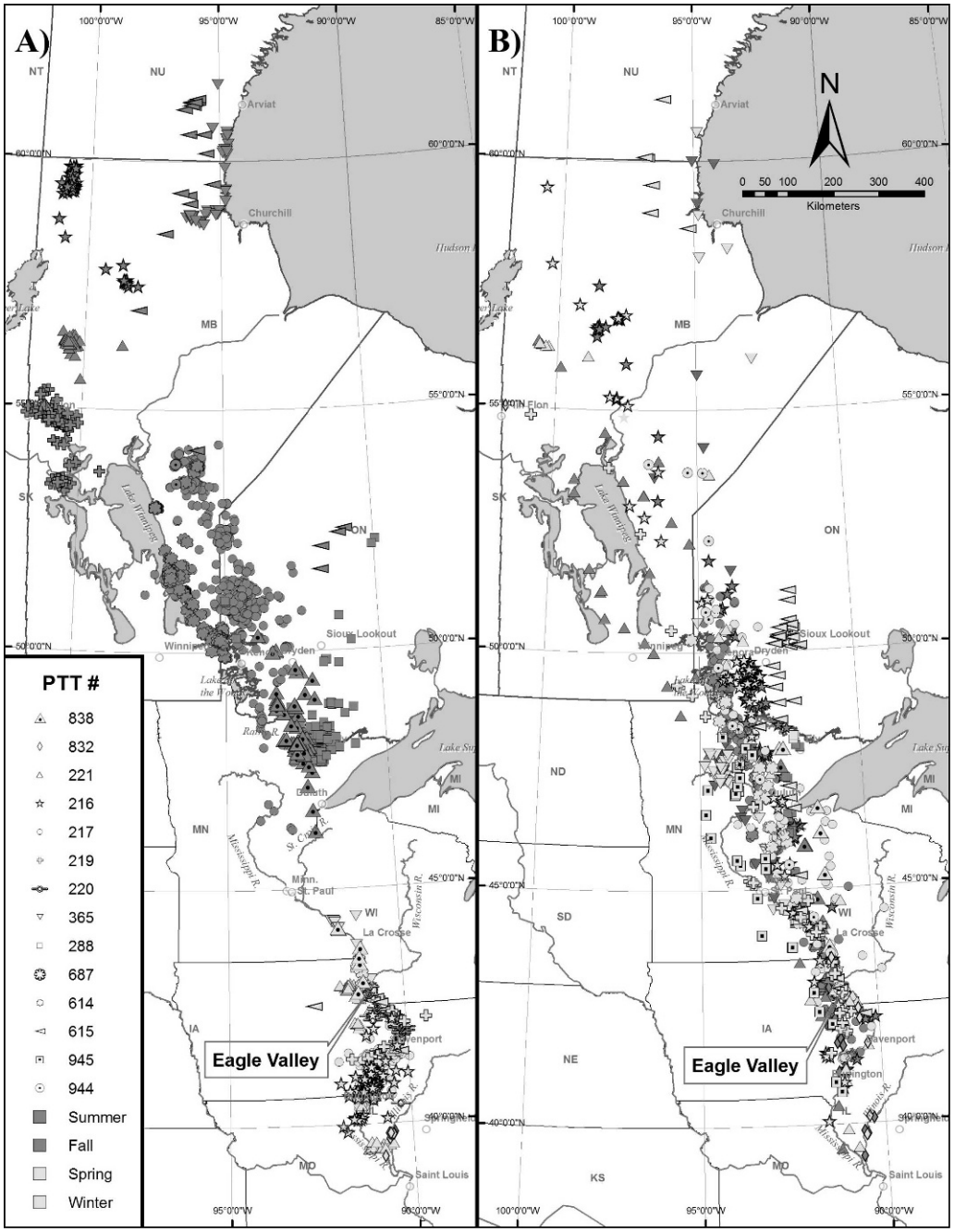


Figure 1. (A) Summer and winter ranges and (B) spring and autumn migration paths of 14 Bald Eagles tracked by satellite from Eagle Valley, Wisconsin, between March 1999 and April 2007.

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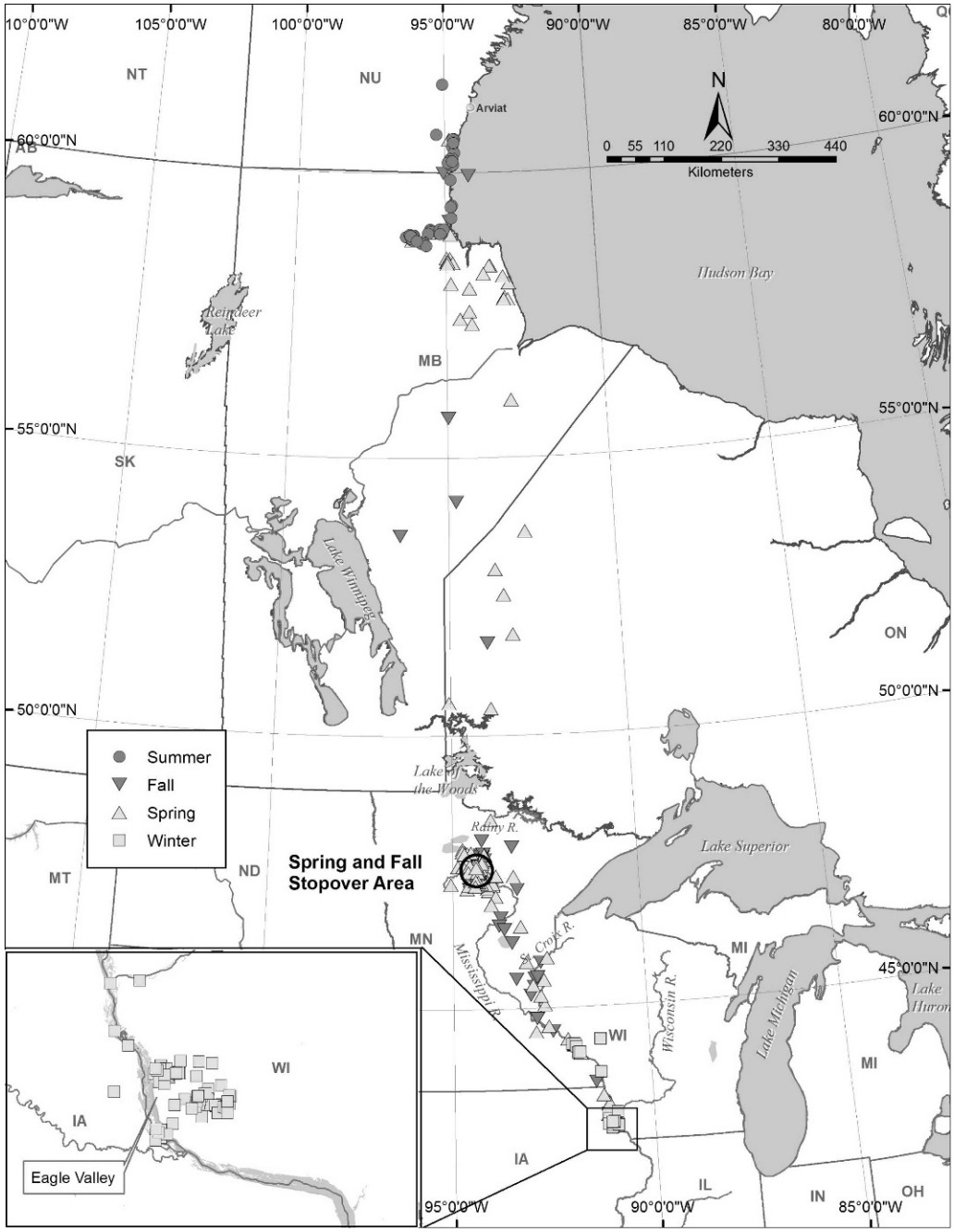


Figure 2. Seasonal locations of nonbreeding adult female Bald Eagle #365 tracked by satellite from Eagle Valley, Wisconsin, between December 2000 and June 2004, illustrating high winter range fidelity and high summer range mobility. Inset shows winter locations only.

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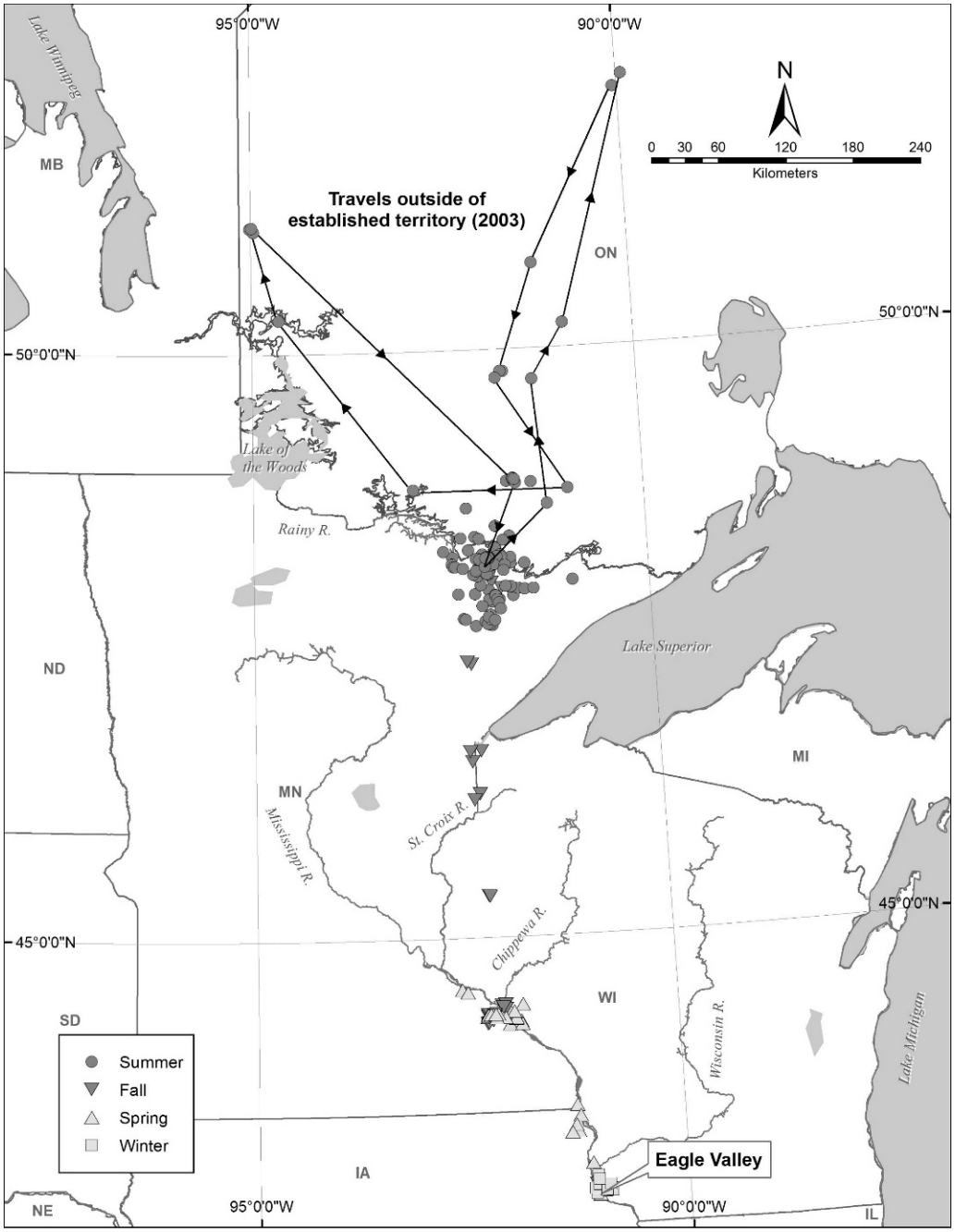


Figure 3. Seasonal locations of adult male Bald Eagle #288 tracked by satellite from Eagle Valley, Wisconsin, between January 2001 and July 2003, illustrating high winter range fidelity and interannual variation of summer range mobility and breeding status.

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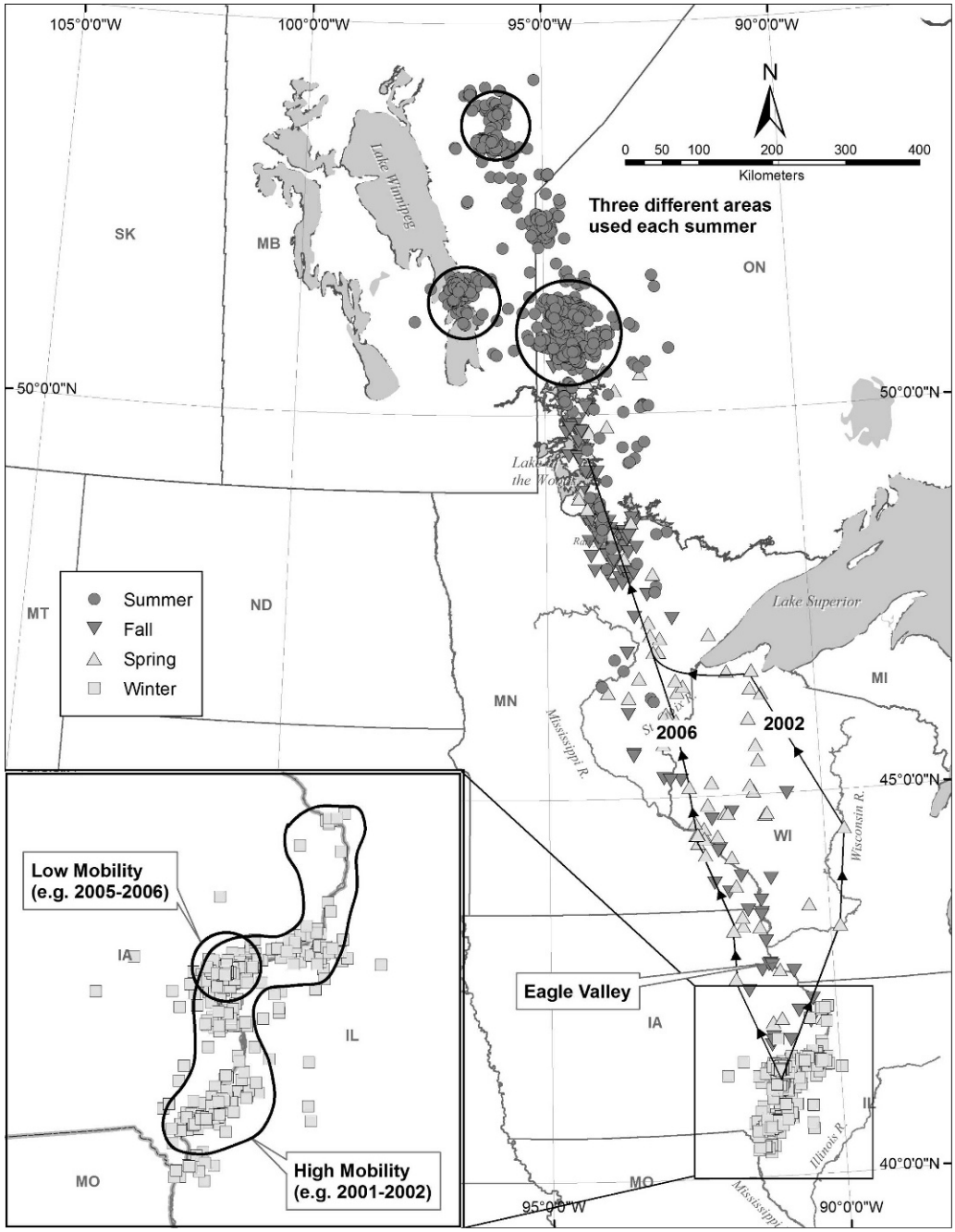


Figure 4. Seasonal locations of nonbreeding adult male Bald Eagle #217 tracked by satellite from Eagle Valley, Wisconsin, between December 1999 and November 2006, illustrating high interannual variation of spring migration routes, winter range mobility, and high summer range fidelity and mobility. All three summer areas were used every year. Inset shows winter locations only.

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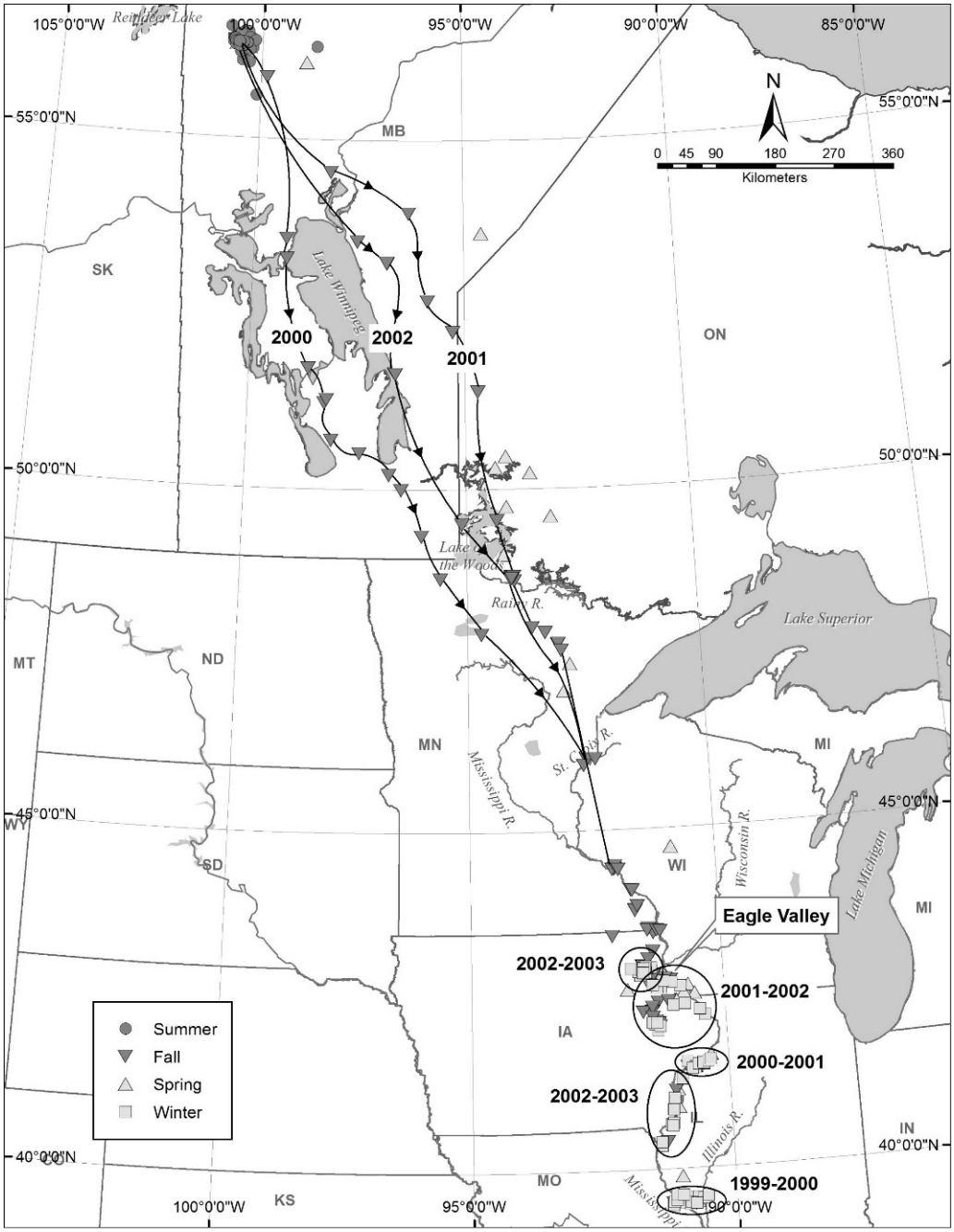


Figure 5. Seasonal locations of breeding adult male Bald Eagle #221 tracked by satellite from Eagle Valley, Wisconsin, between November 1999 and February 2003, illustrating low winter range fidelity, high summer range fidelity and low mobility, and interannual variation of autumn migration routes.

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Table 2. Start and end dates for spring and autumn migrations of Bald Eagles tracked by satellite between 1999 and 2007 from Eagle Valley, Wisconsin, U.S.A.

PTT #, Age-Sex[2]	Spring Migration						Autumn Migration					
	Start Date			End Date			Start Date			End Date[1]		
	n	Mean	SD	*n*	Mean	SD	*n*	Mean	SD	*n*	Mean	SD
838, S-M	2	6-March	1	2	15-March	7	1	15-December	—	1	10-January	—
832, A-F	1	23-January	—	1	17-April	—						
221, A-M	3	14-February[3]	31	2	16-June	3	3	16-October	2	3	13-December	24
216, A-M	2	4-March	9	1	13-June	—	1	25-September	—	1	10-December	—
217, A-M	7	22-March	9	7	5-April[4]	4	7	4-November[5]	7	6	14-December	20
219, A-F	1	11-February	—	1	3-April	—						
220, A-F[6]												
365, A-F	4	8-February	19	4	13-June	4	3	14-September	12	3	20-November	23
288, A-M	3	21-January	2	3	28-February	12	2	25-November	34	2	6-January	4
687, A-F[7]	1	25-March	—									
614, A-F	2	11-March	8	2	23-March	4	1	9-November	—	1	1-December	—
615, A-F	2	5-March	1	1	30-May	—						
945, S-M[8]	1	10-March	—									
944, A-F	1	18-March	—	1	30-March	—						
All eagles	**30**	**26-February**	**21**	**25**	**23-April**	**41**	**18**	**29-October**	**33**	**17**	**15-December**	**18**
All adults	**27**	**24-February**	**23**	**23**	**27-April**	**40**	**17**	**21-October**	**28**	**16**	**11-December**	**16**

[1] Date of capture on winter range not used to calculate mean.
[2] A = adult, F = female, M = male, S = subadult.
[3] No data received between 22 March 2002 and 13 July 2002.
[4] Arrival date to first of three summer ranges.
[5] Date departing southern summer range.
[6] Winter movements only. Lost transmission in January 2000 prior to migration. Traveled 124 km from Eagle Valley to Savanna, IL.
[7] Lost transmission in April 2002 during migration. Traveled 765 km from southernmost winter range to northeast MN.
[8] Traveled 836 km from winter range to northern MN, then was killed in vehicle collision on 6 April 2006. Unknown if migration was completed.

Table 3. Migration characteristics of adult male and female Bald Eagles tracked by satellite between 1999 and 2007 from Eagle Valley, Wisconsin, U.S.A.

	Male			Female				
Movement Behavior	*n*	Mean[1]	SD	*n*	Mean[1]	SD	*t*	*P*
Start of spring migration	4	22-February	26 d	7	26-February	23 d	2.5	0.78
End of spring migration	4	1-May	53 d	6	24-April	34 d	2.6	0.82
Duration of spring migration (d)	4	75	59	6	62	45	2.6	0.72
Interannual variation in spring start dates (d)	4	25	23	3	19	22		*
Interannual variation in spring end dates (d)	3	13	10	2	7	1		*
Interannual variation in spring duration (d)	3	19	11	2	23	24		*
Start of autumn migration	4	26-October	26 d	2	12-October	39 d		*
End of autumn migration	4	19-December	12 d	2	25-November	8 d		*
Duration of autumn migration (d)	4	54	17	2	44	31		*
Interannual variation in autumn start dates (d)	3	24	23	1	24	—		*
Interannual variation in autumn end dates (d)	3	36	27	1	45	—		*
Interannual variation in autumn duration (d)	3	48	5	1	30	—		*

[1] For start and end dates and durations, means are grand averages; i.e., averages across years within individuals (where relevant), averaged across individuals. Interannual variation statistics represent variation across eagles in the extent to which each eagle varied its start and end dates and travel durations across years, measured for each eagle as the range in days between the earliest and latest dates and the shortest and longest durations.

* Small sample sizes precluded statistical comparison.

We tracked seven adult eagles during multiple spring seasons (Table 2). Within individuals, the extent of interannual variation in start dates ranged from 1–55 d (median: 13 d; mean: 22 ± 20.7 d); the extent of variation in end dates ranged from 3–23 d (n = 5 eagles; median: 8 d; mean: 11 ± 7.8 d); and the extent of variation in travel durations ranged from 6–40 d (n = 5 eagles; median: 25 d; mean: 21 ± 14.3 d). Interannual variation in start and end dates was less pronounced in females than in males (Table 3).

Autumn. We tracked six adult eagles (four males, two females) for 1–6 autumn seasons, for a combined 16 complete autumn migrations (Table 2). Onset of autumn migration varied from 4 September to 19 December (median: 25 October; mean: 21 October); autumn migration end dates varied from 28 October to 22 January (median: 12 December; mean: 11 December); and travel durations ranged from 15–77 d (median: 50 d; mean: 51 d) (Tables 2, 4). Start dates for females averaged 14 d earlier than for males, and travel durations for females averaged 10 d shorter than for males (Table 3). Subadult #838 completed a single autumn migration in 26 d between 15 December and 10 January (Tables 2, 4).

We tracked three adult males and one adult female during more than one autumn migration. Within individuals, the extent of interannual variation in start dates ranged from 3–48 d (median: 23 d; mean: 24 ± 18.5 d); the extent of interannual variation in end dates ranged from 6–58 d (median: 45 d; mean: 38 ± 22.4 d); and the extent of interannual variation in travel durations ranged from 30–54 d (median: 45 d; mean: 44 ± 9.9 d). Individual eagles showed greater variation in autumn migration end dates among years than was true for spring migration end dates, whereas interannual variation in start dates and travel durations was similar in spring and autumn.

Adult eagles spent an average of 16 d longer on spring migration than on autumn migration; however, this difference was not significant (t = 2.16, df = 13, P = 0.36) and no clear pattern of differences

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Table 4. Mean spring and autumn migration durations (d) and distances (km) between winter and summer ranges of Bald Eagles tracked by satellite between 1999 and 2007 from Eagle Valley, Wisconsin, U.S.A.

PTT #, Age-Sex[1]	Spring Duration			Autumn Duration			Distance		
	n	Mean	SD	*n*	Mean	SD	*n*	Mean	SD
838, S-M	2	9	6.4	1	26	—	2	599	10
832, A-F	1	85	—				1	2147	—
221, A-M[2]	2	140	4.9	3	59	23.6	3	1840	139
216, A-M	1	109	—	1	76	—	1	2222	—
217, A-M	7	14	8.1	6	40	16.2	7	1479[3]	52
219, A-F	1	51	—				1	1799	—
220, A-F[4]									
365, A-F	4	125	17.9	3	66	16.8	3	1968	34
288, A-M	3	38	13.3	2	42	38.2	3	611	2
687, A-F[5]									
614, A-F	2	12	4.2	1	22	—	2	1092	279
615, A-F	1	86	—				1	2102[3]	—
945, S-M[6]									
944, A-F	1	12	—				1	1294	—
All eagles	**25**	**62**	**49.2**	**17**	**47**	**20.4**	**25**	**1559**	**592**
All adults	**23**	**67**	**48.4**	**16**	**51**	**19.8**	**23**	**1655**	**526**

[1] A = adult, F = female, M = male, S = subadult.
[2] No data received between 22 March 2002 and 13 July 2002.
[3] Farthest distance from winter range to farthest north summer range.
[4] Winter movements only. Lost transmission in January 2000 prior to migration. Traveled 124 km from Eagle Valley to Savanna, IL.
[5] Lost transmission in April 2002 during migration. Traveled 765 km from southernmost winter range to northeastern MN.
[6] Traveled 836 km from winter range to northern MN, then was killed in vehicle collision on 6 April 2006. Unknown if migration was completed.

was evident across individuals (Table 4). Adult males #221 and #216 and adult female #365, all longer-distance migrants (traveling at least 1800 km), took longer to complete spring migration than they did to complete autumn migration every year tracked. Conversely, adult male #217, adult female #614, and subadult male #838, all shorter-distance migrants, took longer to complete their autumn migrations each year tracked. In another case, adult male #288 took longer in spring migration during the first year, but longer in autumn migration during the second year tracked.

Migration Route Fidelity. The data allowed for assessments of interannual fidelity to migration routes for seven adult eagles (Table 2). Within seasons, most eagles showed route fidelity. Noteworthy exceptions included the autumn migrations of adult male #221 along the west side of Lake Winnipeg in 2000, but along the east side in 2001 and 2002 (Fig. 5). In addition, adult male #217 varied the southern portion of his spring route from year to year from as far west as eastern Iowa/southeastern Minnesota to as far east as the Wisconsin River in central Wisconsin, an east-west variation of 214 km (Fig. 4).

Most birds also followed similar routes in spring and autumn. Eagles #221 and #217 again were exceptions. Eagle #221 traveled on different sides of Lake Winnipeg during spring and autumn in 2000, but on the same side during his migrations in 2001. Eagle #217 traveled a more direct route on his southbound than northbound migrations.

Discussion

The eagles we studied demonstrated a roughly north-south movement pattern between winter and summer ranges. Bald Eagles wintering along or near the Upper Mississippi River Valley occupied summer areas farther east than those tracked from wintering areas in western Montana (McClelland et al. 1994), northwestern Washington (Watson and Pierce 2001), and central California (Linthicum 2003, Linthicum et al. 2007), and west of those tracked from winter ranges farther east in Michigan (Grubb et al. 1994) and New York (P. Nye pers. comm.).

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Gerrard et al. (1978) found that no Bald Eagles fledged at Besnard Lake in north-central Saskatchewan dispersed as far east as the Mississippi River Valley, and hypothesized that eagles wintering along the Mississippi River came primarily from east of that natal area. The results of our study supported his hypothesis. Harmata (2002) found that several adult Bald Eagles wintering in south-central Colorado summered in Saskatchewan and western Manitoba in the Churchill River watershed. This area extends east into the westernmost summer ranges of some EV eagles. Thus, it appears that eagles summering around the central to northern Saskatchewan/Manitoba border may choose to migrate nearly south along the Churchill-East Slope migration flyway (Harmata 2002) or southeast to wintering areas along the Mississippi River.

Four 2–3-year-old Bald Eagles tracked from winter ranges along the Wisconsin River in south-central Wisconsin (Hall 2005) summered farther east than the eagles in this study. This suggests there may be some segregation of summering areas for eagles that winter in the EV and Wisconsin River areas, despite the close proximity of the two areas (118 km apart).

Winter and Summer Range Fidelity. Eagles in our study showed variation in the degree of fidelity to and mobility within their winter ranges. Numerous studies have reported high winter-range fidelity among Bald Eagles (Harmata and Stahlecker 1993, McClelland et al. 1994, Linthicum 2003, Linthicum et al. 2007, P. Nye pers. comm.). Linthicum (2003) added that the return to the same winter area might be brief, similar to some of our results. Similarly, Watson and Pierce (2001) reported that 65% of telemetered eagles returned to the Skagit River wintering area in Washington, though none returned to it exclusively. McClelland et al. (1994) noted major interannual shifts in the wintering areas of four eagles, similar to our results for eagle #221 (Fig. 5).

Mandernack (unpubl. data) studied winter roost dynamics at EV for 15 years, observing noteworthy fluctuations in the abundance of wintering eagles, which suggested that a host of variables may interact to influence local eagle densities. These variables include food abundance and accessibility (due to ice or snow cover), weather severity, availability of protected roost sites, and human disturbance levels. These factors and the progression of the seasons lead to ebb and flow in local population levels. Grubb (2003) also found that local weather and prey conditions greatly influenced wintering Bald Eagle numbers in northern Arizona. We suggest that some eagles winter in small geographic areas and display plasticity and adaptability to local conditions (e.g., eagle #365; Fig. 2), whereas other eagles are more mobile, apparently reacting to changing conditions within seasons (e.g., #217; Fig. 4), and some use both strategies in different years (e.g., #217 and #221). Social dominance also may play a role in determining the strategy an individual bird uses, with more dominant individuals claiming limited resources and forcing subordinate individuals to more marginal areas.

All eagles in this study showed strong fidelity to summer ranges; however, the degree of mobility within those ranges varied greatly among individuals. These differences likely reflected variable degrees of pair bonding and breeding status. Overall low mobility suggests breeding or territory establishment (e.g., #221; Fig. 5). Low mobility interspersed with long-distance travels back and forth from an established territory suggests a possible failed pair bond or nesting attempt (e.g., #288, 2003; Fig. 3). Overall high mobility suggests a lack of territory establishment and nonbreeding status (e.g., #365, Fig. 2; #217, Fig. 4). Of 10 radio-tagged adults in Canada, McClelland et al. (1994) reported that three had successful nests and six were paired but did not nest. Watson and Pierce (2001) stated that the ratio of nonbreeding to breeding adults that wintered in Washington was 1:1, reflecting a surplus of mature breeders, which is consistent with our findings. Five of eight EV adults monitored into or through a summer season occupied small territories, suggesting the possibility of breeding. We were unable to visit four such territories to confirm status, but we did visit the fifth site and found the female eagle apparently paired but no nest was found even following an aerial search. Data suggested that two additional adult females may have been breeders, but only two summer data points were available for one (#832) and the PTT of the other (#944) functioned for only 6 wk after arrival on the summer range. Watson and Pierce (1998) reported that nonbreeding adults, like breeders, had spring destinations that were region-specific, but nonbreeders wandered locally after arriving at these areas. The nonbreeding adults in our study that we tracked for multiple years did not wander; rather they visited the same disjunct areas throughout the summer, arriving and departing with remarkable consistency year after year (e.g., #365, Fig. 2; #217, Fig. 4). We speculate that the cost of flight

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between distant locations may be offset by energy gained once there due to reduced competition and/or exploitation of a seasonally abundant food source.

Migration Timing, Duration, and Distance. Determining the timing, duration, and distance of migration is complicated by the difficulty of determining when migration ends and winter or summer travel begins. Lengthy gaps in PTT data due to preset times between on cycles blur start and end times. Migratory ''backtracking'' can obscure the timing and rate of migration. Lengthy stopovers and variability in an individual's migration behavior, whether related to food, weather, or social factors, might further confuse the issue. In our study, spring migration began between mid-January and late-March and took on average 67 d, which is notably longer than reported for eagles in New York (7–39 d; P. Nye pers. comm.), Washington (21 d; Watson and Pierce 2001), and Colorado (15 d; Harmata 2002). In addition, our study revealed wide variation in the spring departure dates of suspected breeders, suggesting that the drive to secure a nest site and breed does not fully explain the differences. Weather and food availability also are drivers of spring migration, and our observations of several eagles ''backtracking'' during migration and stopping over for extended periods suggest this influence. Linthicum et al. (2007) reported no stopover/staging areas where eagles stayed more than 7–10 d on their spring journey. In our study, however, during all 4 yr of tracking, nonbreeding adult female #365 stayed for 2–2.5 mo at the same stopover area in northern Minnesota (Fig. 2) and suspected breeding adult male #216 stayed for 63 d southeast of Kenora, Ontario, before continuing on to northwestern Manitoba. Perhaps the comparatively extended duration of stopovers by some eagles in our study reflects regional differences in the factors that influence migration activity and behavior.

The adult eagles in our study began autumn migration between early-September and mid-December, with a late-October average departure. This is earlier than the late-November average recorded in New York (P. Nye pers. comm.). Variability in onset of autumn migration among regions likely reflects differences in climate and effects on prey availability, with individuals summering at higher latitudes departing earlier. In our study, autumn migration ended between late-October and late-January, which is consistent with other studies (P. Nye pers. comm., Linthicum et al. 2007); however, travel duration for the EV birds averaged longer (51 d) than in other studies (21.5 d, P. Nye pers. comm.; 38 d, Watson and Pierce 2001). Moreover, in our study there was high variability within and among individuals in the duration spent migrating relative to the distance traveled. For example, adult male #288 took only 15 d in 2001 but 69 d in 2002 to cover a similar distance of just over 600 km.

Buehler (2000) suggested that a faster migration pace in spring than in autumn might confer a competitive advantage for nest sites and mates, and other studies have shown faster spring migration times (Watson and Pierce 2001, Linthicum 2003, P. Nye pers. comm.). Not all eagles in our study demonstrated this clear pattern. In fact, there was high variability within and among individuals and in relation to probable breeding status. Two of the four potential breeders and one nonbreeder took considerably longer on spring than on autumn migration. In addition, although autumn migration stopovers occurred, for several eagles spring migration lasted longer than autumn migration due to longer vernal stopover periods. Duration of spring migration stopovers may be a function of prey availability and adequate cover relative to latitudinal climate differences. In our study, the longer-distance migrants took a disproportionately longer time on spring migration than on autumn compared to shorter-distance migrants (Table 4). Foraging opportunities might be limited in the harsh late winter to early spring climate of north-central Canada. This leads to longer spring stopovers at lower latitudes while eagles wait for conditions to improve farther north, resulting in longer spring migration duration.

Females arrived on summer ranges on average one week earlier than males, which is contrary to the generally accepted pattern in which males are the first to arrive on a territory. In addition, our data indicated that females traveled faster than males in both spring and autumn. Both of these results may be attributable to small sample sizes, however, and the long migration durations of two adult males that summered at higher latitudes also may have biased our data.

The migration distances of EV eagles fell within the range of variation observed in other studies. On average, EV eagles migrated longer distances (1655 km) than those farther east (P. Nye pers. comm., range 363–1600 km; Grubb et al. 1994, mean 435 km) and in Washington (Watson and Pierce 2001, mean 1123 km), but shorter distances

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than those tracked in the Intermountain region (McClelland et al. 1994, median 2056 km; Harmata 2002, mean 2019 km). In addition, Linthicum et al. (2007) tracked Canadian eagles that wintered in central and southern California to Great Slave Lake, Northwest Territories, which also was farther than the EV eagles traveled.

Migration Route Fidelity. Overall, the eagles in our study showed fidelity to migration routes, both among years within seasons and across seasons. This was consistent with the results of P. Nye (pers. comm.) and Watson and Pierce (1998, 2001). Linthicum (2007), however, noted evidence of a ''loop migration'' pattern, whereby eagles migrating between California and the Northwest Territories followed a more easterly route in autumn than in spring. In our study, one eagle exhibited a loop migration pattern, but in only one of three years tracked.

In conclusion, our study provided important new information on the movements of Bald Eagles in a region where such knowledge was lacking. It revealed that most eagles that winter along the Upper Mississippi River summer across a broad geographic range from northern Minnesota to central Canada, a range whose western edge extends into the summer range of eagles that winter in south-central Colorado (Harmata 2002). The large latitudinal gradients in environmental variables across such a vast summer range likely contributed to the high variability of migration behavior we observed in our study. Compared to other studies, our results indicated similar degrees of route and range fidelity, but greater variation in migration timing and longer travel durations. Although sample sizes were admittedly modest, observed trends in migration timing, sex-specific comparisons, and subadult compared to adult behavior occasionally were outside the parameters of generally accepted behavioral patterns, or even contrary to them. The spatial and temporal accuracy of PTT data reveals a previously unrecognized level of detail to many such behaviors, thereby encouraging us, and hopefully others, to expand those parameters. Further tracking of eagles with daily GPS data also may reveal finer-scale habitat preferences. Such information is needed to further enhance our understanding of the ecology and conservation needs of Bald Eagles in the Upper Midwest.

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