The Auk 125(1):214–224, 2008
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Printed in USA.

MOVEMENTS OF GOLDEN EAGLES (*AQUILA CHRYSAETOS*) FROM INTERIOR ALASKA DURING THEIR FIRST YEAR OF INDEPENDENCE

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ABSTRACT.—We used satellite telemetry to study year-round movements of two cohorts of juvenile Golden Eagles (*Aquila chrysaetos*) from Denali National Park and Preserve, Alaska. Radiotagged Golden Eagles started autumn migration between 15 September and 5 October and arrived on their winter areas 31 to 86 days later. Cumulative tracking distances during autumn migration ranged from 818 to 4,815 km. Peak tracking velocities during autumn migration reached 261 km day^{-1} in 1997 and 472 km day^{-1} in 1999. Golden Eagles wintered from southern Yukon Territory to southern New Mexico, and most spent the winter within 75 km of the location where they terminated their autumn migration. Spring migration occurred from late March through mid-June. Eagles showed little fidelity to their autumn migration paths as they migrated northwest in spring through western Canada and into Alaska. Duration of spring migration ranged from 24 to 54 days, and cumulative tracking distance during spring migration ranged from 2,032 to 4,491 km. Peak tracking velocities during spring migration reached 284 km day^{-1} in 1998 and 330 km day^{-1} in 2000. In contrast to juvenile Golden Eagles raised at temperate latitudes in North America, juveniles raised in Denali traveled thousands of kilometers across western North American during their first year of independence. Our results suggest that conservation strategies for migratory Golden Eagles from Denali, and perhaps from other areas in northern North America, require a continental approach. *Received 9 November 2006, accepted 9 May 2007.*

Key words: Alaska, *Aquila chrysaetos*, Denali, Golden Eagle, migration, migratory behavior, movements.

Movimientos de Individuos de *Aquila chrysaetos* desde el Interior de Alaska durante su Primer Año de Independencia

RESUMEN.— Utilizamos telemetría satelital para estudiar los movimientos anuales de dos cohortes de águilas juveniles de la especie *Aquila chrysaetos* provenientes del Parque Nacional y Reserva Denali, Alaska. Las águilas marcadas con radiotransmisores comenzaron la migración de otoño entre el 15 de septiembre y el 5 de octubre y llegaron a sus áreas de invernada entre 31 a 86 días después. Las distancias acumulativas registradas durante la migración de otoño variaron entre 818 y 4,815 km. La velocidad más alta registrada durante la migración de otoño alcanzó 261 km día^{-1} en 1997 y 472 km día^{-1} en 1999. Estas águilas invernaron desde el sur del Territorio de Yukón hasta el sur de Nuevo México, y la mayoría pasó el invierno dentro de una distancia de 75 km desde los puntos en que terminaron su migración de otoño. La migración de primavera ocurrió desde fines de marzo hasta mediados de junio. Las águilas mostraron poca fidelidad a sus rutas migratorias de otoño, en sus migraciones de primavera hacia el noroeste por el oeste de Canadá hacia Alaska. La duración de la migración de primavera fue de 24 a 54 días, y las distancias acumulativas registradas durante la migración de primavera fueron de 2,032 a 4,491 km. Las velocidades más altas registradas durante la migración de primavera alcanzaron 284 km día^{-1} en 1998 y 330 km día^{-1} en 2000. De modo contrario a las águilas juveniles de esta especie criadas en latitudes templadas de Norteamérica, los juveniles de Denali viajaron miles de kilómetros por el oeste de Norteamérica durante su primer año de independencia. Nuestros resultados sugieren que las estrategias de conservación para *A. chrysaetos* de Denali, y probablemente de otras áreas del norte de Norteamérica, requieren de un enfoque continental.

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The Auk, Vol. 125, Number 1, pages 214–224. ISSN 0004-8038, electronic ISSN 1938-4254. © 2008 by The American Ornithologists' Union. All rights reserved. Please direct all requests for permission to photocopy or reproduce article content through the University of California Press's Rights and Permissions website, http://www.ucpressjournals.com/reprintInfo.asp. DOI: 10.1525/auk.2008.125.1.214

LITTLE IS KNOWN about the movements or survival of raptors in the period between leaving the natal area and entering a breeding population. Golden Eagles (*Aquila chrysaetos*) raised at latitudes >60°N in western North America are usually migratory, yet little is known about their migration routes, wintering areas, and areas they use before they enter a breeding population (Kochert et al. 2002). One of the densest known populations of nesting Golden Eagles in North America occurs in Denali National Park and Preserve, Alaska (hereafter "Denali"; McIntyre and Adams 1999, Kochert et al. 2002). Encounters with individuals banded as nestlings in Denali suggest that Golden Eagles raised there are long-distance migrants with wintering areas extending from eastern Colorado to north-central Mexico (C. L. McIntyre unpubl. data). Although encounters with Golden Eagles banded in Denali have identified some wintering areas, the year-round movements of juvenile Golden Eagles from Denali and other northern latitudes in North America have not been studied (Watson 1997, Kochert et al. 2002).

Documenting year-round movements of wide-ranging birds is essential for identifying factors that influence their survival and for developing robust conservation strategies for their populations (Steenhof et al. 1984, 2005; Higuchi et al. 2004). This may be especially important for species that exhibit delayed sexual maturity, such as Golden Eagles (Watson 1997), which may not enter a breeding population until years after they leave their natal areas. In 1997, we initiated an extensive satellite-tracking study of juvenile Golden Eagles from Denali to estimate their survival and describe their year-round movements. That study showed that juvenile Golden Eagles from Denali have relatively low survival rates (McIntyre et al. 2006). Here, we examine tracking results of radiotagged juvenile Golden Eagles during their first year of independence and compare their movements during autumn migration, winter, spring migration, and summer.

METHODS

Field procedures.—We radiotagged Golden Eagle nestlings when they were ≥56 days of age in late July and early August in 1997 ($n = 22$), 1998 ($n = 5$), and 1999 ($n = 21$) at nesting areas in the northern foothills of the Alaska Range in northeastern Denali in central Alaska (63°36′N, 149°39′W). We entered nests using standard rock-climbing techniques, banded all nestlings with U.S. Geological Survey (USGS) rivet aluminum leg bands, and recorded a series of morphological characteristics including mass and length of footpad (McIntyre et al. 2006). We estimated nestling age using photographic aging guides (Hoechlin 1976) and determined their sex using mass and footpad length following Edwards and Kochert (1986). We radiotagged nestlings that were in apparently good physical condition and with mass ≥3,600 g.

We used 95-g satellite-received transmitters (PTTs; Microwave Telemetry, Columbia, Maryland) powered by lithium batteries with an expected life of two years (P. Howey pers. comm.). Duty cycles were 8 h on and 72 h off in 1997, and 8 h on and 48 h off in 1998 and 1999. We glued a 9-g VHF radio transmitter (model 3PN, Advanced Telemetry Systems, Isanti, Minnesota) to the PTT to help locate dead Golden Eagles (McIntyre et al. 2006). We attached the dual transmitters to nestlings using a backpack-style body harness (Buehler et al. 1991, Steenhof et al. 2006) constructed from 13-mm tubular Teflon ribbon (Bally Ribbon, Bally, Pennsylvania) and incorporated a biodegradable link made of cotton thread so that the radios would eventually fall off the birds. When attached, the PTTs rested on the dorsal surface along the midline of the back between the bird's wings, with the antenna angled at ~45° from the PTT posterior. The dual transmitters and harness weighed ~106 g (<3% of the mass of the nestling at deployment), within conventional guidelines of bird telemetric studies (Caccamise and Hedin 1985).

TABLE 1. Argos satellite locations by location-quality class before and after accuracy filtering, obtained from radiotagged juvenile Golden Eagles from Denali National Park and Preserve, Alaska, during their first year of independence.

Argos location-quality class	All Argos locations		All filtered locations		Best filtered location per duty cycle	
	n	(%)	*n*	(%)	*n*	(%)
3	154	1.3	154	2.2	136	7.0
2	569	4.7	569	8.0	416	21.4
1	1,944	16.1	1,944	27.2	833	42.8
0	5,458	45.2	3,024	42.3	451	23.2
A	1,315	10.9	777	10.9	60	3.1
B	1,745	14.4	436	6.1	18	0.9
Z	897	7.4	235	3.3	31	1.6
Total	12,082	100.0	7,139	100.0	1,945	100.0

Data collection and preparation.—We determined the location and status (alive or dead) of radiotagged Golden Eagles using the Argos data collection and location system (Argos 1996). We categorized a PTT as a mortality if it remained motionless for more than two consecutive duty cycles, unless we determined otherwise, or as a failure if we lost complete contact with it within the expected lifespan of its power source. We attempted to retrieve all motionless PTTs (McIntyre et al. 2006).

We obtained 12,082 relocations (Table 1), including 2,667 standard-class locations (LC = 3, 2, and 1) and 9,415 auxiliary-class locations (LC = 0, A, B, and Z). Service Argos estimated accuracy of standard-class locations using high-power PTTs under ideal ambient conditions as 1-sigma error radii of 250, 500, and 1,500 m for LC 3, 2, and 1, respectively. Accuracy of auxiliary-class locations is highly variable and undocumented by Service Argos (Argos 1996). Empirical tests of relatively low-power wildlife PTTs under a variety of environmental settings have reported slightly poorer accuracy for standard-class locations (Harris et al. 1990, Vincent et al. 2002), but acceptable accuracy, in our opinion, for interpreting continental-scale migration data. However, 78% of our data set was auxiliary-class locations, which have broad and unsatisfactory error variances (Vincent et al. 2002, Liaubet and Malardé 2003). Although filtering methods can improve robustness of auxiliary-class locations, most published algorithms are for marine and terrestrial species that are far less mobile or that move more slowly than migrating birds (McConnell et al. 1992, Keating 1994, Hays et al. 2001, Austin et al. 2003).

We used a hybrid filtering strategy developed by Douglas (2006) that evaluated the Argos auxiliary-class locations using

two independent filtering methods. The first required that, to be retained, auxiliary-class locations have at least one other location that was both consecutive in time and redundant in space, which we defined as <10 km. The second evaluated movement rates and turning angles; an auxiliary-class location was rejected if its vector length (from the previous retained location) was >10 km and its rate was >100 km h^{-1} or if its internal turning angle was suspiciously acute. The first filtering method has merits for relatively sedentary animals; however, because of the improbability of acquiring spatially redundant locations of a migrating bird, we created a hybrid of the two methods in which all locations that passed the first filter were retained and considered "anchor points." If the distance between two consecutive anchor points was >20 km, locations that passed the second filter during the intervening period were individually evaluated with respect to three directionality tests: (1) azimuth to the anchor point and azimuth to the candidate location differed by <20°, (2) passing through the candidate location did not increase the total distance traveled by >20%, and (3) the internal turning angle formed by the candidate location was >150°. Candidate locations with LC values of 0 and A had to pass two directionality tests and LC B and Z locations had to pass all three tests.

We did not filter the Argos standard-class locations, and we manually removed 25 clearly aberrant auxiliary-class locations before filtering. The spatial-redundancy filter retained 4,008 of 9,390 auxiliary-class locations. The rate-angle filter included 464 additional auxiliary-class locations because they passed the directionality tests. The final hybrid data set contained 2,667 standard-class and 4,492 auxiliary-class locations (Table 1). From this data set, we selected one location per duty cycle on the basis of best LC. In cases of LC ties, we selected the best location based on a sequential rule-set: the highest Argos IQX value, the most messages received during the satellite overpass, the highest IQY value, and the earliest date–time. The resulting filtered data set of "best" LC locations per duty cycle contained 1,945 records (71% standard-class and 29% auxiliary-class locations) and was used for all analyses and graphics presented here unless otherwise stated. We calculated the great-circle (orthodrome) distance and direction of each vector formed by two consecutive locations (hereafter termed a "leg"). Hence, the migratory journey (i.e., the tracking path) for each individual was represented as a series of legs connecting the best locations per duty cycle.

Data summaries and analyses.—Our summaries and analyses are based on Golden Eagles radiotagged in 1997 and 1999. We omitted individuals from the 1998 cohort because of the small tracking-sample size ($n = 3$). Results are based on individuals that survived each season of their first year of independence (autumn migration, winter, spring migration, and summer) with a functioning PTT or until mortality or PTT failure.

We defined the seasonal movement periods using the following criteria: (1) autumn migration started when Golden Eagles permanently left their natal areas and ended when they stopped moving consistently southward away from the natal areas and started omnidirectional movements of ≤15 km per duty cycle for three or more consecutive duty cycles, (2) spring migration started with consistent unidirectional northward movements of >15 km per duty cycle away from the winter area, (3) winter movements occurred between the end of the first autumn migration and the start of the first spring migration, and (4) summer movements occurred between the end of the first spring migration and the start of the second autumn migration. We assumed that individuals gained independence when they initiated their first autumn migration (McIntyre and Collopy 2006). We defined "migratory stopovers" as movements of ≤15 km for more than one duty cycle during autumn and spring migrations, but with movements of >15 km per duty cycle after the stopover. We tested for differences in movement patterns within seasons between two cohorts (1997 and 1999), between sexes, and between individuals that survived and those that died during their first year of independence. We could not determine actual dates of departure and arrival because of our three-day duty cycle; hence, we interpolated departure and arrival dates as midtimes between their respective outbound and inbound locations.

We report distance moved as the sum of the length of all legs during each season, and direction moved during migration as the mean of the azimuths of all legs during each season. We report movement rates as tracking velocity, because sampling was intermittent. In one analysis of diurnal movements, we examined lengths and velocities of within-duty-cycle vectors, but in all other cases, we analyzed between-duty-cycle relocations so that the reported tracking velocities represent average daily progress across the landscape, as opposed to in-flight speed.

We investigated relationships between peak migratory tracking velocities and wind conditions using daily averaged zonal and meridional 850-millibar (mb) and 700-mb wind-speed estimates from the National Centers for Environmental Prediction (NCEP) reanalysis data set (see Acknowledgments). The NCEP wind data nearest a leg's starting location, ending location, and interpolated midpoint location were averaged to characterize the prevailing spatiotemporal wind conditions associated with each movement.

For all statistical tests, we used S-PLUS, version 6.0 (Insightful, Seattle, Washington) and applied a 0.05 alpha-level for reporting statistical significance. We summarized movement directions using ORIANA, version 2 (Kovach Computing Services, Pentraeth, United Kingdom). Except where noted otherwise, values reported are means ± SD.

Results

Autumn migration.—Twenty-eight juvenile Golden Eagles started their first autumn migration between 15 September and 5 October (Table 2) and flew eastward through eastern Alaska and southeast through western Canada (Fig. 1). The autumn migration corridor (the zonal distance between the outermost tracking legs of all migrating Golden Eagles) increased from <100 km at the Alaska–Yukon border (~62°N latitude) to 740 km at 60°N to >1,100 km at 50°N latitude (Fig. 1).

Golden Eagles ended their first autumn migration from late October to December (Table 2), 31–86 days after starting migration ($\bar{x} = 60.3 \pm 14.9$ days; Table 3). Duration of autumn migration did not differ by cohort ($Z = -0.71$, $P = 0.48$), sex ($Z = -0.53$, $P = 0.59$), or survival ($Z = 0.49$, $P = 0.63$). Cumulative tracking distance in autumn migration ranged from 818 to 4,815 km ($\bar{x} =$ 2,692 ± 934 km), with no difference between cohort ($t = -1.17$, df = 25, $P = 0.25$; Table 4). Males traveled farther than females

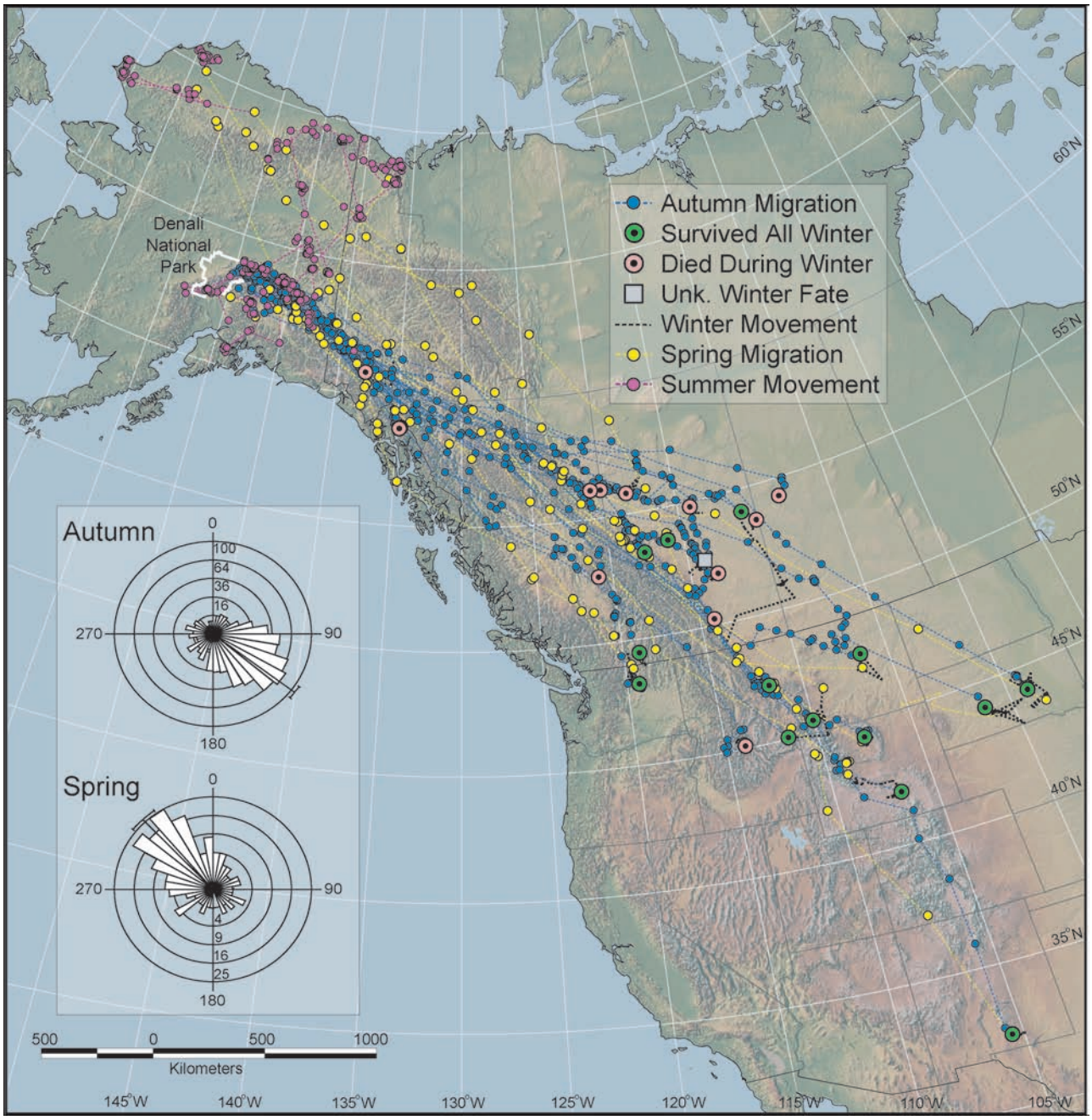


FIG. 1. Movements of juvenile Golden Eagles from Denali National Park and Preserve, Alaska, during their first year of independence, as determined by satellite telemetry. Points depict the highest-quality Argos location obtained during each PTT duty cycle. Lines represent legs between consecutive locations (orthodromes depicted as straight lines in this gnomonic map projection). Inset displays circular frequency histograms that sum the number of autumn and spring-migration tracking vectors within 10° azimuth intervals on concentric axes. Radial lines denote the mean migration azimuth (±95% confidence interval) for all legs.

Table 2. Start and end dates of autumn migration for 1997 and 1999 cohorts of juvenile Golden Eagles (n = 28) from Denali National Park and Preserve, Alaska, as determined by satellite telemetry. SD is reported as number of days.

	Start			End		
Group	Mean	SD	Range	Mean	SD	Range
Cohort						
1997	22 September	4.7	15 September–1 October	24 November	12.9	8 November–21 December
1999	26 September	5.1	19 September–5 October	22 November	18.7	30 October–24 December
Sex						
Female	21 September	4.2	19 September–2 October	23 November	15.8	30 October–21 December
Male	25 September	5.6	15 September–5 October	26 November	14.9	8 November– 24 December
Survival status						
Survived first year	23 September	5.0	19 September–2 October	14 November	4.8	8–22 November
Died during first year	25 September	4.7	15 September–5 October	27 November	16.0	30 October–24 December

Table 3. Duration (days) of autumn (n = 28 individuals) and spring migrations (n = 12) for juvenile Golden Eagles from Denali National Park and Preserve, Alaska, as determined by satellite telemetry.

	Autumn migration (days)			Spring migration (days)		
Group	Mean	SD	Range	Mean	SD	Range
Cohort						
1997	61.2	12.0	48–86	46	8.5	31–54
1999	57.5	18.7	31–86	37	7.4	24–45
Sex						
Female	59.4	16.6	31–86	41.5	9.7	24–52
Male	61.3	12.9	48–86	41.6	8.8	31–54
Survival status						
Survived first year	52.3	8.1	37–59	39.8	10.3	24–54
Died during first year	62.4	15.7	31–86	43.2	7.9	31–52

during autumn migration ($t = -2.12$, df = 26, $P = 0.04$), as did individuals that survived their first year of independence ($t = -2.73$, df = 26, $P = 0.01$; Table 4). Tracking distance and time elapsed in completing autumn migration were not correlated ($r^2 = 0.05$).

Overall, autumn migration was highly directional to the southeast; the mean azimuth of all legs from natal areas to wintering areas (n = 568 legs) was 127.3 ± 50.6° (95% confidence interval [CI]: 123.1–131.3°)(Fig. 1, inset). Differences between the total tracking-path distance (reported above) and the direct straight-line distance between natal areas and wintering areas ranged from 75 to 712 km ($\bar{x}$ = 234 ± 126.3 km, n = 27), and did not differ by cohort ($t = -1.3$, df = 24, $P = 0.19$) or sex ($t = -1.51$, df = 24, $P = 0.14$). Overall, the autumn-migration tracking paths were 9.0 ± 4.0% (range: 5–17%) longer than if the birds had flown in straight lines directly to their wintering areas.

Duration of migratory stopovers during autumn migration ranged from 2 to 19 days ($\bar{x}$ = 4.9 ± 3.5 days). Most individuals (89%) made at least one stopover during autumn migration ($\bar{x}$ = 2.3 ± 1.5 stops, range: 1–7). Duration of a migratory stopover was longer for individuals that made a single stop (range: 3–19 days, $\bar{x}$ = 7.3 ± 5.2, n = 8) than for those that made multiple stops (range: 2–16 days, $\bar{x}$ = 4.3 ± 2.5, n = 17; t = 2.8, df = 55, P = 0.01).

Peak diurnal movements (in autumn and spring) occurred primarily at midday (Fig. 2). Among within-duty-cycle movement vectors that spanned >1 h and extended >50 km (n = 58), velocities ranged from 16 to 73 km h^{-1} for periods ranging from 1 to 5 h. The higher velocity range (e.g., >60 km h^{-1}, n = 5 vectors) represents our best minimum estimates of short-term sustained flight speed. Apparent nocturnal movements of <10 km (Fig. 2) probably resulted from imprecise location of stationary individuals, especially given the 10-km tolerance we permitted during the data-filtering process. Long-term tracking velocities

Table 4. Cumulative tracking distance (km) for 1997 and 1999 cohorts of juvenile Golden Eagles from Denali National Park and Preserve, Alaska, during autumn (n = 28 individuals) and spring migrations (n = 12), as determined by satellite telemetry. SD is reported as number of days.

	Autumn migration (km)			Spring migration (km)		
Group	Mean	SD	Range	Mean	SD	Range
Cohort						
1997	2,599	731	1,052–3,802	3,067	783	2,032–4,091
1999	3,000	1,041	1,035–4,815	3,369	1,001	2,411–4,491
Sex						
Female	2,387	874	1,035–3,802	3,018	870	3,032–4,153
Male	3,100	887	1,872-4,815	3,498	885	2,270–4,491
Survival status						
Survived first year	3,220	504	2,511–3,936	3,477	812	2,426–4,182
Died during first year	2,549	980	818–4,815	2,959	922	2,032–4,491

TABLE 5. Start and end dates of spring migration for 1997 and 1999 cohorts of juvenile Golden Eagles ($n = 12$ individuals) from Denali National Park and Preserve, Alaska, as determined by satellite telemetry. SD is reported as number of days.

	Start			End		
	Mean	SD	Range	Mean	SD	Range
Group						
1997	10 April	10.3	27 March–22 April	28 May	15.7	10 May–13 June
1999	23 April	9.9	10 April–8 May	30 May	12.1	12 May–13 June
Sex						
Female	17 April	12.8	27 March–8 May	29 May	12.9	12 May–13 June
Male	15 April	11.7	3–30 April	29 May	15.6	10 May–13 June
Survival status						
Survived first year	21 April	11.1	10 April–8 May	2 June	12.8	12 May–13 June
Died during first year	12 April	11.7	27 March–26 April	26 May	14.2	10 May–13 June

during autumn migration reached 261 km day^{-1} in 1997 and 472 km day^{-1} in 1999 (Fig. 3). Prevailing jet-stream winds over western North America generally favored autumn migration trajectories (Fig. 4A–B).

Total migration distance and allocation of movement during migration varied among individuals (Fig. 5A–D). Aggressive movements (steep slope) were more prevalent earlier in the migration period, stopover events (plateaus) occurred throughout migration, and the rate of movement decreased toward the end of autumn migration (Fig. 5A–D). We used distance–duration curves plotted on proportional axes to examine spatiotemporal migration patterns and subjectively partitioned the curves into four groups: a very aggressive start with a prolonged slow end (logarithmic); a somewhat aggressive start with a shorter slow end (relaxed logarithmic); a constant rate throughout (linear); and a slow start, aggressive middle, and slow end (sigmoid) (Fig. 5E–H). More than 50% of individuals exhibited an aggressive start and a drawn-out end (illustrated in Fig. 5E). Only 11% moved at a constant rate throughout their entire autumn migration (Fig. 5G).

Winter movements.—Juvenile Golden Eagles wintered across a vast area of western North America, 671–4,545 km from their natal areas ($\bar{x} = 2458 \pm 864$ km; Fig. 1). The mean azimuth between natal areas and winter areas averaged $109.3 \pm 7.0^\circ$ (range: $95.4 - 120.9^\circ$). No individuals wintering >55°N latitude survived the winter, and those wintering >49°N were less likely to survive than those wintering to the south ($\chi^2 = 8.11$, df = 1, $P = 0.04$). Although 28 individuals completed their first autumn migration, only 14 survived their first winter. Of these, most remained <50 to 75 km from the location where they terminated their autumn migration (Fig. 6).

Spring migration.—Twelve juvenile Golden Eagles completed spring migration. These individuals migrated north from late March through mid-June (Table 5), with most sustained movements occurring after mid-April (Fig. 7A). Tracking-path distances in spring migration ranged from 2,032 to 4,491 km ($\bar{x} = 3{,}218 \pm$

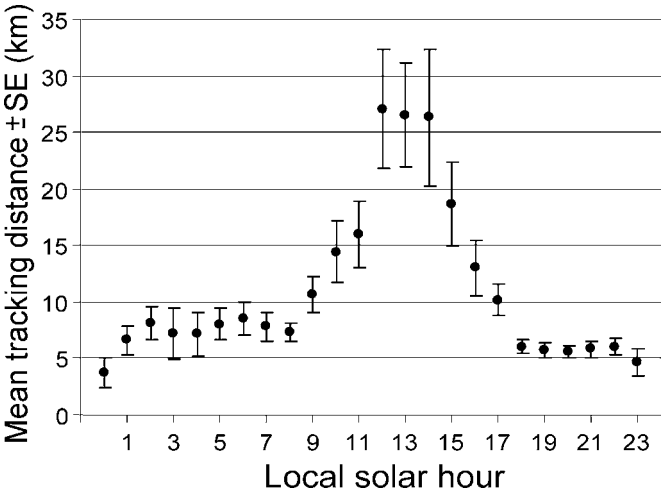


FIG. 2. Average tracking distance of radiotagged juvenile Golden Eagles derived from sequential satellite relocations 1–4 h apart during autumn and spring migrations. Local solar hour was assigned to each vector by subtracting 4 clock-minutes from Coordinated Universal Time (UTC) vector midtime for every degree of longitude west of Greenwich, and rounding.

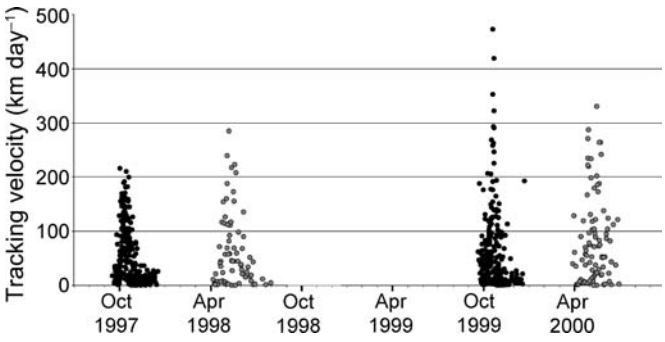


FIG. 3. Tracking velocity of two cohorts (1997, 1999) of radiotagged juvenile Golden Eagles from Denali National Park and Preserve, Alaska, during autumn (black dots) and spring (gray dots) migrations. Data were derived from sequential satellite-telemetry relocations (legs) averaging 3.1 ± 2.1 days apart.

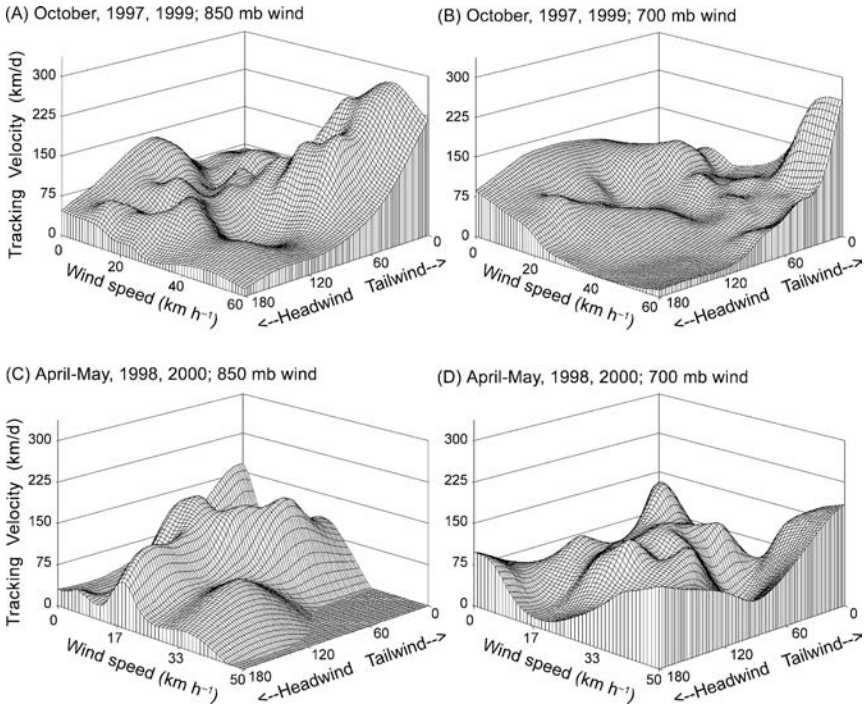


FIG. 4. Tracking velocity of radiotagged juvenile Golden Eagles from Denali National Park and Preserve, Alaska, during peak movements in autumn (top) and spring (bottom) migrations in relation to wind speed and direction at 850 mb (left, ~1,500 m altitude) and 700 mb (right, ~3,000 m altitude). Wind direction is plotted in relation to its angle of incidence with the tracking leg.

871 km), with no difference between cohorts ($t = -0.58$, df = 10, $P = 0.57$), sexes ($t = -0.93$, df = 10, $P = 0.37$), or survival ($t = -1.02$, $P = 0.33$) (Table 4). Differences between spring-migration tracking paths (see above) and direct straight-line distances between winter and summer areas (range: 1,945–4,359 km; $\bar{x} = 2{,}981 \pm 832$ km) among individuals ranged from 87 to 648 km ($\bar{x} = 216 \pm 169$ km) and did not differ by cohort ($t = -1.30$, df = 90, $P = 0.23$) or sex ($t = -0.84$, df = 9, $P = 0.43$). Overall, individuals traveled 6.0 ± 4.0% (range: 3–15%) farther along their spring-migration tracking path than if they had flown in straight lines directly to their summer areas.

Spring migration was highly directional to the northwest; the mean azimuth of all legs from the winter areas to summer areas ($n = 166$) averaged 316.8 ± 53.2° (95% CI: 308.6–325.0°) (Fig. 1, inset). Some individuals tended to retrace their autumn migration route early in spring migration, but most showed little fidelity to their autumn migration paths until they approached Alaska (Fig. 1).

Average start date of spring migration was 13 days earlier in 1998 than in 2000 (Table 5). Proportional distance–time signatures for spring migration varied, with an apparent dependency between cohorts (Fig. 7B); individuals from the 1997 cohort progressed more slowly during the early portion of the spring migration than individuals of the 1999 cohort. Initiation of major spring movements coincided with ~14 h of daylight (Fig. 7C).

Spring migration required 24 to 54 days ($\bar{x} = 41.5 \pm 8.9$) and did not differ by cohort ($Z = 1.68$, $P = 0.09$), sex ($Z = 0.08$, $P = 0.94$), or survival ($Z = 0.40$, $P = 0.69$) (Table 3). Cumulative tracking distance and time elapsed in completing spring migration were not correlated ($r^2 = 0.17$). Duration of spring migratory stopovers ranged from three to six days ($\bar{x} = 3.7 \pm 1.5$ days), with most individuals (84%) making only one or two stopovers.

Peak tracking velocities during spring migration reached 284 km day^{-1} in 1998 and 330 km day^{-1} in 2000 (Fig. 3). Peak spring movements were not associated with strong tail winds (Fig. 4C–D).

Summer movements.—Twelve juvenile Golden Eagles spent their first summer in Alaska or the northern Yukon (Figs. 1 and 8), usually >250 km from their natal areas. Females spent their first summer somewhat closer to their natal areas than males (Fig. 8). During summer, most individuals wandered >200 km from the terminus of their spring migration (Fig. 9) and visited different places for various amounts of time.

Discussion

Migratory movements.—Juvenile Golden Eagles raised in Denali traveled thousands of kilometers across western North America during their first year of life. Radiotagged adult Golden Eagles from the Hudson Bay region of Canada made similar long-distance migrations in eastern North America (Brodeur et al. 1996). By contrast, Golden Eagles originating at lower latitudes in North America appear to move more locally during the nonbreeding season (Steenhof et al. 1984, Harmata 2002, Kochert et al. 2002).

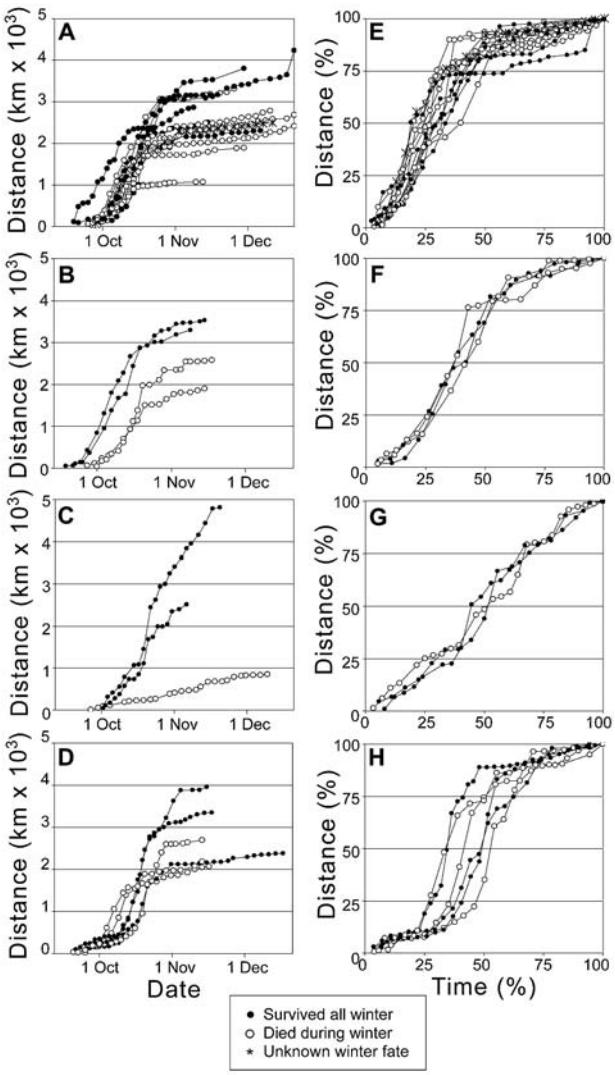


FIG. 5. Cumulative progression of 28 radiotagged juvenile Golden Eagles from Denali National Park and Preserve, Alaska, during autumn migration. Movements are shown as absolute distance over time (A–D) and proportion distance over proportion time (E–H). Migration data were subjectively partitioned into four distinct groups with similarly proportioned distance–time signatures.

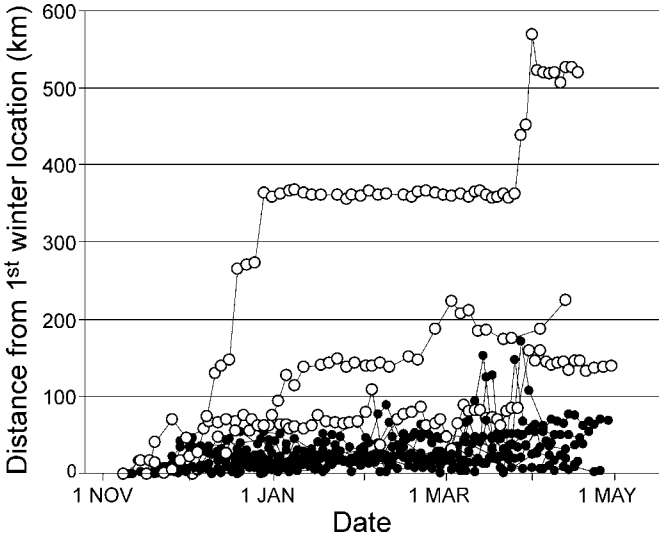


FIG. 6. Distance from first winter location to all subsequent winter locations for 14 radiotagged juvenile Golden Eagles from Denali National Park and Preserve, Alaska. Open symbols highlight three individuals that made one or more sustained departures from their initial winter location.

Juveniles moved mainly at midday, when updrafts were more likely to favor soaring–gliding flight (Kerlinger 1989), and peak movements during autumn migration coincided with favorable tail winds. Golden Eagles often use soaring–gliding flight rather than powered flight during migration and are expected to adjust their flight speed either to minimize energy expended or to maximize distance traveled (Kerlinger 1989). We suspect that individuals took advantage of tail winds when they were available, but our spring tracking data suggest that lack of tail winds did not impede their migratory progress.

Rates of movement varied across the migration period; during autumn migration, most individuals moved more rapidly earlier in their migrations and substantially more slowly as they ended migration. During spring migration, rates of movement differed by cohort, with the 1997 cohort exhibiting slower rates of movement earlier in their northward migrations than the 1999 cohort. Juveniles completed spring migration in fewer days and with fewer stopovers compared with autumn migration; we hypothesize that the experience that eagles gained during autumn migration and winter may explain this. However, defining the actual end dates of spring migration was problematic, because Golden Eagles did not migrate to a specific summering area and remain there for the summer; rather, they tended to stop in one area for a while and then make substantial movements to other areas during summer. Thus, we may have underestimated the duration and length of spring migration.

Close clustering of migration start dates suggests that environmental factors triggered the onset of sustained migratory movements of juveniles in autumn and spring. By contrast, the dispersion of ending dates for both autumn and spring migration suggests that individuals continued migrating until they found adequate resources.

Juveniles moved in similar geographic directions during distinct migration periods but used different migration routes and exhibited different migratory behaviors and strategies. Individuals generally exhibited little directional scatter along their migration routes. The variance surrounding the average bearings between natal and winter areas was attributable to movement of individuals eastward across the Canadian Shield or southward through British Columbia. The variance surrounding the average bearings between winter and summer areas was attributable to eagles drifting northward across the Yukon. By contrast, juvenile Osprey (*Pandion haliaetus*) exhibited directional scatter and diverted from the general course during autumn migration (Hake et al. 2001). Individual Golden Eagles in our study used different migration

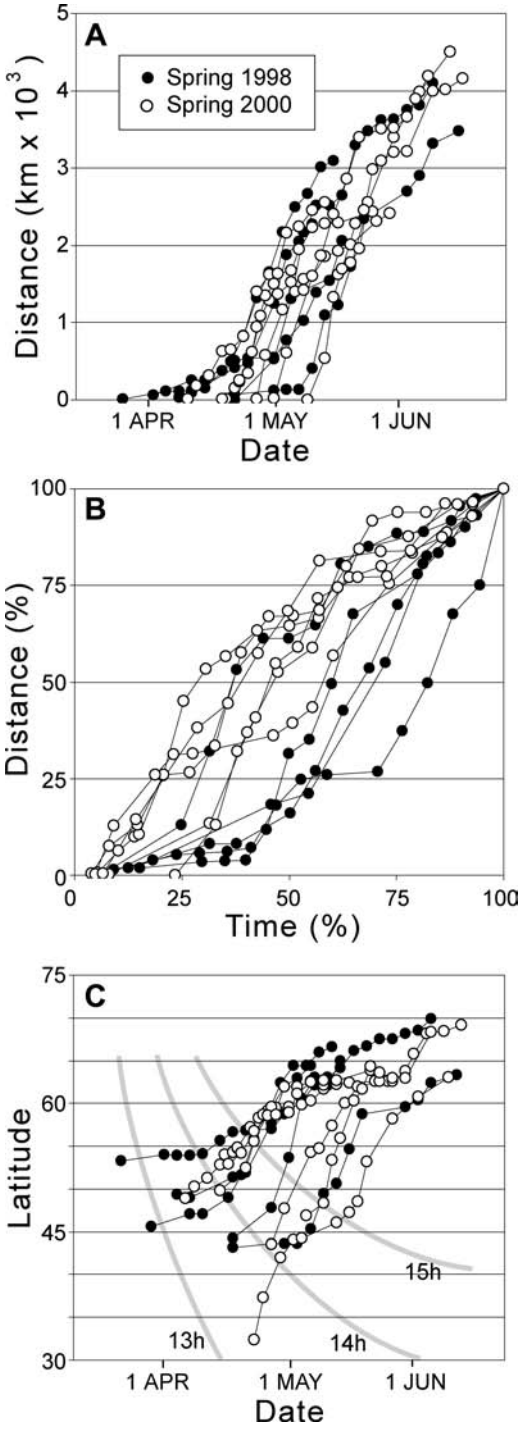


Fig. 7. Cumulative progression of 12 radiotagged juvenile Golden Eagles from Denali National Park and Preserve, Alaska, during spring migration. Movements are shown as (A) absolute distance over time; (B) proportional distance over proportional time; and (C) latitude over time with superimposed reference curves (gray) for 13, 14, and 15-h day-length.

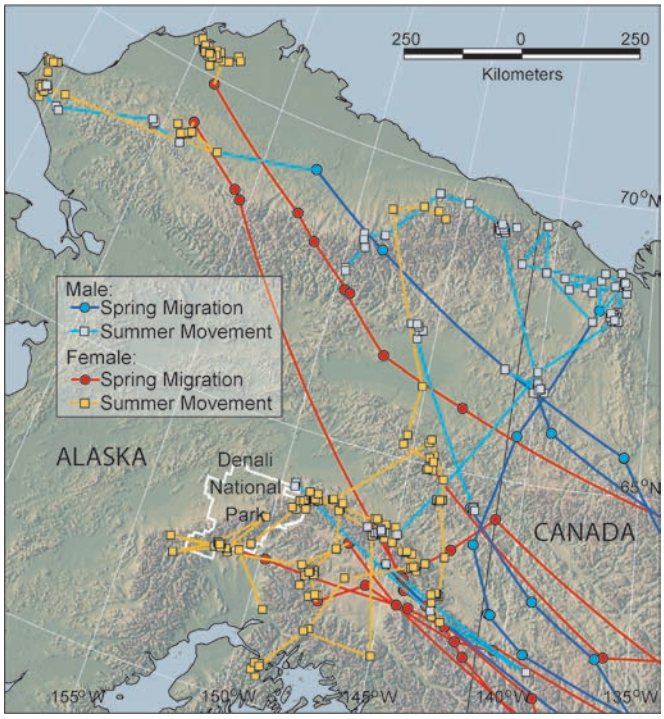


Fig. 8. Spring migration and summer movements of 12 radiotagged juvenile Golden Eagles from Denali National Park and Preserve, Alaska. Note movements to northern Alaska and the apparent difference between movements of males and females in relation to latitude and distance to Denali National Park and Preserve.

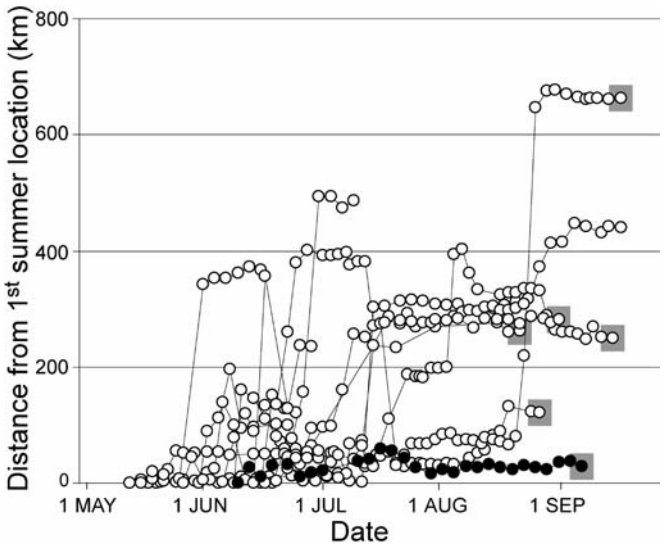


Fig. 9. Distance from first summer location to all subsequent summer locations for 12 radiotagged juvenile Golden Eagles from Denali National Park and Preserve, Alaska. Solid circles highlight one individual with strong fidelity to a single summer locality. Terminal shaded squares denote six radiotagged individuals that survived summer.

routes in autumn and spring, which suggests that their migration is complex and warrants further investigation (Hake et al. 2003, Chernetsov et al. 2004).

Most breeding Golden Eagles in Denali return to the study area in late March and complete their clutches by mid-April (McIntyre and Adams 1999). By contrast, most juveniles in the present study did not start migrating north until late March or early April, and most did not return to Alaska until mid-May through mid-June. Juvenile Steller's Sea-Eagles (*Haliaeetus pelagicus*) also reached summering sites after adults (Ueta et al. 2000). Juvenile Golden Eagles returning to Alaska likely exhibit different migratory strategies than adults that may be returning to Alaska to defend their territory and establish a nest.

Winter movements.—Most juvenile Golden Eagles wintered within or east of the Rocky Mountains, which is consistent with data on encounters with Golden Eagles banded as nestlings in Denali (C. L. McIntyre unpubl. data). Three juveniles wintered in central Alberta, and two juveniles wintered west of the Rocky Mountains in southern British Columbia and north-central Washington, which extends the documented wintering range of Denali's Golden Eagles.

Golden Eagles attempting to overwinter in the southern Yukon and southeast coastal Alaska died within two months of ending their autumn migration. Reports of Golden Eagles overwintering in southeast Alaska and the southern Yukon are rare, and winter observations of this species in the southern Yukon often occur during years of high abundance of Snowshoe Hares (*Lepus americanus*) (B. Bennett pers. comm.). Reports of starving and dead Golden Eagles in the southern Yukon in winter often coincide with extremely cold temperatures, and recovered carcasses of many radiotagged individuals that attempted to overwinter at northern latitudes showed signs of starvation (McIntyre et al. 2006). Thus, overwintering at northern latitudes may be a poor strategy for juveniles from northern latitudes.

Summer movements.—Juveniles did not exhibit a strong degree of homing to their natal areas. By contrast, migratory Bald Eagles (*H. leucocephalus*) radiomarked in the Greater Yellowstone Ecosystem were relocated at least once each year $\leq$1.6 km from their natal nests, usually in spring, autumn, or both (Harmata et al. 1999).

In contrast to their rather sedentary behavior in winter, juvenile Golden Eagles made extensive movements during summer and rarely settled into one area for very long. The large proportion of juvenile Golden Eagles from Denali that summered in and north of the Brooks Range in the northern Yukon and northern Alaska was one of our most surprising results. We suspect that these individuals were exploiting the region's spatially and temporally heterogeneous food resources (King 1970, Whitten et al. 1992). This finding illustrates the importance of this region not only for Golden Eagles nesting or raised in the local area, but also for those raised hundreds of kilometers to the south.

Conservation implications.—Conservation strategies for migratory birds often rely on site-based approaches for identifying areas used during migration, molting, staging, and winter (e.g., North American Waterfowl Management Plan). Because Golden Eagles from Denali and Hudson Bay (Brodeur et al. 1996), and perhaps from other areas in Alaska and northwestern Canada, range extensively across North America, we propose that conservation strategies for the migratory populations of this species aspire to a continental approach (e.g., Yukon-to-Yellowstone Conservation Initiative;see Acknowledgments).

Historical, current, and potential habitat changes (Kochert and Steenhof 2002, Kochert et al. 2002, Knick et al. 2003) across North America provide a convincing rationale for carefully monitoring Golden Eagle population trends (McCaffery and McIntyre 2005). Monitoring programs for Golden Eagle populations across North America should include studies on nesting grounds, during migration, and during winter (Kochert and Steenhof 2002). Our results point out potential limitations of using site-specific counts of migratory Golden Eagles as the only tool for monitoring their populations. For instance, juveniles from Denali used a "flyway" much broader than individual flyways described by Hoffman and Smith (2003), and they exhibited substantial variation in routes used during autumn and spring migrations. Before adopting migration counts as a primary tool for monitoring migratory Golden Eagle populations, more research is needed to document the variability among migration routes and migratory behaviors of individuals from different populations.

Our study provided new information on the movements of migratory juvenile Golden Eagles across western North America, but much remains to be learned about the year-round movements of all age classes. Our results cannot be applied to older age classes of Golden Eagles because they may behave differently as they age and gain experience, especially when approaching maturity or when entering a breeding population. Priority topics for future studies of Alaska Golden Eagles include (1) determining breeding dispersal of juveniles from their natal areas to their breeding areas, (2) identifying movement patterns of other age classes, and (3) identifying areas used throughout the year by all age classes.

ACKNOWLEDGMENTS

The U.S. Geological Survey (USGS) and the U.S. National Park Service provided funding for this study, with additional support from the USGS Forest and Rangeland Ecosystem Science Center and Denali National Park and Preserve. A. Lovaas, D. Fenn, S. Martin, G. Olson, P. Anderson, and P. Hooge provided important administrative support. Our study benefited greatly from the assistance of C. Grand, P. Grand, J. Reichert, B. Shott, and J. D. Swed, who helped us climb to nests. We appreciate the comments of M. Kochert, M. McGrady, K. Oakley, R. Ritchie, one anonymous reviewer, and, particularly, K. Steenhof, that improved the manuscript. The Oregon State University Animal Care and Use Committee approved our capture, handling, and attachment protocols (AUF no. 1962). The National Centers for Environmental Prediction (NCEP) reanalysis data set is available at www.cdc.noaa.gov. For information on the Yukon-to-Yellowstone Conservation Initiative, see www.y2y.net. Use of trade names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

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Associate Editor: K. Steenhof