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POSTFLEDGING DEPENDENCE PERIOD OF MIGRATORY GOLDEN EAGLES (*AQUILA CHRYSAETOS*) IN DENALI NATIONAL PARK AND PRESERVE, ALASKA

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Abstract.—The postfledging dependence period is not well documented for many species of raptors, including Golden Eagles (*Aquila chrysaetos*). From 1997 to 1999, we used satellite telemetry to estimate the length of the postfledging dependence period, and the finite survival rate of fledglings during that period, for migratory Golden Eagles in Denali National Park and Preserve, Alaska. Length of the postfledging dependence period averaged 50.1 days and ranged from 39 to 63 days. The postfledging dependence period was longer for Golden Eagles that hatched earlier, but hatching date did not influence the date they departed their natal area. Average date of departure from the natal area was 25 September. The departure period spanned a 17-day period from 15 September to 5 October, and coincided with a series of environmental changes including decreases in day length, temperature, and prey diversity. Probability of survival during the postfledging dependence period was 0.98 (95% CI = 0.94 to 1.00). *Received 18 April 2005, accepted 8 November 2005.*

Key words: Alaska, *Aquila chrysaetos*, Denali, Golden Eagle, postfledging dependence period, survival.

Período de Dependencia Posterior al Emplumamiento de *Aquila chrysaetos* en el Parque Nacional y Reserva Denali, Alaska

Resumen.—El período de dependencia posterior al emplumamiento no ha sido bien documentado en muchas especies de rapaces, incluyendo a *Aquila chrysaetos*. Desde 1997 hasta 1999 usamos telemetría satelital para estimar la duración del período de dependencia posterior al emplumamiento y la tasa finita de supervivencia de los volantones durante este período para el águila migratoria *A. chrysaetos* en el Parque Nacional y Reserva Denali, Alaska. La duración del período de dependencia posterior al emplumamiento promedió 50.1 días y varió entre 39 y 63 días. El período fue más largo para las águilas que eclosionaron más temprano, pero la fecha de eclosión no influenció la fecha de partida del área natal. La fecha promedio de partida desde el área natal fue el 25 de septiembre. El período de partida se extendió por un período de 17 días (desde el 15 de septiembre hasta el 5 de octubre) y coincidió con una serie de cambios ambientales, incluyendo la disminución en la extensión del día, en la temperatura y en la diversidad de presas. La probabilidad de supervivencia durante el período de dependencia posterior al emplumamiento fue 0.98 (95% IC = 0.94 a 1.00).

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The postfledging dependence period is an important stage of life for fledgling raptors. During this period, fledglings acquire adequate food reserves before migration (Wood et al. 1998), improve their flight skills (Bustamante and Hiraldo 1989), and develop hunting skills (Newton 1979, Weathers and Sullivan 1989, Bustamante 1993), while often free of the additional pressures of securing food (Amar et al. 2000). Despite its importance, the postfledging dependence period is one of the least-studied life-history stages of many raptor species, apparently because of difficulties associated with monitoring fledglings after they leave the nest (McFadzen and Marzluff 1996, Wood et al. 1998). Advances in radiotelemetry, however, are providing scientists with new tools to overcome some of these difficulties.

Factors regulating the length of the postfledging dependence period in raptors vary among species (Bustamante 1994). Parents may control the length of this period by reducing food-provisioning (Watson 1997) or exhibiting aggressive behavior toward their offspring (Alonso et al. 1987). By contrast, fledglings may lose interest in their parents once they are able to fend for themselves (Brown 1966) and may leave their natal areas as food supply decreases (McCollough 1986) or when migration starts (Bustamante and Hiraldo 1989).

Estimates of the length of the postfledging dependence period for Golden Eagles (*Aquila chrysaetos*) range from 30 to 180 days and are based on small sample sizes from studies where Golden Eagles are sedentary or short-distance migrants (Walker 1987, Bahat 1992, Watson 1997, Grant and McGrady 1999, O'Toole et al. 1999, Kochert et al. 2002). By contrast, Golden Eagles from northern latitudes of North America generally complete annual long-distance migrations (Kochert et al. 2002). Compared with Golden Eagles originating in temperate latitudes, fledgling Golden Eagles raised in northern latitudes in North America do not have the option of lingering in their natal areas throughout the winter (Kochert et al. 2002); they must migrate or chance overwintering in severe Arctic or sub-Arctic regions where winters are often extremely cold and food resources are limited.

Estimating survival during different life-history stages is essential for understanding population dynamics of raptors (McFadzen and Marzluff 1996, Zelenak et al. 1997, Bennetts et al. 1999), yet few raptor studies include estimates of survival during the postfledging dependence period. Many raptor studies include estimates of nesting success, but equating nesting success with recruitment can lead to erroneous conclusions about trends of individual populations over time (McFadzen and Marzluff 1996).

We used satellite telemetry to describe movements and estimate survival of migratory juvenile Golden Eagles from Denali National Park and Preserve, Alaska (hereafter "Denali"). Here, we report on the length of the postfledging dependence period and calculate finite survival rate of fledglings during this period. We tested the null hypotheses that length of the postfledging dependence period and survival within this period did not vary by year, sex, or brood size (1 or >1). We also tested for an effect of hatching date on length of the postfledging dependence period and date of departure from natal areas.

Methods

Study area.—The study was conducted in the northern foothills of the Alaska Range in northeastern Denali in central Alaska (63°36'N, 149°39'W). Rugged, mountainous terrain interspersed by broad glacial valleys and upland areas characterized the 2,100-km^2 study area. Elevations ranged from 427 m in the lowlands and river bottoms to 1,372 m along the foothill summits.

Field procedures.—We radiotagged nestlings in late July and early August just before they fledged. We entered nests using standard rock-climbing techniques; banded nestlings with federal leg bands; and measured the mass and length of their footpad, hallux, and culmen. We noted external physical condition of nestlings and estimated the fullness of their crop as empty, 25%, 50%, or 100%. We determined sex of nestlings using mass and footpad length (Edwards and Kochert 1986) and estimated their age by comparing their feather development with photographic aging guides (Hoechlin 1976, C. L. McIntyre unpubl. data).

We only radiotagged nestlings that were ≥56 days of age (≥80% of their estimated age at fledging; Steenhof 1987), in apparently good physical condition, and with mass ≥3,600 g at deployment. Nestling mass at deployment

ranged from 3,600 g to 4,400 g; the dual transmitters were <3% of nestling mass at deployment (Caccamise and Hedin 1985). We attempted to tag equal numbers of males and females among years, but only visited nests where we presumed the likelihood of injury or loss from premature fledging to be low.

We attached the dual transmitters to nestlings using a backpack harness (Buehler et al. 1991) constructed from 13-mm Teflon ribbon (Bally Ribbon Mills, Bally, Pennsylvania). The harness contained a biodegradable link made of cotton embroidery thread so that the dual transmitters would eventually fall off the Golden Eagles. The Oregon State University Institutional Animal Care and Use Committee approved our capture, handling, and radiotagging protocols (AUF no. 1962).

Telemetry equipment.—We used 95-g satellite-received transmitters (platform transmitting terminals [PTTs]; model PTT-100, Microwave Telemetry, Columbia, Maryland) that contained sensors to monitor battery voltage, movement, and temperature. The PTTs transmitted 8 h every 48 h during the postfledging dependence period, and the expected life span of PTTs was 2.5 years (P. Howey pers. comm.). We glued 9-g conventional radiotransmitters (VHF; model 3PN, Advanced Telemetry Systems, Isanti, Minnesota) to the side of PTTs and secured the VHF antenna to the body-harness shoulder-strap to ensure that it did not interfere with the PTT antennae. The VHFs transmitted only after PTTs remained motionless >48 h. We used VHF radio signals to locate mortalities.

Collecting satellite telemetry data.—We obtained data for eagles from ARGOS (Fancy et al. 1988, Harris et al. 1990) every two days. We determined the status of radiotagged Golden Eagles as alive, dead, or radio-failure using information on location, temperature, movement, and battery voltage. We categorized a PTT as radio-failure if we lost complete contact with it. If a PTT remained motionless for two or more duty cycles, we retrieved it as soon as possible to determine the Golden Eagle's fate.

Estimating the length of the postfledging dependence period.—No fledglings permanently moved out of their parents' nesting territory (defined as the fledglings' natal area) until the onset of autumn migration (C. L. McIntyre unpubl. data). Therefore, we defined the postfledging dependence period as the time between fledging and onset of autumn migration (Newton 1979, Rohner and Hunter 1996). We estimated date of departure as the midpoint between the last date that a Golden Eagle was within its natal area and the first date it was not. We estimated length of the postfledging dependence period as number of days between estimated fledging date and estimated departure date.

Statistical analyses.—We calculated the length of the postfledging dependence period and finite survival rate using data collected in all years. We radiotagged all nestlings in broods with >1 young, when possible, to determine whether departure dates differed between siblings. We estimated finite survival rate and its variance using the binomial method (White and Garrott 1990) and present estimates of survival as proportions with 95% confidence intervals (CI). We tested for equal probability of survival between sexes using Fisher's exact test and compared the length of the postfledging dependence period and departure date using Mann-Whitney tests. We did not use data from 1998 to test for differences in the length of the postfledging dependence period among years, because we radiotagged only five nestlings that year. We examined the length of the postfledging dependence period and departure date in relation to hatching date using simple linear regression and compared departure dates of sibling groups using a *t*-test. We used square-root transformation for all count data but report means as untransformed values for clarity.

We used S-PLUS, version 6.0 (Insightful, Seattle, Washington), for all statistical analyses. Unless otherwise noted, we report variation around the mean as standard deviation (±1 SD) and used $\alpha = 0.05$ as the level of significance for statistical tests.

Results

We radiotagged 48 nestlings from 1997 to 1999 (Table 1). We could not radiotag an equal number of nestlings in all years because nest accessibility and productivity varied among years, and many nestlings in 1998 did not achieve required mass for deploying PTTs. We observed all radiotagged Golden Eagles one to three times after fledging and did not note any apparent sign of increased stress or unusual behavior caused by

Table 1. Attributes of 48 radiotagged nestling Golden Eagles, Denali National Park and Preserve, Alaska, 1997–1999.

	Number of Golden Eagles			
Group	1997	1998	1999	Total
Sex				
Female	12	4	13	29
Male	10	1	8	19
Brood size				
One	5	2	6	13
Two	17	3	14	34
Three	0	0	1	1
Total	22	5	21	48

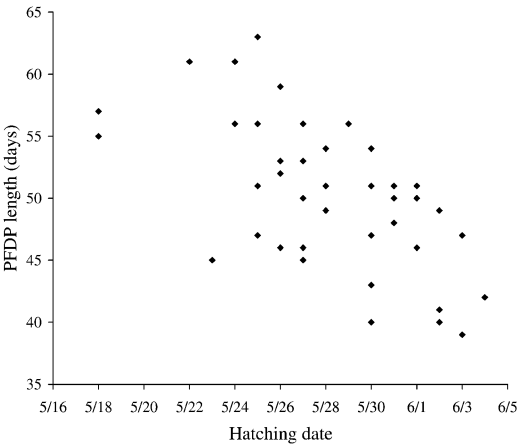

Fig. 1. Length of the Golden Eagle postfledging dependence period (PFDP) in relation to estimated hatching date (16 May–5 June), Denali National Park and Preserve, Alaska (F = 23.7, df = 1 and 42, $P < 0.001$, $r^2 = 0.36$). Data are pooled among years.

the harness and dual transmitters. We censored three PTTs from our data set, including one PTT that failed, one shed PTT that the Golden Eagle tore off soon after fledging, and one PTT with an unknown fate that we could not recover on an inaccessible mountainside. Aside from the one failure, the PTTs performed as expected throughout the study.

Length of the postfledging dependence period.—Length of the postfledging dependence period averaged 50.1 ± 5.7 days (Table 2) and did not differ by year, sex, or brood size (Table 2). Hatching date did not affect departure date (F = 0.64, df = 1 and 42, $P = 0.42$, $r^2 = 0.02$), but Golden Eagles that hatched earlier generally had a longer postfledging dependence period than those that hatched later (Fig. 1).

Average departure date was 25 September ± 4.6 days (Table 3). Departure dates did not vary by year, sex, or brood size (Table 3). The temporal pattern of departure was linear in 1997 and 1999 and corresponded to decreases in day length (Fig. 2).

On average, siblings departed their natal areas 4.3 ± 3.8 days apart (range = 1 to 13 days). Average number of days between departure dates for individuals from mixed-sex sibling groups (4.0 ± 3.0 days, n = 5) and same-sex sibling groups (4.6 ± 4.9 days, n = 7) did not differ (t-test = 0.20, df = 10, $P = 0.80$).

Survival.—Finite survival rate during the postfledging dependence period was 0.98 (95% CI = 0.94 to 1.00). Finite survival rate was similar for

Table 2. Length of the Golden Eagle postfledging dependence period (days) in Denali National Park and Preserve, Alaska, 1997–1999. Z statistics and related P values are for Mann-Whitney tests for year, sex, and brood size between 1997 and 1999.

	n	Mean ± SD	Minimum	Maximum	Z	P
Year						
1997	21	48.4 ± 5.2	39	56	–1.18	0.24
1998	3	50.6 ± 1.5	49	52		
1999	20	51.8 ± 6.3	41	63		
Sex						
Female	27	50.5 ± 5.7	39	61	0.71	0.48
Male	17	49.5 ± 5.9	40	63		
Brood size						
One	12	49.7 ± 5.7	41	61	–0.29	0.76
Two or three	32	50.3 ± 5.8	39	63		
Total	44	50.1 ± 5.7	39	63		

TABLE 3. Departure dates of fledgling Golden Eagles from their natal areas in Denali National Park and Preserve, Alaska, 1997–1999. *Z* statistics and related *P* values are for Mann-Whitney tests for year, sex, and brood size between 1997 and 1999.

Group	Mean ± SD	Minimum	Maximum	*Z*	*P*
Year					
1997	24 September ± 4.5 days	15 September	1 October	–1.61	0.11
1998	27 September ± 2.3 days	25 September	29 September		
1999	26 September ± 4.9 days	19 September	5 October		
Sex					
Female	26 September ± 4.4 days	19 September	2 October	0.82	0.41
Male	25 September ± 5.2 days	15 September	5 October		
Brood size					
One	27 September ± 3.8 days	20 September	2 October	1.28	0.19
Two or three	25 September ± 4.8 days	15 September	5 October		
Total	25 September ± 4.6 days	15 September	5 October		

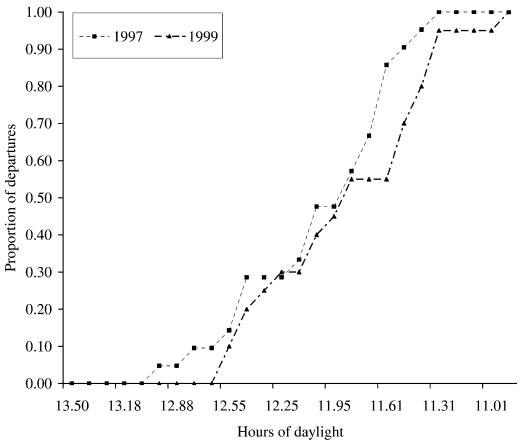

FIG. 2. Proportion of fledgling Golden Eagles departing their natal areas in relation to day length, Denali National Park and Preserve, Alaska. The *x* axis shows the number of hours of daylight every three days from 10 September (farthest left) to 15 October (farthest right), 1997–1999.

females (0.96, 95% CI = 0.89 to 1.00) and males (1.00) ($P = 0.45$). Finite survival rate of eagles was 1.00 in 1997 and 1999, and 0.75 (95% CI = 0.33 to 1.00) in 1998. Estimates of survival in 1998, however, were based on a sample of four radiotagged Golden Eagles. The single mortality documented in the present study occurred in 1998; a female Golden Eagle died approximately five weeks after fledging. We found the thoroughly scavenged carcass ~1,500 m from its natal nest but could not determine the cause of death.

DISCUSSION

Length of the postfledging dependence period.—Our results are consistent with Kessel's (1989) suggestion that the length of the postfledging dependence period for Golden Eagles in western and northern Alaska is <2 months. Our findings are not surprising; the Golden Eagle nesting season in interior Alaska is relatively short (McIntyre and Adams 1999), and Golden Eagles migrate out of the area in September and October (C. L. McIntyre unpubl. data). Departure dates were similar among years, and initiation of migration of fledglings from Denali was associated with decreasing daylight, a factor that remains constant among years. Prey diversity also decreased at this time as Arctic ground squirrel (*Spermophilus parryii*) and hoary marmot (*Marmota caligata*) began hibernation and Willow Ptarmigan (*Lagopus lagopus*) dispersed out of the area. We suspect that decreasing daylight and prey diversity also influenced parental behavior, but we do not know whether departure of parent Golden Eagles from their nesting territories influenced departure of their offspring.

Our results suggest that the postfledging dependence period for fledgling Golden Eagles that undertake long-distance migration is shorter than that for sedentary or short-distance migrants. The postfledging dependence period in Denali was shorter than reported for sedentary or short-distance migrant Golden Eagles in temperate latitudes (Walker 1987, Bahat 1992, Watson 1997, Grant and McGrady 1999, O'Toole et al. 1999, Kochert et al. 2002). No other

estimates of length of the postfledging dependence period of migratory Golden Eagles are available for comparison, but migratory populations of Peregrine Falcons (*Falco peregrinus*; Sherrod 1983) had shorter postfledging dependence periods than resident populations.

Our results suggest that fledgling Golden Eagles in Denali have little time to prepare for their long and extended migratory journeys, and that their postfledging dependence period is constrained by the onset of migration (see Meiri and Yom-Tov 2004). Golden Eagles that hatched earlier remained in their natal areas and did not depart on their migratory journeys earlier than those that hatched later. An earlier hatching date may provide fledglings with more time to improve their flight and hunting skills, which would be beneficial for survival during their next stages of life. Because of the brevity of the postfledging dependence period, we suspect that fledglings in Denali rely primarily on their parents for food during the postfledging dependence period (Robertson 1985, Bustamante and Hiraldo 1989, Donazar and Ceballos 1990, Hunt et al. 1992, Wood et al. 1998).

Survival.—Ours is the first study to estimate survival of fledgling migratory Golden Eagles during the postfledging dependence period. Our results suggest that survival of these large-bodied, long-distance migratory raptors is high during the postfledging dependence period. Unfortunately, there are few other empirically derived estimates of survival of Golden Eagles during this period with which to compare our results (Watson 1997, Kochert et al. 2002). However, fledglings of other large-bodied raptors, including Bald Eagle (*Haliaeetus leucocephalus*; Buehler et al. 1991, Wood et al. 1998) and Ferruginous Hawk (*Buteo regalis*; Zelenak et al. 1997) also exhibited high survival during the postfledging dependence period.

The present study occurred over a relatively short time, when primary prey species of Golden Eagles in Denali, including snowshoe hare (*Lepus americanus*) and Willow Ptarmigan, were abundant (McIntyre and Adams 1999, C. L. McIntyre unpubl. data). As with many other northern carnivores, cyclic populations of snowshoe hare and Willow Ptarmigan affect breeding success of Golden Eagles in Denali; laying rate and overall productivity is highest when prey is abundant and lowest when prey is limited (McIntyre and Adams 1999). We suspect that survival of fledgling Golden Eagles during the postfledging dependence period in Denali may be lower in years when prey is limited. For instance, survival of juvenile and adult Northern Goshawks (*Accipiter gentilis*) and Great Horned Owls (*Bubo virginianus*) in southwest Yukon, Canada, decreased in years when snowshoe hare populations declined (Doyle and Smith 1994, Rohner and Hunter 1996). Further, survival of juvenile Tawny Owls (*Strix aluco*) in Argyll, Scotland, declined in relation to declines in their main food supply (Petty and Thirgood 1989).

We also suspect that weather may affect survival of fledglings during the postfledging dependence period in Denali. Weather conditions vary substantially within and among years in our sub-Arctic study area (National Park Service [NPS] unpubl. data). The single mortality documented in this study occurred in 1998 when productivity and nestling mass were low despite high prey abundance. Low productivity and lower body mass of nestlings in 1998 coincided with one of the wettest and coolest summers recorded in Denali since 1930 (NPS unpubl. data). We hypothesize that increased rainfall and more days with precipitation in 1998 may have influenced provisioning rates and that cooler weather may have increased energetic needs of nestlings, resulting in overall poorer physiological condition of nestlings (Dawson and Bortolotti 2000, Redpath et al. 2002). Therefore, we suspect that prolonged periods of wet and cold weather during the nesting season may decrease the probability of survival of fledglings during the postfledging dependence period.

Future research questions.—Our results provide new insights about the Golden Eagle postfledging dependence period, but many questions remain. (1) What is the role of parents during the postfledging dependence period, and how does it affect survival of fledglings? (2) Do parents depart their nesting territory before their offspring, and does their departure influence departure of their offspring? (3) Do mass and physiological condition of fledglings influence their survival during the postfledging dependence period? (4) Does sibling competition continue during the postfledging dependence period, and does it affect survival? (5) How do weather and prey abundance affect fledgling survival during and after the postfledging dependence period? (6) Does survival during the postfledging dependence period vary

substantially across the range of Golden Eagles, and is the probability of survival different for resident and migratory populations? Clearly, a better understanding of factors affecting survival of fledgling Golden Eagles during the postfledging dependence period will require longer studies of both fledglings and their parents across the range of this species.

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