

PATTERNS IN NESTING AREA OCCUPANCY AND REPRODUCTIVE SUCCESS OF GOLDEN EAGLES (*AQUILA CHRYSAETOS*) IN DENALI NATIONAL PARK AND PRESERVE, ALASKA, 1988–99

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ABSTRACT.—Annual territory occupancy and reproductive success of nesting Golden Eagles (*Aquila chrysaetos*) were monitored at 58–76 nesting areas in Denali National Park and Preserve, Alaska since 1988. Data were collected annually using two standardized aerial surveys and follow-up foot surveys. Aerial surveys were conducted during the early incubation period (late April) to determine occupancy and nesting activities and late in the nestling period (late July) to count fledglings and determine nesting success. All aerial surveys were conducted using a Bell 206B Jet Ranger helicopter with one or two experienced observers and an experienced wildlife pilot. Aerial surveys were the most time- and cost-efficient means to survey the 1800-km² study area. Average flight time during late April surveys was 12.8 flight hr (over 3 d) and during late July was 5.3 flight hr on 1 d. Duration of surveys depended on nesting activities. Foot surveys were useful for making longer observations in areas where territory occupancy could not be determined during aerial surveys. Annual occupancy rates averaged 83%. Laying rates, success rates, and overall population productivity varied significantly over the study period. Fledgling production varied greatly over the 12-yr period from a low of 9 fledglings in 1994 to a high of 70 fledglings in 1999. Laying rates, mean brood size, and overall population productivity were significantly correlated with abundance of cyclic snowshoe hare (*Lepus americanus*) and Willow Ptarmigan (*Lagopus lagopus*) populations. Cyclic prey did not influence occupancy rates. Most territories were occupied more than 8 yr, but four remained vacant throughout the study. Productivity varied greatly among nesting territories. More than 50% of all fledglings were produced at 17 nesting areas and >75% of all fledglings were produced at 35 nesting areas.

KEY WORDS: Golden Eagle; *Aquila chrysaetos*; reproduction; Denali National Park; Alaska.

Patrones en la ocupación del área de anidamiento y el éxito reproductivo de las águilas reales (*Aquila chrysaetos*) en el parque nacional y coto de caza de Denali, Alaska, 1988–99

RESÚMEN.—La ocupación anual del territorio y el éxito reproductivo de águilas reales (*Aquila chrysaetos*) durante la anidación fueron monitoreados en 58–76 áreas de anidación en el parque nacional y coto de caza de Denali, Alaska desde 1988. Los datos fueron colectados anualmente usando dos estudios aéreos estandarizados y prosiguiendo con estudios a pie. Los estudios aéreos fueron desarrollados durante el periodo temprano de incubación (a finales de abril) para determinar la ocupación y las actividades de anidamiento, y durante el periodo tardío de anidación (a finales de Julio) para contar los polluelos y determinar el éxito reproductivo. Todos los estudios aéreos fueron hechos usando un helicóptero Bell 206B Jet Ranger con uno o dos observadores experimentados y un piloto experimentado en vida silvestre. Los estudios aéreos fueron los medios tiempo-costos más eficientes para estudiar los 1800-km² del área de estudio. El tiempo promedio de vuelo durante los estudios de finales de abril fue 12.8 vuelos hora (cerca de 3 días) a finales de julio fue 5.3 vuelos hora cerca de 1 día. La duración de los estudios dependió de las actividades de anidación. Los estudios a pie fueron útiles para hacer observaciones más largas en áreas donde la ocupación del terreno no pudo ser determinada durante los estudios aéreos. Las tasas de ocupación anual promedian 83% y no varían significativamente en el tiempo. Las tasas de postura, las de éxito y la productividad total de la población variaron significativamente durante el periodo de estudio. La producción de polluelos varió grandemente durante el periodo de 12 años desde un nivel bajo de 9 polluelos en 1994 hasta uno alto de 70 polluelos en 1999. Las tasas de postura, la media del tamaño de la nidada, y la productividad de toda la población estuvieron correlacionadas significativamente con la abundancia de las poblaciones cíclicas de liebres “zapatos de nieve” (*Lepus americanus*) y del urogallo de sauce (*Lagopus lagopus*). Las presas cíclicas no influenciaron las tasas de ocupación. La mayoría de territorios fueron ocupados por más de 8 años,

pero 4 permanecieron vacantes a través de todo el estudio. La productividad varió grandemente entre los territorios de anidamiento. Mas del 50% de todos los polluelos se produjeron en 17 áreas de anidación y >75% de todos los polluelos fueron producidos en 35 áreas de anidación.

[Traducción de César Márquez y Victor Vanegas]

Few long-term studies have examined the reproductive characteristics of Golden Eagles (*Aquila chrysaetos*) at high latitudes in North America (McIntyre and Adams 1999). Breeding populations in northern North America are migratory, spending ≥ 5 mo migrating to, wintering in, and returning from temperate latitudes thousands of kilometers from their nesting areas (Gabrielson and Lincoln 1959, Palmer 1988, Brodeur et al. 1996). Many breeding populations depend on cyclic prey and have few alternate prey sources early in the nesting season. This life history strategy is common among birds breeding at northern latitudes and entails high energy demands for migration immediately before annual reproductive efforts. Furthermore, Golden Eagles arrive at their northern breeding areas in late winter when abundance and diversity of their prey is at its lowest annual level.

Golden Eagle reproduction is tied to the abundance of its principal prey (Tjernberg 1983, Bates and Moretti 1994, Steenhof et al. 1997). Snowshoe hare (*Lepus americanus*) and Willow Ptarmigan (*Lagopus lagopus*) are common food sources available to breeding Golden Eagles in interior Alaska early in the nesting season (McIntyre unpubl. data). Hare and ptarmigan experience large amplitude population cycles in Alaska (Buckley 1954, Weeden 1959). From May–August, breeding Golden Eagles in interior Alaska prey heavily upon arctic ground squirrel (*Spermophilus parryi*), as well as hoary marmot (*Marmota caligata*), snowshoe hare, and Willow Ptarmigan (Murie 1944, McIntyre and Adams 1999). Ground squirrels and marmots are obligate hibernators and do not emerge from hibernation until mid-April and early May, long after most eagles have completed their clutches.

In this paper, I describe the reproductive characteristics and evaluate relationships between reproductive components and abundance of cyclic prey of a northern, migratory Golden Eagle population that nests in Denali National Park, Alaska. I also report on patterns of nesting area occupancy and productivity.

METHODS

Study Area. The 1800-km² study area, centered at 63°35'N and 149°30'W is in Denali National Park on the

north side of the Alaska Range in interior Alaska (Denali). Most of the study area is within a federally designated Wilderness Area and an internationally recognized World Biosphere Reserve. Human activities occur primarily in summer and are concentrated along a gravel road that traverses the study area.

Mountains, broad glacial river valleys, low rolling tundra, and upland areas dominate the study area landscape. Elevations in the study area range from 350–2500 m. Most of the study area is above treeline (800 m). Mountains south of the study area exceed 2500 m in elevation and are permanently covered with ice and snow. Sheldon (1930), Dixon (1938), and Murie (1944, 1963) provide detailed descriptions of the vegetation and geology of the study area.

The region has a subarctic montane climate with temperatures ranging from -47°C – 32°C . Average annual precipitation is 38 cm, including about 200 cm of snowfall. During 1988–99, snow cover persisted at lower elevations from mid-September through mid-May, an average of 210 d (National Park Service unpubl. data).

Breeding pairs of Golden Eagles return to Denali during late February to early April (Murie 1944, McIntyre 1995). Most clutches are completed by mid-April and nestlings usually fledge in late July and early August (McIntyre 1995). Autumn migration starts in late September and continues into October.

Terminology. I followed terminology recommended by Postupalsky (1983), Newton and Marquiss (1982), and Steenhof (1987) to describe occupancy and activities at nesting areas. An area where at least one nest was found and where no more than one pair of Golden Eagles nested in one year was considered a nesting area. Nests were assigned to unique nesting areas based on their history of use and location. A nesting area was considered occupied if a territorial pair or evidence of a territorial pair (such as an incubating bird, nest construction, or nest maintenance) was observed; otherwise the area was deemed unoccupied.

A territorial pair of Golden Eagles that laid eggs was termed a laying pair (Steenhof et al. 1997). I did not flush birds off nests to count eggs and presumed that incubating birds had eggs. Nestlings that reached 51 days-of-age (or 80% of the mean age at first flight) were considered fledglings (Steenhof 1987). Laying pairs that produced ≥ 1 fledgling were considered successful pairs.

Surveys. I surveyed the study area twice annually by helicopter to find territorial and laying pairs of Golden Eagles and to count fledglings. Additional observations were conducted by dogsled in March and on foot throughout the nesting season to supplement aerial surveys. Another experienced observer usually assisted me with each survey.

During the first aerial surveys each year, we checked all known nests within each nesting area to determine occupancy and describe nesting activities. We also searched for new nests and nesting areas. These surveys

were conducted on two to five consecutive days in late April and early May. Most clutches were completed at this time and hatching had not yet occurred. Nesting areas not classified as occupied during this survey were revisited later in the nesting season to confirm their status. The second annual surveys were conducted in late July or early August to count fledglings and document nesting success. By this time of year, most nestlings were >51-days-old, but few had fledged.

All surveys were flown at 30–40 km/hr and we periodically hovered to observe nest contents. A minimum distance of >100 m was maintained between the helicopter and nest structures during all aerial surveys. We landed and made observations from vantage points on the ground when we could not determine occupancy or nesting activities from the helicopter. We used binoculars (10 × 40) during all aerial surveys, and binoculars and spotting scopes (15–45×) during ground observations. I followed recommendations made by Fyfe and Olendorff (1976) to avoid disturbing adults and nestlings during field activities.

I report annual reproductive performance of Golden Eagles in Denali using four components: (1) occupancy rate, as the proportion of nesting areas surveyed that were occupied by territorial pairs; (2) laying rate, as the proportion of territorial pairs that laid eggs; (3) success rate, as the proportion of laying pairs that produced ≥1 fledgling; and (4) mean brood size, as the average brood size for successful pairs. Population productivity is reported as the mean number of fledglings produced annually per territorial pair.

Index of Prey Abundance. I developed indices of population change of snowshoe hare and Willow Ptarmigan on a broad scale by recording the number of each species observed annually during routine field activities. Annual indices of abundance for snowshoe hare and Willow Ptarmigan were highly correlated in our study ($R^2 = 0.95$, $N = 12$ yr, $P < 0.0001$). Therefore, I used mean number of snowshoe hares observed per field day as our index of spring prey abundance. Results and conclusions were identical when Willow Ptarmigan or combinations of these prey species were used in the analyses.

Statistical Analyses. I used chi-square analyses to test for differences in occupancy rate, laying rate, and success rate among years. Analysis of variance (ANOVA) was used to test for differences in mean brood size among years. I used Pearson's correlation to test for a relationship between Golden Eagle reproduction and spring prey abundance. All statistical tests were run using Statistix® software (Analytical Software 1992). All tests are considered significant at the 0.05 level.

RESULTS

I monitored 56–76 nesting areas annually (Table 1), and the same 62 nesting areas for ≥10 yr. Although I attempted to survey all known nesting areas each year, weather conditions during aerial survey in several years prevented me from making observations at all nesting areas.

Overall, occupancy rate averaged 83% and varied significantly among years ($\chi^2_{11} = 22.72$, $P =$

0.02). Of the 62 nesting areas monitored for ≥10 yr, 49 (79%) were occupied ≥10 years and 38 were occupied for 12 consecutive yr. Laying rate was the most variable reproductive component we measured ($\chi^2_{11} = 82.01$, $P < 0.001$), ranging from 33% in 1994 to 90% in 1989. Success rate also varied slightly ($\chi^2_{11} = 19.97$, $P = 0.05$) from a low of 42% in 1994 to a high of 88% in 1996. Annual mean brood size averaged 1.45 fledglings per successful pair and varied significantly among years ($F_{11,291} = 1.98$, $P < 0.05$). Population productivity ranged from 0.16–1.16 fledglings per territorial pair. A total of 455 fledglings were produced during the 12-yr period; 406 fledglings were produced at 62 nests monitored for ≥10 yr. A total of 17 (27%) of 62 nests monitored for ≥10 yr produced 50% of all fledglings from 1988–99. The most productive nesting area produced 15 fledglings over 12 yr, with 8 successful nesting attempts and a mean brood size higher than the population mean (1.88 compared to 1.45).

Annual indices of abundance for snowshoe hare and Willow Ptarmigan were highly correlated during the study period ($R^2 = 0.95$, $N = 12$ yr, $P < 0.001$). The number of hares observed per day annually ranged from 0.7–8.12. The number of ptarmigan observed per day annually ranged from 3–22. Abundance of both species was lowest in 1994.

Occupancy rate and success rate did not change in relation to spring prey abundance (occupancy: $R^2 = 0.04$, $P = 0.89$; success: $R^2 = 0.35$, $P = 0.25$). Laying rate and mean brood size were affected by the abundance of cyclic prey (laying rate: $R^2 = 0.83$, $P = 0.009$; mean brood size: $R^2 = 0.71$, $P = 0.0091$). Because of the significant positive relationships for both laying rate and mean brood size, population productivity also was affected significantly by prey abundance ($R^2 = 0.81$, $P = 0.001$).

DISCUSSION

My results suggest that reproductive success of migratory Golden Eagles in interior Alaska is influenced by fluctuating numbers of prey available to eagles early in the nesting season. I could explain 83% of the variation in Golden Eagle productivity with changes noted in the abundance of spring prey.

Laying rate was the most important factor influencing population productivity of Golden Eagles in Denali during this study. Laying rate varied widely compared to other components of reproduction and was most closely related to spring prey abun-

Table 1. Summary of reproductive characteristics of Golden Eagles (*Aquila chrysaetos*) in Denali National Park, Alaska, 1988–99.

YEAR	NESTING AREAS SURVEYED	NESTING AREAS OCCUPIED	PAIRS WITH EGGS	TOTAL FLEDGLINGS	OCCUPANCY RATE (%)	LAYING RATE (%)	SUCCESS RATE (%)	FLEDGLINGS PER OCCUPIED TERRITORY	MEAN BROOD SIZE
1988	56	47	37	38	83.93	78.72	75.68	0.81	1.36
1989	66	50	45	58	75.76	90.00	77.78	1.16	1.66
1990	66	46	38	47	69.70	82.61	73.68	1.02	1.68
1991	66	51	35	43	77.27	68.63	82.86	0.84	1.48
1992	70	57	36	26	81.43	63.16	52.78	0.46	1.37
1993	68	55	25	23	80.88	45.45	68.00	0.42	1.35
1994	68	58	19	9	85.29	32.76	42.11	0.16	1.13
1995	68	59	27	25	86.76	45.76	70.37	0.42	1.32
1996	72	62	26	30	86.11	41.94	88.46	0.48	1.30
1997	72	63	45	54	87.50	71.43	73.33	0.86	1.64
1998	70	62	34	31	88.57	54.84	61.76	0.50	1.48
1999	76	71	55	71	93.42	77.46	78.18	1.00	1.65

dance. Laying rates were lowest when the spring prey populations were at their lowest level.

Overall, success of laying pairs in Denali was not influenced by spring prey abundance. Before and during laying, snowshoe hare and Willow Ptarmigan constitute most of the available prey for Golden Eagles in Denali (McIntyre and Adams 1999). The importance of these species in the diet of eagles in Denali, however, probably decreases as arctic ground squirrels and hoary marmots emerge from hibernation. However, success rate of eagles in Denali was lowest in years when hare and ptarmigan were at the lowest level of their population cycles. Additionally, mean brood size declined significantly only in years when cyclic prey were scarce. At Kluane Lake, Canada, densities of arctic ground squirrels are strongly correlated with hare abundance (Boutin et al. 1995). If this situation exists in Denali and other areas in Alaska, I expect low success rates and smaller broods of eagles during population lows of hares.

Golden Eagles show great dietary plasticity (Watson 1997). However, the lack of alternate prey may limit diet diversity of Golden Eagles during the early nesting season in northern areas. Few alternate prey are available for Golden Eagles in March and early April in interior Alaska. In Denali, carrion is scarce and carcasses of ungulates are quickly scavenged by terrestrial carnivores (Adams unpubl. data). Throughout interior Alaska, where few alternate prey occur, I expect productivity of Golden Eagles to fluctuate in synchrony with cyclic hare populations. Few empirical data, beyond our study, are available to test this hypothesis. However, Golden Eagles nesting along the Porcupine River in interior Alaska were more successful in years when snowshoe hare were abundant (Ritchie and Curatolo 1982). Similarly, Golden Eagles in southwestern Alaska reared young only in the years when hare densities were high (Petersen et al. 1991).

Occupancy rates of eagles in Denali remained relatively stable over the study period and did not change in relation to abundance of cyclic prey. Most (75%) nesting areas monitored for ≥ 10 yr were occupied in all years. Golden Eagles are long-lived and it may be advantageous for them to protect nesting areas for future breeding attempts, even when prey conditions are unfavorable for producing and rearing young (Newton 1979, Steenhof et al. 1997). These results are consistent with other long-term Golden Eagle studies (Brown and Watson 1964, Steenhof et al. 1997, Watson 1997).

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