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# REPRODUCTIVE CHARACTERISTICS OF MIGRATORY GOLDEN EAGLES IN DENALI NATIONAL PARK, ALASKA[1]

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*Abstract.* We describe reproductive characteristics of Golden Eagles (*Aquila chrysaetos*) breeding in Denali National Park, Alaska during an entire snowshoe hare (*Lepus americanus*) cycle, 1988–1997. Data on nesting eagles were collected at 58 to 72 nesting areas annually using two aerial surveys. Surveys were conducted during the incubation period to determine occupancy and nesting activities and late in the nestling period to count nestlings and determine nesting success. Annual occupancy rates of nesting areas did not vary significantly, whereas laying rates, success rates, and mean brood size varied significantly over the study period. Fledgling production for the study population varied sevenfold during the ten-year period. Laying rates, mean brood size, and overall population productivity were significantly correlated with abundance of cyclic snowshoe hare and Willow Ptarmigan (*Lagopus lagopus*) populations. Reproductive rates of Golden Eagles in Denali were similar to those of Golden Eagles from other high latitude study areas in North America, but lower than for Golden Eagles from temperate zone study areas in North America.

*Key words*: *Alaska,* Aquila chrysaetos, *cyclic prey, Denali National Park, Golden Eagles, reproductive characteristics.*

## INTRODUCTION

Our current understanding of reproductive performance of Golden Eagles (*Aquila chrysaetos*) in North America is largely based upon studies from resident populations in temperate latitudes (Palmer 1988, Steenhof et al. 1997, Watson 1997). However, breeding populations in northern North American are migratory, spending ≥ 5 months 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). 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. Therefore, productivity of northern populations of Golden Eagles could be markedly lower than their temperate counterparts.

Reproduction of Golden Eagles is related to the abundance of their principal prey (Tjernberg 1983, Bates and Moretti 1994, Steenhof et al. 1997). Snowshoe hare (*Lepus americanus*) and Willow Ptarmigan (*Lagopus lagopus*) are the common food sources available to breeding Golden Eagles in interior Alaska early in the nesting season (McIntyre, unpubl. data). Both hare and ptarmigan experience large-amplitude population cycles in Alaska (Buckley 1954, Weeden 1959). During the nestling cycle (May–August), breeding Golden Eagles in interior Alaska prey heavily upon arctic ground squirrel (*Spermophilus parryii*), as well as hoary marmot (*Marmota caligata*), snowshoe hare, and Willow Ptarmigan (Murie 1944, McIntyre, unpubl. data). 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. Because snowshoe hares and Willow Ptarmigan constitute most of the prey available to Golden Eagles prior to and during egg-laying, we hypothesized that productivity of eagles would vary widely with the abundance of these important prey species and would closely follow their population cycles.

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Few studies have examined the reproductive characteristics of Golden Eagles at high latitudes in North America. Northern breeding populations of Golden Eagles are migratory. Many of these breeding populations depend on cyclic prey and have few alternate prey sources early in the nesting season. Therefore, we hypothesized that productivity of these populations would be lower than that of Golden Eagles nesting in temperate latitudes.

In this paper we 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. We also compare reproductive characteristics of Denali's Golden Eagles with characteristics of the species in more southerly latitudes in North America.

## METHODS

### STUDY AREA

The 1,800-km$^2$ study area (centered at 63°35′N, 149°30′W) is in Denali National Park on the north side of the Alaska Range in interior Alaska. 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 m to 2,500 m above sea level. Most of the study area is above treeline (800 m) and is bounded on the south by the Alaska Range, on the north by the northern slope of foothills of the Alaska Range, on the east by the Nenana River, and on the west by Boundary and Glacier Creeks. Mountains to the south exceed 2,500 m in height and are permanently snow and ice covered. 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 to 32°C. Average annual precipitation is 38 cm, including about 200 cm of snowfall. During 1988 to 1997, snow cover persisted at lower elevations from mid-September through mid-May, an average of 210 days (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 by early August (McIntyre 1995). Autumn migration starts in late September and continues into October.

The study area supports a variety of mammals and birds, including many used as prey by Golden Eagles (Murie 1944, McIntyre 1995). Three ptarmigan species, Willow, Rock (*L. mutus*), and White-tailed (*L. lecurus*), live in the study area. Willow Ptarmigan, the most common and widely distributed species (Dixon 1938, Murie 1963), demonstrate 9- to 11-year cyclic fluctuations in numbers (Weeden 1959). Snowshoe hare inhabit forested areas and willow thickets in the study area. Populations of snowshoe hares in interior Alaska fluctuate on 8- to 11-year cycles (Buckley 1954). Hoary marmot are found at higher elevations in loosely-formed colonies. Arctic ground squirrels are abundant; their colonies are distributed throughout the study area.

### TERMINOLOGY

We used recommendations 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). Because we did not flush birds off nests to count eggs, we 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 ≥ one fledgling were considered successful pairs.

### SURVEYS

We 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.

During the first aerial survey each year we attempted to check all previously 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 at least twice during the nesting season to confirm their status.

The second annual survey was conducted on one day 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. At nests where fledging occurred before the second survey, we landed the helicopter and made observations to locate and count fledglings.

All aerial surveys were flown at 30–40 km $hr^{-1}$; we periodically hovered to observe nest contents. A minimum distance of at least 65 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. We followed recommendations made by Fyfe and Olendorff (1976) to avoid disturbing adults and nestlings during field activities.

We 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. We report population productivity as the mean number of fledglings produced annually per territorial pair.

## INDEX OF PREY ABUNDANCE

We attempted to obtain 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. Similar data on black-tailed jackrabbits (*Lepus californicus*) in Idaho provided results comparable to abundance estimates from spotlighting transects (Steenhof et al. 1997). Annual indices of abundance for snowshoe hare and Willow Ptarmigan were highly correlated in our study ($R^2 = 0.94$, $n = 10$ years, $P < 0.001$; Fig. 1A). Therefore, we used mean number of snowshoe hares observed per field day as our index of prey abundance. Results and conclusions were identical when Willow Ptarmigan or combinations of these prey species were used in the analyses.

## STATISTICAL ANALYSES

We 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. We conducted logistic regressions for reproductive components expressed as proportions (occupancy rate, laying rate, and success rate), and stepwise multiple linear regression for mean brood size and population productivity to test for a relationship between Golden Eagle reproduction and abundance of cyclic prey. Logistic regression procedures use model [$p = (e^{\beta_0+\beta_1 X}) \div (1 + e^{\beta_0+\beta_1 X})$], where $p$ is the reproductive component of interest, X is the prey index, and $\beta_0$ and $\beta_1$ are model parameters. Models were evaluated by change-in-deviance procedures using a likelihood ratio test ($G^2$; Feinberg 1980). For linear regression analyses of mean brood size or population productivity versus prey abundance, we tested addition of a quadratic term to the basic linear model ($Y = \beta_0 + \beta_1 X + \beta_2 X^2$) to allow for curvature in the relationship. We evaluated linear regression with $F$-tests, and model parameters with $t$-tests (Zar 1984). We compared the averages of annual estimates of mean brood size and population productivity for Golden Eagle populations from northern (> 55°N) and temperate study areas reported in nine published studies (Table 1). Because we predicted lower values for northern populations, we used one-tailed $t$-tests. All statistical tests were run using Statistix® software (Analytical Software 1992). All tests are considered significant at the 0.05 level.

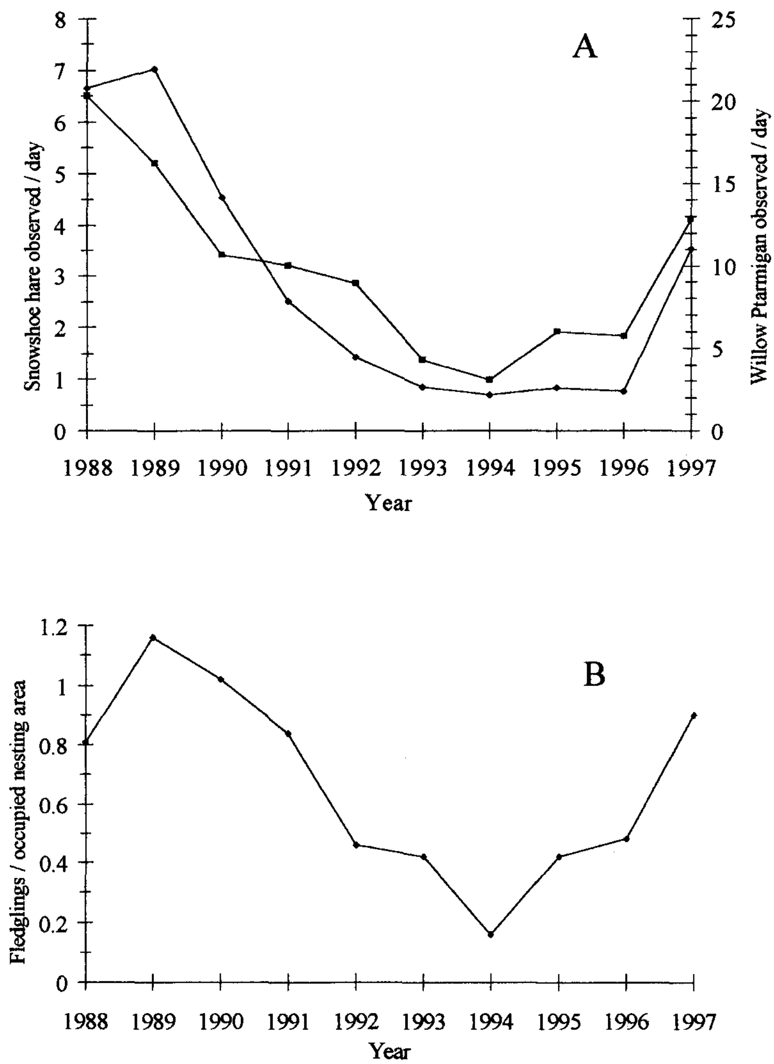


FIGURE 1. Numbers of Willow Ptarmigan (solid diamonds) and snowshoe hare (solid squares) observed annually (A) and overall annual population productivity for Golden Eagles (B), Denali National Park, Alaska, 1988–1997.

## RESULTS

We monitored 56 to 72 nesting areas annually (Table 2). The number of known nesting areas increased from 56 in 1988 to 72 in 1997. We attributed this to our increased familiarity with the study area and not to an increase in nesting areas in the study area. Although we attempted to survey all known nesting areas each year, weather conditions during the first aerial survey in 1993, 1994, and 1995 prohibited us from making observations at four nesting areas.

Occupancy rate averaged 81% and did not vary significantly among years (Table 2; $\chi^2_9 = 12.9$, $P = 0.12$). Laying rate was the most variable reproductive component we measured ($\chi^2_9 = 70.4$, $P < 0.001$), ranging from 33% in 1994 to 90% in 1989 (Table 2). Success rate also varied significantly ($\chi^2_9 = 18.1$, $P < 0.01$) from a low of 42% in 1994 to a high of 88% in 1996 (Table 2). Annual mean brood size averaged 1.43 fledglings per successful pair (Table 2) and varied significantly among years ($F_{9,232} = 1.98$, $P < 0.05$). Population productivity ranged from 0.16 to 1.16 fledglings per territorial pair (Fig. 1B).

TABLE 1. Mean brood size and productivity data from Golden Eagle populations in North America.

| Study area | Latitude | Years | Nesting areas per year | Mean brood size | Fledglings per territorial pair | Reference |
|---|---|---|---|---|---|---|
| Arctic National Wildlife Refuge, AK | 69.5°N | 3 | 8–14 | 1.22 | NP[a] | Young et al. 1995 |
| Northwest Territories, Canada | 68°N | 4 | 10–20 | 1.30 | 0.63 | Poole and Bromley 1988 |
| Porcupine River, AK | 67°N | 4 | 3–9 | 1.50 | NP | Ritchie and Curatolo 1982 |
| Denali National Park, AK | 63.5°N | 10 | 46–63 | 1.43 | 0.66 | This study |
| Saskatoon River, Saskatchewan, Canada | 50.5°N | 25 | 1–8 | 1.46 | NP | Houston 1985 |
| SE Montana/N Wyoming | 45°N | 11 | 10–30 | 1.30 | 0.78 | Phillips et al. 1990 |
| N Wyoming | 44°N | 5 | 85–140 | 1.48 | 0.81 | Phillips and Beske 1990 |
| SE Oregon | 43.5°N | 16 | 5–18 | 1.70 | NP | Thompson et al. 1992 |
| SW Idaho (Snake River) | 43°N | 24 | 28–35 | 1.57 | 0.79 | Steenhof et al. 1997 |

[a] NP = data not presented in source paper.

Annual indices of abundance for snowshoe hare and Willow Ptarmigan were highly correlated in our study (Fig. 1A; $R^2 = 0.94$, $n = 10$ years, $P < 0.001$). The number of hares observed per day annually ranged from 0.7 to 7.1. The number of Ptarmigan observed per day annually ranged from 3 to 21. Abundance of both species was lowest in 1994.

Occupancy rate and success rate were not affected by prey abundance (Fig. 2A and 2C; occupancy: $G^2_1 = 2.8$, $P = 0.1$; success: $G^2_1 = 3.1$, $P = 0.08$). Laying rate and mean brood size were affected by the abundance of cyclic prey (Fig. 2B and 2D; logistic regression model for laying: $\beta_0 = -0.46$, $\beta_1 = 0.37$, $G^2_1 = 69.41$, $P < 0.001$; multiple regression model for mean brood size: $Y = 1.1 + 0.21X - 0.02X^2$, $F_{2,7} = 7.75$, $P = 0.02$). However, laying rate and mean brood size did not increase after the prey index reached $\geq 2.2$ hares day$^{-1}$ (Fig. 2B and 2D). Because of the significant positive relationships for both laying rate and mean brood size, population productivity also was affected significantly by prey abundance (Fig. 2D; multiple regression model for population productivity: productivity = 0.13 + 0.32(prey index) − 0.03(prey index)$^2$, $F_{2,7} = 20.13$, $P < 0.001$, $R^2 = 0.85$).

Mean brood size was 12% lower in northern populations compared to those in temperate latitudes (1.38 vs. 1.56 fledglings per successful pair; one-tailed $t$-test, $t_{98} = 3.1$, $P < 0.001$). Population productivity was 25% lower for northern populations (0.66 vs. 0.87 fledglings per occupied nesting area; one-tailed $t$-test, $t_{66} = 1.9$, $P = 0.03$).

## DISCUSSION

During this study we examined the influence of natural changes in snowshoe hare and Willow Ptarmigan abundance on Golden Eagle reproduction. Our 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. We could explain nearly 90% of the variation in Golden Eagle productivity with changes we noted in the abundance of snowshoe hares and Willow Ptarmigan.

We noted large changes in the abundance of snowshoe hare and Willow Ptarmigan and synchrony in the peak and declines of these species during this study. Similar synchrony in hare and ptarmigan was recorded at Kluane Lake, Yukon,

TABLE 2. Reproductive characteristics of Golden Eagles in Denali National Park, Alaska, 1988–1997.

| Year | Nesting areas surveyed | Nesting areas occupied | Pairs with eggs | Pairs with fledglings | Total fledglings | Occupancy rate (%) | Laying rate (%) | Success rate (%) | Mean brood size | Fledglings per occupied nesting area |
|---|---|---|---|---|---|---|---|---|---|---|
| 1988 | 56 | 47 | 37 | 28 | 38 | 84 | 79 | 76 | 1.36 | 0.81 |
| 1989 | 66 | 50 | 45 | 35 | 58 | 76 | 90 | 78 | 1.66 | 1.16 |
| 1990 | 66 | 46 | 38 | 28 | 47 | 70 | 83 | 74 | 1.68 | 1.02 |
| 1991 | 66 | 51 | 35 | 29 | 43 | 77 | 69 | 83 | 1.48 | 0.84 |
| 1992 | 70 | 57 | 36 | 19 | 26 | 81 | 63 | 53 | 1.37 | 0.46 |
| 1993 | 68 | 55 | 25 | 17 | 23 | 81 | 45 | 68 | 1.35 | 0.42 |
| 1994 | 68 | 58 | 19 | 8 | 9 | 85 | 33 | 42 | 1.13 | 0.16 |
| 1995 | 68 | 59 | 27 | 19 | 25 | 87 | 46 | 70 | 1.32 | 0.42 |
| 1996 | 72 | 62 | 26 | 23 | 30 | 86 | 42 | 88 | 1.30 | 0.48 |
| 1997 | 72 | 63 | 45 | 36 | 57 | 88 | 71 | 80 | 1.58 | 0.90 |
| Mean | — | — | — | — | — | 81 | 62 | 71 | 1.43 | 0.66 |
| CV | — | — | — | — | — | 7% | 31% | 19% | 13% | 48% |

Canada (Boutin et al. 1995). Population peaks and lows of hares in Denali and Kluane occurred during the same years, suggesting that these prey species fluctuate in synchrony over a large geographic area.

Laying rate was the most important factor influencing population productivity of Golden Eagles in Denali during our study. Laying rate varied widely compared to other components of reproduction and was most closely related to abundance of snowshoe hares and Willow Ptarmigan. Laying rates were lowest when the hare population was at its lowest level. Laying rate also was the most important reproductive param-

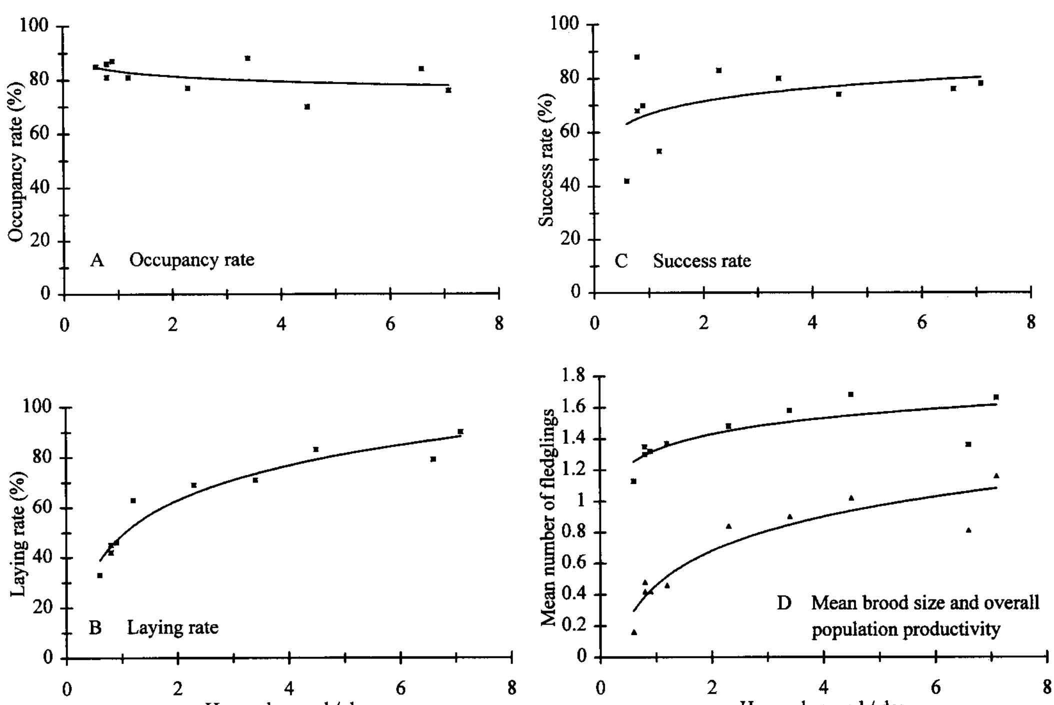


FIGURE 2. Reproductive components vs. index of prey abundance for Golden Eagles, Denali National Park, Alaska, 1988–1997. Occupancy rate (A) and success rate of laying pairs (C) were not affected by the prey index. Laying rate (B), mean brood size (D, solid squares), and overall population productivity (D, solid triangles) were significantly affected by the prey index.

eter influencing population productivity of Golden Eagles in Idaho over a 25-year period (Steenhof et al. 1997).

Overall success of laying pairs in Denali was not influenced by the abundance of snowshoe hare and Willow Ptarmigan. We suggest that success of laying pairs depends more upon abundance and availability of arctic ground squirrel and hoary marmot than hare or ptarmigan. Arctic ground squirrels and hoary marmots formed > 80% of the prey remains, in terms of biomass, collected at 212 occupied Golden Eagle nests in Denali from 1987 to 1997 (McIntyre, unpubl. data). Prior to and during laying, snowshoe hare and Willow Ptarmigan constitute most of the available prey for Golden Eagles in Denali (McIntyre, unpubl. data). The importance of hare and ptarmigan 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 were strongly correlated with hares (Boutin et al. 1995). If this situation exists in Denali and other areas in Alaska, we expect low success rates and smaller broods of eagles during population lows of hares. We suggest that the quadratic relationship shown in Figure 2B and 2D may have resulted from correlations between population densities of hares and arctic ground squirrels in Denali.

Golden Eagles show great dietary plasticity (Watson 1997). Golden Eagles in Idaho diversified their diets when the abundance of their main prey declined (Steenhof and Kochert 1988). 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 early 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, we 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 stable over our study period and were not affected by changes in cyclic prey. Our results are consistent with other long-term Golden Eagle studies (Brown and Watson 1964, Steenhof et al. 1997, Watson 1997). Golden Eagles are long-lived and there may be advantages to protecting nesting areas for future breeding attempts, even when prey conditions are unfavorable for producing and rearing young (Newton 1979, Steenhof et al. 1997).

Golden Eagles in northern study areas had smaller broods and produced fewer fledglings overall than eagles in temperate areas. Although our analyses were limited by small and unbalanced sample sizes, these data suggest that productivity of migratory Golden Eagles is lower than non-migratory eagles in western North America. We hypothesize that lower productivity in migratory eagles arises from a combination of energetic costs associated with migration, severe climatic conditions, and limited alternate prey on the breeding grounds. Northern breeding Golden Eagles commonly migrate > 3,000 km from wintering grounds to breeding grounds prior to nesting (Brodeur et al. 1996, McIntyre, unpubl. data). Although Golden Eagles can move quickly and economically over long distances, migration is energetically demanding (Wood et al. 1998) and may entail energetic costs reflected in reduced productivity. Costs of migration might be most pronounced in years when prey abundance in nesting areas is low. Additionally, Golden Eagles in many northern breeding areas begin egg laying when mean daily temperatures remain well below 0°C (Poole and Bromley 1988, McIntyre 1995). Severe climatic conditions may exacerbate effects of decreased prey availability on Golden Eagle productivity (Steenhof et al. 1997). Finally, many northern breeding populations of Golden Eagles have few alternate prey to buffer effects of low snowshoe hare and Willow Ptarmigan abundance during cyclic lows. The lack of alternate prey may affect laying in years when cyclic prey species are low and may subsequently reduce overall productivity of northern breeding populations.

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