IBIS The International Journal of Avian Science
*Ibis* (2012), **154**, 124–135

# Ecological and environmental correlates of territory occupancy and breeding performance of migratory Golden Eagles *Aquila chrysaetos* in interior Alaska

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Understanding relationships between environmental conditions and reproductive parameters is important when interpreting variation in animal population size. The northwestern North American population of Golden Eagles *Aquila chrysaetos canadensis* initiates courtship and nesting in early spring when prey diversity is low and weather conditions are severe. Snowshoe Hare *Lepus americanus* and Willow Ptarmigan *Lagopus lagopus*, the primary prey of Golden Eagles early in their nesting season in interior Alaska, both exhibit cyclical fluctuations in abundance, providing the opportunity to investigate such relationships. We used Bayesian hierarchical models to explore variation in territory occupancy, nesting rates, nesting success and productivity of Golden Eagles from 1988 to 2010 in Denali National Park and Preserve, Alaska, in relation to annual and site-specific parameters including prey abundance, weather conditions, elevation and human activity. We also investigated the long-term fluctuations of breeding performance over the course of the study. The abundance of Hares influenced both the number of Eagles that laid eggs and the number of Eagles that produced fledglings. The conditions on the breeding ground did not explain observed declines in nesting rates and fledgling production, suggesting that other factors such as change in the age structure of the population, increased intraspecific competition or deterioration of migration and wintering habitat are driving the long-term trends of these parameters.

**Keywords:** breeding biology, long-term study, population monitoring, prey abundance, weather.

Prey abundance is one of the primary factors driving the reproductive success of raptors (Newton 1979, Krebs *et al.* 2001), but weather and human activities can also affect reproduction (Steenhof *et al.* 1997, Steidl & Anthony 2000). Variation in breeding performance related to prey cycles, weather and human disturbance may obscure trends in the reproduction of long-lived species, and long-term studies are necessary to assess adequately their population parameters. The data required for assessments of long-lived predator and prey species of interest must be collected over decades (Arthur & Prugh 2010), and such datasets are rare. However, when collected and analysed in a continuous and rigorous manner, they provide unique opportunities to investigate complex predator–prey relationships, identify patterns, and increase knowledge of species and their environmental associations (Newton 1998, Sundell *et al.* 2004, Anthony *et al.* 2008).

Raptors exhibiting specialized diets show strong responses to changes in the abundance of their primary prey (Newton 1998) and have few alternative food sources when their primary prey decline in abundance. Raptors that prey heavily on species that exhibit cyclical patterns in abundance also show strong responses to changes in prey abundance, with reproduction increasing when prey abundance is high and decreasing when it is low (Doyle & Smith 1994, Steenhof *et al.* 1997, McIntyre & Adams 1999, Whitfield *et al.* 2009).

Snowshoe Hare *Lepus americanus* and Willow Ptarmigan *Lagopus lagopus* exhibit large-amplitude population cycles across North America (Boutin *et al.* 1995, Hodges *et al.* 2001, Krebs *et al.* 2001, Martin *et al.* 2001). Changes in the abundance of

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Snowshoe Hare influence reproduction of many predators including Canada Lynx *Lynx canadensis*, Coyote *Lupis latrans*, Great Horned Owl *Bubo virginianus* and Northern Goshawk *Accipiter gentilis* (Krebs *et al.* 2001), while changes in the abundance of Willow Ptarmigan influence the reproduction of Gyrfalcon *Falco rusticolus* (Booms *et al.* 2008). In interior Alaska, nesting Golden Eagles *Aquila chrysaetos* are heavily dependent on both prey species, particularly during the early nesting season (McIntyre & Adams 1999).

Golden Eagles are long-lived raptors, exhibiting high fidelity to nesting territories and relatively low reproductive rates (Kochert *et al.* 2002, Pedrini & Sergio 2002, Watson 2010). The relative importance of prey species consumed by Golden Eagles during the nesting season varies by region (Kochert *et al.* 2002, Watson 2010) but the availability of live prey is an important component of successful reproduction (Watson 2010). In many areas, Golden Eagles exhibit higher nesting success and produce more fledglings when their primary prey is abundant and weather conditions are favourable (Steenhof *et al.* 1997, Kochert *et al.* 2002, Watson 2010). Patterns in the reproductive success of Golden Eagles nesting in western North America often closely followed the cycles of leporid prey (e.g. rabbits and hares; Steenhof *et al.* 1997, McIntyre & Adams 1999, Kochert *et al.* 2002).

Migratory Golden Eagles that nest at high latitudes (> 60°N) in northwestern North America return to their nesting grounds from late February to early April (Kochert *et al.* 2002) when the diversity of prey is low and weather conditions are often severe and highly variable. In this region of northwestern North America, the diversity, availability, and abundance of prey species for Golden Eagles varies temporally across the nesting season (McIntyre & Adams 1999, Krebs *et al.* 2001). Furthermore, the diversity and abundance of species available as live prey to Golden Eagles in this region are lowest during the early nesting season when Eagles are establishing nesting territories and laying eggs. The diversity and abundance of prey increases over the nesting season as obligate hibernators emerge and prey species produce offspring, but the diversity of species available as prey for Golden Eagles in the high latitudes of North America is probably lower than in other areas of the species' range (Kochert *et al.* 2002, Watson 2010).

One of the highest nesting densities of Golden Eagles in North America occurs in Denali National Park and Preserve, Alaska (henceforth Denali; Kochert *et al.* 2002). In this area, Snowshoe Hare and Willow Ptarmigan are the two most common species of live prey available to Golden Eagles during courtship, egg-laying, and incubation (McIntyre & Adams 1999). Rock Ptarmigan *Lagopus muta* and White-tailed Ptarmigan *Lagopus leucura* also occur in the area, but are relatively rare compared with Willow Ptarmigan (C. McIntyre unpubl. data). Arctic Ground Squirrel *Spermophilus parryii* and Hoary Marmot *Marmota caligata* are also consumed by nesting Golden Eagles, but these obligate hibernators are not available as a food source until after most Eagles lay their eggs (McIntyre & Adams 1999). To a lesser degree, Golden Eagles also consume carrion and Dall's Sheep *Ovis dalli* lambs, but neither is commonly available early in the Eagle's nesting season.

Here, we examine the extent to which prey abundance, weather conditions, elevation and potential human activity influenced variation in territory occupancy, nesting probability, nest success and fledgling production in a large population of migratory Golden Eagles. Our analysis builds on the dynamics of the predator–prey relationship identified by McIntyre and Adams (1999) and the relationships between human activity and Eagle nesting success described by Martin *et al.* (2009). We address four specific questions related to the effects of ecological and environmental correlates on the occupancy of nesting territories and reproductive success of Golden Eagles: (1) which reproductive stages are most influenced by the abundance of Snowshoe Hare and Willow Ptarmigan and does the availability of these two prey species differentially affect reproductive output; (2) do extended periods of low temperatures, precipitation (e.g. blizzards, rain storms) or extensive snow cover in the early nesting season negatively influence nesting success; (3) do isolated or nesting territories at higher elevations exhibit higher levels of occupancy and nesting success; and (4) is there any evidence of systematic change in the territory occupancy and nesting success over our study period?

## METHODS

### Study area

The 2100-km$^2$ study area, centred at 63°35′89″N, 149°38′29″W, was in the northern foothills of the

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Alaska Range in Denali. Elevations of foothill summits ranged from 607 to 1372 m and most of the study area was above the treeline (> 800 m). Steep-sided mountains, large swift-running glacial rivers, broad glacially carved valleys, open tundra and scrublands, and extensive riparian gravel bars dominated the study area (McIntyre *et al.* 2006). All known Golden Eagle nests in the study area were on cliffs and rock outcrops. A gravel road transected the study area, and travel along the road and within the study area occurred mainly from late May through mid-September.

## Terminology

Terminology describing nesting territories and nesting activities followed Steenhof and Newton (2007). A nesting territory was a specific area that contained, or historically contained, one or more nests within the nesting season home-range of a mated pair of Golden Eagles, and where only one pair of Eagles nested in a given year. Golden Eagles often use traditional nesting territories for decades (Watson 2010) and we assigned individual nests to unique nesting territories based on their history of use and proximity to other nests (McIntyre & Adams 1999). We considered a nesting territory occupied if we observed: (1) two Eagles that appeared to be paired; (2) at least one Eagle exhibiting territorial behavior; (3) an incubating Eagle in a nest; (4) eggs or eggshells in a nest; (5) a recently constructed, refurbished or decorated nest; or (6) nestlings or fledglings in or near the nest. We calculated annual nesting territory occupancy as the proportion of nesting territories occupied in relation to those that we observed during our surveys. We presumed that nests where we observed incubating Eagles contained eggs and we defined a nest with eggs as an occupied nest. We calculated annual nesting rates (NEST) as the proportion of occupied nesting territories that contained an occupied nest. A successful nest was one where at least one fledgling was raised. We calculated annual nesting success (SUCCESS) as the proportion of occupied nests where at least one fledgling was raised. We assumed that nestlings fledged 10 weeks after hatching (McIntyre & Collopy 2006) and considered nestlings that reached 7 weeks of age as fledglings unless we found evidence that they did not fledge after this time. We based this standard minimum age on our observations that indicated that mortality of nestlings after this time was minimal until actual fledging (C. McIntyre unpubl. data). For comparative purposes, we calculated two annual measurements of fledgling production including the number of fledglings per successful nest (mean brood size, MBS) and the number of fledglings produced per occupied nesting territory (overall population production, PROD).

## Measuring territory occupancy, nesting success and production

We conducted two standardized aerial surveys and supplemental ground-based surveys annually to document occupancy of nesting territories, nesting activities, nesting success and production of fledglings from 1988 to 2010. The occupancy survey (Fraser *et al.* 1983) was conducted in late April and early May after most clutches were completed and before hatching occurred (McIntyre & Adams 1999) to document occupancy of nesting territories and nesting activities. The production survey (Fraser *et al.* 1983) was conducted in mid- to late July, after most nestlings reached 7 weeks of age but before many fledged, to document nesting success and fledgling production.

During the occupancy survey, we attempted to observe all nests within all nesting territories and also searched for new or previously undocumented nests and nesting territories. We did not intentionally flush incubating Eagles off their nest to count eggs, and Eagles rarely flushed (< 0.5%) off their nests during our surveys. We conducted additional aerial and ground surveys at all nesting territories when we did not find evidence of occupancy during our initial annual observations. All occupied nests located during the occupancy survey were revisited during the production survey. During the production survey, we noted the contents of the nest (e.g. number of nestlings or fledglings, addled eggs, empty) and estimated the age of each nestling to the nearest week using a photographic guide of known age nestlings in Denali (C. McIntyre unpubl. data).

One or two experienced observers conducted all aerial surveys from a Bell Jet Ranger helicopter (1988–2000), a Hughes 500 helicopter (2006) or a Robinson R-44 helicopter (all other years). During all surveys and fieldwork (e.g. nest visits), we classified Golden Eagles with white in their wings or tail as subadults and all others as adults (Jollie 1947, Steenhof *et al.* 1983).

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## Explanatory variables

*Abundance of Snowshoe Hare and Willow Ptarmigan*

We calculated annual abundance indices of Snowshoe Hare (HARE) and Willow Ptarmigan (PTARM) as the number of adults of each species detected each day during routine fieldwork from mid-April to late June (McIntyre & Adams 1999). We assumed that the indices were correlated with actual abundance. Sampling error undoubtedly influenced these indices, but we are confident that the observed variation in abundance (> 10-fold) was sufficient to render this a minor concern. Similar counts of Snowshoe Hare were highly correlated with abundance estimates generated from faecal pellet counts (Arthur & Prugh 2010). Similar counts of Black-tailed Jackrabbits *Lepus californicus* in Idaho provided results comparable with abundance estimates generated from data collected by spotlighting transects (Steenhof *et al.* 1997), suggesting that these indices usually provide reliable measures of relative abundance and the frequency and amplitude of the cycles (Arthur & Prugh 2010).

*Extreme weather events*

We obtained weather data from the Denali weather station at the eastern edge of the study area. We expected that weather conditions would affect nesting Golden Eagles differently at different stages of the nesting season (Steenhof *et al.* 1997, Watson 2010) and assumed that Eagles would react negatively to extreme weather events. We used the number of pairs of consecutive days when the temperature was below specific levels or with measurable precipitation to represent extreme weather events during three stages of the nesting season including: (1) March–April (courtship, nest building and refurbishment, egg-laying, and early incubation); (2) April–June (incubation and early brood-rearing); and (3) May–June (late incubation and early brood-rearing). Weather variables for March and April included the number of pairs of consecutive days when the temperature did not reach −17.8 °C (0 °F; Steenhof *et al.* 1997) (TEMP1) and the number of pairs of consecutive days with precipitation (PRECIP1). Weather variables for April–June included the number of pairs of consecutive days when the temperature did not reach −17.8 °C (TEMP2) and the number of pairs of consecutive days with precipitation (PRECIP2). Weather variables for May–June included the number of pairs of consecutive days when the temperature did not reach 0 °C (TEMP3) and the number of pairs of consecutive days with measurable precipitation (PRECIP3). We also created a variable for the last day with continuous snow cover (SNOW).

*Potential human disturbance*

Human activities near occupied eagle nests can negatively influence nesting success by causing eagles to abandon their eggs (Watson 2010) or decrease nest attendance (Steidl & Anthony 2000). Based on our experience of the study area, we presumed that most human activities occurred ≤ 2 km from roads and established hiking routes from June to August. We assumed that nesting territories ≤ 2 km from roads and hiking routes were more vulnerable to potential human disturbance and that this would be reflected in decreased rates of occupancy, nesting and nesting success. Proximity to roads and hiking routes (HUMAN) was treated as a categorical variable (1 = roads and hiking routes ≤ 2 km from nesting territory centroid; 0 = roads and hiking routes > 2 km from nesting territory centroid). The nesting centroid was calculated as the mean latitude and longitude of all known nests within each nesting territory (Kochert *et al.* 1999).

*Elevation*

Open landscapes with sparse, dwarf or short vegetation dominated nesting territories located at higher elevations in the study area (McIntyre *et al.* 2006). We hypothesized that open landscapes would favour detection and accessibility of prey (Pedrini & Sergio 2001a) and that this would potentially enhance the hunting success and nesting success of Golden Eagles (Carrete *et al.* 2006, Sergio *et al.* 2006, Watson 2010). Therefore, we used the elevation of the nesting territory centroid as a surrogate habitat variable (ELEV) and assumed that it was a realistic index of the openness of the landscape within each nesting territory.

## Data analyses

We conducted separate analyses to investigate variation in occupancy of nesting territories ($\Psi$) and four reproductive parameters including nesting (NEST), nesting success (SUCCESS), mean brood size (MBS) and fledglings per occupied nesting territory (PROD). We selected combinations of these

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variables *a priori* for each analysis based on the variables we expected to influence each stage of nesting. For instance, weather conditions were not expected to affect occupancy of nesting territories and were not included in the models examining variations in Ψ. All continuous covariates, except year, were standardized to have a mean = 0 and sd = 1 to improve convergence. We included the variables HARE, PTARM, ELEV and HUMAN to investigate variation in Ψ. We included the variables HARE, PTARM, HUMAN, TEMP1, PRECIP1 and SNOW to investigate variation in NEST and the variables HARE, PTARM, ELEV, HUMAN, TEMP2, PRECIP2, TEMP3, PRECIP3 and SNOW to investigate variation in SUCCESS. We included the variables HARE, HUMAN, TEMP2, TEMP3, PRECIP3 and SNOW to investigate variation in MBS and the variables HARE, PTARM, ELEV, PRECIP1 and TEMP2 to investigate variation in PROD.

We used hierarchical models (Gelman *et al.* 2004) to estimate Ψ, NEST, SUCCESS, MBS and PROD. All response parameters, except for MBS and PROD, were treated as a binomial (0 = absent/failure, 1 = present/success) variable and were constructed using logistic regression in an occupancy model framework (MacKenzie *et al.* 2006). We modelled MBS and PROD as a Poisson variable using loglinear regression models (Link *et al.* 2006). We did not estimate detection probability for each nesting stage and assumed that detectability of occupied nesting territories, nesting pairs, successful pairs and fledglings was equal to 1 in all years. Violations of this assumption would result in underestimates of occupancy and/or success; however, detection was likely to be high (> 0.90) and consistent during all stages in all years (Martin *et al.* 2009), so we expected bias to be low.

We constructed and fitted models using program R (R Development Core Team 2009), R2WINBUGS package (Sturtz *et al.* 2005) and WINBUGS 1.4.1 (Spiegelhalter *et al.* 2004). We used the deviance information criterion (DIC), which is analogous to the use of Akaike's information criterion (AIC) as described by Burnham and Anderson (2002), and which helps balance the tradeoff between model complexity and model fit, to select among competing models (Spiegelhalter *et al.* 2002). After using DIC values to identify the best fitting fixed-effects model for each nesting stage, we added random effects of site (e(SITE)) and year (e(YEAR)) to help explain remaining heterogeneity in the data. We believed this was warranted because unmodelled heterogeneity can result in overly precise parameter estimates (Flint *et al.* 1995, Schmidt *et al.* 2010), leading to unrealistic conclusions. Appropriate estimates of uncertainty associated with our parameters allowed us to more confidently assess the effects of covariates and identify meaningful trends in the parameters of interest. This approach also allowed us to account for missing data due to unequal sampling among years. By estimating missing values along with other model parameters (Gelman *et al.* 2004), we could include all data, regardless of monitoring history. We assessed model fit using the Bayesian *P*-value, comparing the fit of the empirical data with model-based predictions (Gelman *et al.* 2004). This value indicates how likely the observed data are in comparison with data simulated from the posterior distributions, with values approaching 0 or 1 indicating lack of fit (Gelman *et al.* 2004, Schmidt *et al.* 2010). All parameter estimates are presented as means and 95% credible intervals on the logit scale and were produced using the model with the lowest DIC. Predicted probabilities of occupancy, nesting, nesting success and production are presented on the real scale with 95% credible intervals. Summary statistics for prey indices, territory occupancy and reproductive parameters are reported as means with standard deviations.

## RESULTS

We monitored 66–89 (mean = 79 ± 7.3) Golden Eagle nesting territories annually (Table 1). Poor survey conditions in some years and a temporary change in the study area boundaries in 1994–97 prevented us from monitoring all known nesting territories each year. The number of known nesting territories increased over time, resulting from the discovery of previously undocumented, rather than newly established, territories in the study area.

Abundance indices of Snowshoe Hare and Willow Ptarmigan tracked the amplitude and frequency of their population cycles and showed little additional variation between years (Fig. 1). The timing and frequency of the highs and lows of the cycles of each species were similar in most years, but the amplitudes differed markedly, especially during later years (Fig. 1).

Apparent occupancy rate was high across the study period (range = 0.81–0.93, mean = 0.86 ± 0.04; Table 1) and the best approximating model

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**Table 1.** Summary of survey effort, observed numbers of occupied nesting territories, nesting pairs, successful pairs and fledglings, calculated rates of nesting and nesting success, and estimates of mean brood size and fledglings per occupied nesting territory of Golden Eagles, Denali National Park and Preserve, Alaska, 1988–2010.

| Year | Nesting territories surveyed | Nesting territories occupied | Occupied nests | Successful nests | Fledglings | Occupancy rate | Nesting rate | Nesting success | Mean brood size | Fledglings per occupied nesting territory |
|---|---|---|---|---|---|---|---|---|---|---|
| 1988 | 68 | 60 | 43 | 35 | 49 | 0.88 | 0.72 | 0.81 | 1.40 | 0.82 |
| 1989 | 68 | 58 | 51 | 43 | 70 | 0.85 | 0.88 | 0.84 | 1.63 | 1.21 |
| 1990 | 72 | 58 | 48 | 34 | 53 | 0.81 | 0.83 | 0.71 | 1.56 | 0.91 |
| 1991 | 75 | 62 | 44 | 37 | 55 | 0.83 | 0.71 | 0.84 | 1.49 | 0.89 |
| 1992 | 82 | 69 | 39 | 18 | 25 | 0.84 | 0.57 | 0.46 | 1.39 | 0.36 |
| 1993 | 87 | 72 | 33 | 20 | 28 | 0.83 | 0.46 | 0.61 | 1.40 | 0.39 |
| 1994 | 66 | 56 | 20 | 9 | 11 | 0.85 | 0.36 | 0.45 | 1.22 | 0.20 |
| 1995 | 67 | 56 | 27 | 19 | 24 | 0.84 | 0.48 | 0.70 | 1.26 | 0.43 |
| 1996 | 68 | 61 | 26 | 23 | 28 | 0.90 | 0.43 | 0.88 | 1.22 | 0.46 |
| 1997 | 83 | 69 | 48 | 35 | 58 | 0.83 | 0.70 | 0.73 | 1.66 | 0.84 |
| 1998 | 82 | 66 | 34 | 22 | 33 | 0.80 | 0.52 | 0.65 | 1.50 | 0.50 |
| 1999 | 81 | 72 | 52 | 42 | 69 | 0.89 | 0.72 | 0.81 | 1.64 | 0.96 |
| 2000 | 82 | 70 | 53 | 34 | 51 | 0.85 | 0.76 | 0.64 | 1.50 | 0.73 |
| 2001 | 81 | 68 | 44 | 23 | 31 | 0.84 | 0.65 | 0.52 | 1.35 | 0.46 |
| 2002 | 82 | 73 | 10 | 4 | 4 | 0.89 | 0.14 | 0.40 | 1.00 | 0.05 |
| 2003 | 83 | 71 | 25 | 13 | 19 | 0.86 | 0.35 | 0.52 | 1.46 | 0.27 |
| 2004 | 82 | 73 | 32 | 16 | 20 | 0.89 | 0.44 | 0.50 | 1.25 | 0.27 |
| 2005 | 86 | 76 | 41 | 28 | 38 | 0.88 | 0.54 | 0.68 | 1.36 | 0.50 |
| 2006 | 88 | 80 | 63 | 51 | 76 | 0.91 | 0.79 | 0.81 | 1.49 | 0.95 |
| 2007 | 89 | 81 | 60 | 46 | 73 | 0.91 | 0.74 | 0.77 | 1.59 | 0.90 |
| 2008 | 86 | 75 | 51 | 34 | 52 | 0.87 | 0.68 | 0.67 | 1.53 | 0.69 |
| 2009 | 80 | 74 | 61 | 42 | 67 | 0.93 | 0.82 | 0.69 | 1.60 | 0.91 |
| 2010 | 80 | 75 | 51 | 36 | 49 | 0.94 | 0.68 | 0.71 | 1.36 | 0.65 |

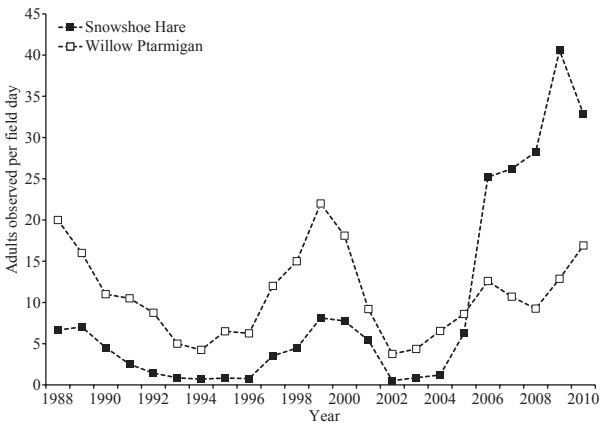



**Figure 1.** Annual abundance indices of Snowshoe Hare and Willow Ptarmigan in Denali National Park and Preserve, Alaska, 1988–2010. The indices represent the number of adult Snowshoe Hare and adult Willow Ptarmigan observed per field day from mid-April through June each year.

(Table 2) indicated that the probability of occupancy increased slightly throughout the study period ($\beta_{TREND}$ = 0.04, CI = 0.02–0.07; Fig. 2a). We did not detect a relationship between occupancy and elevation or human activity. The precision ($\tau$) of the random site effect was low ($\tau_{SITE}$ = 0.13), indicating that the amount of variability at the site level was high after accounting for the covariates, and contributed to the uncertainty in the effects of elevation and human activity (Table 2). The Bayesian *P*-value indicated model fit was adequate (*P* = 0.37).

Apparent nesting rates were highly variable across the study period (range = 0.14–0.88, mean = 0.61 ± 0.19; Table 1). The estimated probability of nesting was positively related to prey abundance, although Snowshoe Hare abundance ($\beta_{HARES}$ = 0.65, CI = 0.25–1.05) appeared to be twice as influential as that of Willow Ptarmigan ($\beta_{PTARM}$ = 0.36, CI = 0.07–0.65; Table 3). The best approximating model (Table 3) also indicated that the probability of nesting declined through time ($\beta_{TREND}$ = −0.06, CI = −0.12 to −0.003). We did not detect a relationship between nesting rates and human activity or extended precipitation events. Model selection results also supported inclusion of year ($\tau_{YEAR}$ = 4.20) and site ($\tau_{SITE}$ = 3.49), random effects which contributed

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**Table 2.** Selection results for models describing variation in nesting territory occupancy probability (Ψ) of Golden Eagles in Denali National Park and Preserve, Alaska, 1988–2010. Models were compared using the deviance information criterion (DIC) with lower ΔDIC values indicating higher support.

| Model | DIC | ΔDIC |
|---|---|---|
| $\Psi_{TREND + HUMAN + ELEV + e(SITE)}$ | 1039.9 | 0.0 |
| $\Psi_{TREND + HUMAN + ELEV}$ | 1854.3 | 814.4 |
| $\Psi_{TREND + HUMAN + ELEV + HARE}$ | 1854.7 | 814.8 |
| $\Psi_{TREND + ELEV}$ | 1855.4 | 815.5 |
| $\Psi_{TREND + HUMAN + ELEV + HARE + PTARM}$ | 1855.9 | 816.0 |
| $\Psi_{TREND + HUMAN}$ | 1858.7 | 818.8 |
| $\Psi_{TREND}$ | 1862.6 | 822.7 |
| $\Psi_{ELEV}$ | 1863.2 | 823.3 |
| $\Psi_{TREND + HARE}$ | 1863.4 | 823.5 |
| $\Psi_{HARE}$ | 1864.1 | 824.2 |
| $\Psi_{HUMAN}$ | 1866.2 | 826.3 |
| $\Psi_{CONSTANT}$ | 1870.2 | 830.3 |

Variables included in the models were: annual change (TREND), distance to human activity (HUMAN), elevation of nesting centroid (ELEV), annual Hare abundance index (HARE) and annual Ptarmigan abundance index (PTAR).

to the uncertainty in the direction of the effects of human activity and precipitation. The fit of the best approximating model was determined to be adequate ($P = 0.44$).

Apparent nest success ranged from 0.40 to 0.88 ($\bar{x} = 0.67 \pm 0.14$) annually (Table 1). We found no relationship between nesting success and any of the covariates included in our models (Table 4). The credible intervals for all covariates included in the model addressing nesting success overlapped zero, indicating uncertainty in the magnitude and direction of the covariate effects (Table 4).

There was little evidence for any variation in mean brood size relative to the covariates we considered. Estimates from the constant model indicated that mean brood size averaged 1.5 (CI = 1.4–1.6) and did not change through time. In contrast, the number of fledglings produced per occupied nesting territory decreased through time ($\beta_{TREND} = -0.02$, CI = −0.03 to −0.005; Fig. 2b), was positively related to the abundance of Snowshoe Hares ($\beta_{HARES} = 0.15$, CI = 0.05–0.25) and Willow Ptarmigan ($\beta_{PTARM} = 0.09$, CI = 0.02–0.17), and decreased in relation to extended periods of cold weather during April–June ($\beta_{TEMP2} = -0.09$, CI = −0.16 to −0.03; Table 5). DIC did not support the inclusion of random year and site effects, suggesting that the included covariates explained a majority of the variation in the

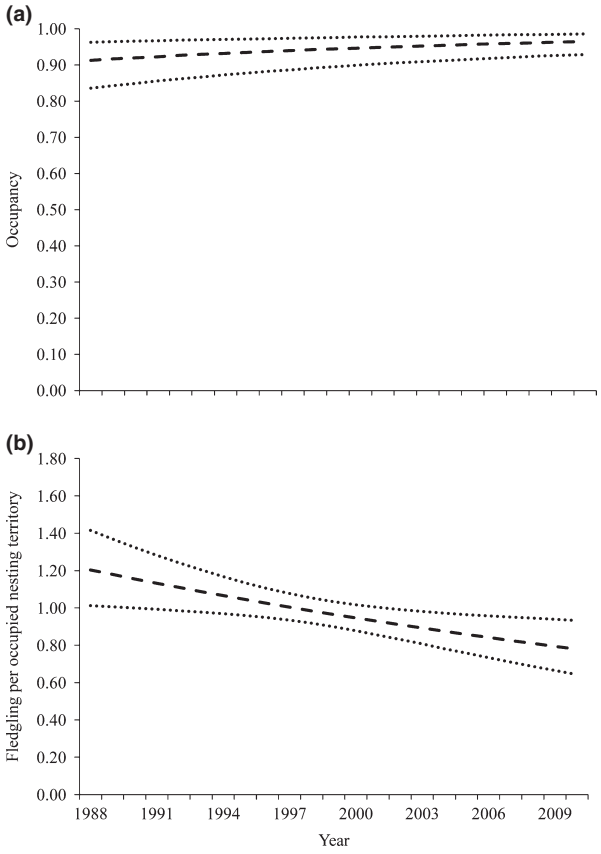



**Figure 2.** Trends in the probability of nesting territory occupancy (a) and fledgling production (b) of Golden Eagles, Denali National Park and Preserve, Alaska, 1988–2010. All estimates were based on the best approximating model for each stage and assumed mean values for all covariates.

data (Table 5). Based on the best approximating model (Table 5), overall fledgling production given occupancy declined by 0.4 fledglings per occupied nesting territory at mean covariate values. This model also fitted the data based on the Bayesian *P*-value ($P = 0.33$).

## DISCUSSION

We demonstrate several novel and formerly undocumented aspects of Golden Eagle ecology related to the cyclical behavior of their primary prey and overall declines in probability of nesting and fledgling production in Denali over time. Snowshoe Hare and Willow Ptarmigan abundance were independently important for nesting (egg-laying), providing new insights into the complexities of predator–prey interactions, the temporal variation in prey availability in this system, and the dietary

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**Table 3.** Selection results for models describing variation in nesting probability (NEST) for Golden Eagles in Denali National Park and Preserve, Alaska, 1988–2010. Models were compared using the deviance information criterion (DIC) with lower ΔDIC values indicating higher support.

| Model | DIC | ΔDIC |
|---|---|---|
| $NEST_{HARES + TREND + PTARM + HUMAN + PRECIP1 + e(YEAR) + e(SITE)}$ | 1880.5 | 0.0 |
| $NEST_{HARES + TREND + PTARM + HUMAN + PRECIP1 + e(SITE)}$ | 1913.4 | 32.9 |
| $NEST_{HARES + TREND + PTARM + HUMAN + PRECIP1 + e(YEAR)}$ | 1919.1 | 38.6 |
| $NEST_{HARES + TREND + PTARM + HUMAN + PRECIP1}$ | 1947.9 | 67.4 |
| $NEST_{HARES + TREND + PTARM + HUMAN}$ | 1948.7 | 68.2 |
| $NEST_{TREND + HARES + PTARM + HUMAN + TEMP1}$ | 1950.1 | 69.6 |
| $NEST_{HARES + TREND + PTARM + HUMAN + SNOW}$ | 1950.7 | 70.2 |
| $NEST_{HARES + TREND + PTARM}$ | 1952.5 | 72.0 |
| $NEST_{HARES + TREND + HUMAN}$ | 1979.3 | 98.8 |
| $NEST_{HARES + TREND}$ | 1982.7 | 102.2 |
| $NEST_{HARES}$ | 2041.0 | 160.5 |
| $NEST_{CONSTANT}$ | 2109.8 | 229.3 |
| $NEST_{TREND}$ | 2111.9 | 231.4 |

Variables included in the model were: annual Hare abundance index (HARE), annual change (TREND), annual Ptarmigan abundance index (PTARM), distance to human activity (HUMAN), pairs of consecutive days with measurable precipitation during March and April (PRECIP1), number of consecutive pairs of days when the temperature did not reach –17.3 °C during March and April (TEMP1), and the last day with continuous snow cover (SNOW).

**Table 4.** Selection results for models describing variation in nesting success (SUCCESS) of Golden Eagles in Denali National Park and Preserve, Alaska, 1988–2010. Models were compared using the deviance information criterion (DIC) with lower ΔDIC values indicating higher support.

| Model | DIC | ΔDIC |
|---|---|---|
| $SUCCESS_{TREND + HARES + PTARM + TEMP2 + e(YEAR)}$ | 1146.5 | 0.0 |
| $SUCCESS_{TREND + HARES + PTARM + TEMP2 + e(YEAR) + e(SITE)}$ | 1148.5 | 2.0 |
| $SUCCESS_{TREND + HARES + PTARM + TEMP2}$ | 1150.7 | 4.2 |
| $SUCCESS_{TREND + HARES + PTARM + TEMP3}$ | 1151.7 | 5.2 |
| $SUCCESS_{TREND + HARES + PTARM + SNOW}$ | 1152.8 | 6.3 |
| $SUCCESS_{TREND + HARES + PTARM}$ | 1155.2 | 8.7 |
| $SUCCESS_{TREND + HARES + PTARM + PRECIP3}$ | 1156.6 | 10.1 |
| $SUCCESS_{TREND + HARES + PTARM + PRECIP2}$ | 1156.6 | 10.1 |
| $SUCCESS_{TREND + HARES + HUMAN + PTARM}$ | 1157.2 | 10.7 |
| $SUCCESS_{TREND + HARES}$ | 1158.7 | 12.2 |
| $SUCCESS_{TREND + HARES + HUMAN}$ | 1160.6 | 14.1 |
| $SUCCESS_{TREND + HARES + ELEV}$ | 1160.8 | 14.3 |
| $SUCCESS_{HARES}$ | 1171.0 | 24.5 |
| $SUCCESS_{CONSTANT}$ | 1171.5 | 25.0 |
| $SUCCESS_{TREND}$ | 1171.9 | 25.4 |

Variables included in the model were: annual Hare abundance index (HARE), annual change (TREND), annual Ptarmigan abundance index (PTARM), number of pairs of consecutive days when the temperature did not reach 0 °C from April to June (TEMP2), number of pairs of consecutive days with measurable precipitation from April to June (PRECIP2), last date with continuous snow cover (SNOW), number of pairs of consecutive days with measurable precipitation during May and June (PRECIP3), distance to human activity (HUMAN), and elevation of nesting centroid (ELEV).

specialization of Golden Eagles during a critical time of their nesting season. Although past work identified Snowshoe Hare and Willow Ptarmigan abundance as important for Golden Eagle reproduction in Denali (McIntyre & Adams 1999, Martin *et al.* 2009), this is the first study to explore the individual importance of both of these species to overall breeding performance.

Predators are frequently classified as generalists or specialists, with the latter exhibiting strong numerical responses to changes in prey abundance (Hanski *et al.* 1991). Golden Eagles are often considered dietary generalists (Kochert *et al.* 2002, Watson 2010) but several studies have illustrated that some individuals have relatively specialized diets, whereas others have broader diets (Whitfield *et al.* 2009). Our results, as well as those of Nyström *et al.* (2006) in northern Sweden, suggest that Golden Eagles had a highly specialized diet during the early part of the nesting season when live prey was limited to essentially two highly cyclical species (Snowshoe Hare and Willow Ptarmigan in Denali, Rock and Willow Ptarmigan in Sweden). We suggest that Golden Eagles nesting at high latitudes or elevations where the diversity of prey is low may exhibit similar temporal dietary specialization. Furthermore, the diet of Golden Eagles in southwest Idaho expanded when the abundance of their principal prey decreased (Steenhof & Kochert 1988). In contrast, the lack of species diversity in northern breeding areas during the early nesting season limits the dietary expansion of Golden Eagles when their principal prey are at the low phase of their cycles.

The environmental conditions affecting the probability of nesting were also the primary drivers of overall fledgling production. This was not surprising because our measurement of production, fledglings per occupied nesting territory, was a product of all three independent measurements of

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**Table 5.** Selection results for models describing variation in the number of fledglings per occupied territory (PROD) of Golden Eagles in Denali National Park and Preserve, Alaska, 1988–2010. Models were compared using the deviance information criterion (DIC) with lower ΔDIC values indicating higher support.

| Model | DIC | ΔDIC |
|---|---|---|
| $PROD_{HARE + TREND + PTARM + TEMP2}$ | 2356.5 | 0.0 |
| $PROD_{HARE + TREND + PTARM + TEMP2 + PRECIP1}$ | 2357.4 | 0.9 |
| $PROD_{HARE + TREND + PTARM + TEMP2 + e(YEAR)}$ | 2357.8 | 1.3 |
| $PROD_{HARE + TREND + PTARM}$ | 2362.1 | 5.6 |
| $PROD_{HARE + TREND + PTARM + PRECIP1}$ | 2363.6 | 7.1 |
| $PROD_{HARE + TREND + HUMAN + PTARM}$ | 2364.3 | 7.8 |
| $PROD_{HARE + TREND + PTARM + ELEV}$ | 2364.6 | 8.1 |
| $PROD_{HARE + TREND}$ | 2366.9 | 10.4 |
| $PROD_{HARE}$ | 2376.0 | 19.5 |
| $PROD_{CONSTANT}$ | 2377.6 | 21.1 |
| $PROD_{HUMAN}$ | 2379.0 | 22.5 |
| $PROD_{TREND}$ | 2379.2 | 22.7 |

Variables included in the model were: annual Hare abundance index (HARE), annual change (TREND), annual Ptarmigan abundance index (PTARM), number of pairs of consecutive days when the temperature did not reach 0 °C from April to June (TEMP2), number of days with measurable precipitation in March and April (PRECIP1), distance to human activity (HUMAN) and elevation of nesting centroid (ELEV).

reproduction (proportion of pairs with eggs, proportion of pairs that raise fledglings and brood size at fledging; Steenhof *et al.* 1997). In Denali, fledgling production was influenced primarily by the proportion of females that laid eggs. These findings are consistent with those of Steenhof *et al.* (1997), who found a similar relationship for Golden Eagles in southwest Idaho.

Others have noted synchrony in the highs and lows of the Snowshoe Hare and Willow Ptarmigan cycles (McIntyre & Adams 1999, Martin *et al.* 2001), and although we observed similar patterns, it was not as consistent during later years of the study. Despite this synchronicity in abundance, Snowshoe Hares accounted for 60% more variation in overall reproduction of Golden Eagles than did Willow Ptarmigan. A possible explanation for this is the difference in the behaviour and availability of Snowshoe Hare and Willow Ptarmigan during late winter and early spring, the time when Eagles are returning to Denali, establishing their nesting territories and laying eggs. Snowshoe Hares are resident, occupying relatively small seasonal home-ranges (Hodges *et al.* 2001) and are available when Eagles return to their nesting territories in late winter and spring. In contrast, Willow Ptarmigan leave their nesting grounds in autumn, form segregated male and female flocks in winter, and return to their nesting areas from mid- to late March to April (Weeden 1965). As such, the availability of adult Willow Ptarmigan is probably lowest during the earlier stages of the Eagle's nesting season and increases over the nesting season. In contrast, the availability of adult Snowshoe Hare remains relatively constant across the early stages of the Eagle's nesting season.

Occupancy of nesting territories remained stable over the study period, and variation in prey abundance did not influence occupancy. These results are consistent with those from other Golden Eagle studies that noted high rates of nesting territory occupancy with low interannual variation, even when the abundance of primary prey fluctuated (Steenhof *et al.* 1997, Watson 2010).

In our models of nesting success, all credible intervals overlapped zero, suggesting uncertainty in the magnitude and direction of the effects of the covariates. This was likely to be due to variation in the sample size of successful nests. For instance, only a small proportion of nests contained eggs and fledged young in years when Snowshoe Hare and Willow Ptarmigan abundance was low, so any additional negative effects on the success of the remaining nests would be more difficult to detect. We also suspect that Eagles in Denali prey less on Snowshoe Hare and Willow Ptarmigan after Arctic Ground Squirrel and Hoary Marmot emerge from hibernation and become available as prey (Murie 1944, C. McIntyre unpubl. data), but we had no data on the abundance of these two species in the study area to use as a covariate in our models of nest success.

We also found weak evidence that fledgling production was negatively affected by extended periods of low temperatures during the incubation and early nestling period. Low temperatures can reduce Golden Eagle reproduction by increasing energy demands (Watson 2010) or influencing the behaviour of prey (Steenhof *et al.* 1997). This suggests that long-term shifts to more extreme weather conditions in the region could result in decreased reproductive output by Golden Eagles.

We did not find any evidence that elevation or human activity influenced nesting success and fledgling production, but nesting territories at higher elevations or > 2 km from human activity exhibited slightly higher probabilities of occupancy. We initially suspected that nesting territories at higher elevations may favour

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detection of prey and potentially enhance hunting and reproductive success of Golden Eagles (Carrete *et al.* 2006), but it appears that this effect is weak. Support for the human disturbance effect may indicate that nesting territories further from roads and trails are less vulnerable to human disturbance (Kaisanlahti-Jokimäki *et al.* 2008, Martin *et al.* 2009). However, we expect that the current levels of human activity in Denali during the parts of the nesting season when Eagles are most likely to abandon their nests (April to early June) are very low and have no substantial effect on the territorial population.

Overall, we found strong relationships between breeding and environmental conditions on the breeding grounds, suggesting that the processes influencing these parameters were primarily dependent on the temporal heterogeneity in the environment of the breeding grounds (Katzner *et al.* 2005). However, consistent declines in the probability of nesting and fledgling production were not explained by the local environmental variables we included in our models. Thus, other factors, possibly acting on the population as a whole, are driving the declines in the breeding performance of Golden Eagles in Denali. In the Italian Alps, density-dependent processes acted negatively upon breeding parameters of Golden Eagles (Fasce *et al.* 2011), although we did not find any evidence of a decrease in nesting rates or overall population production (mean number of fledglings per occupied nesting territory) in relation to the slight increase in occupancy rates in Denali. We offer three potential explanations for the declines in the probability of nesting and overall population production: changes in the age structure of the nesting population, increased intraspecific competition and disturbance, and decreased breeding condition of adults resulting from deterioration of habitat on wintering areas and migration routes (i.e. carry-over effects).

Changes in the age structure of the nesting population could lead to decreased rates of nesting and success. Sub-adult Golden Eagles lay eggs and reproduce at lower rates than adults (Sánchez-Zapata *et al.* 2000, Pedrini & Sergio 2001b, Watson 2010) and an increase in the proportion of sub-adults in the territorial population could lead to decreased nesting rates and fledgling production. Further, increased age of territory holders could also lead to decreased nesting rates and fledgling production (Penteriani *et al.* 2009).

Behavioural interference including increased territorial encounters over limited nest-sites or foraging habitats may also lead to decreased nesting or production (Haller 1982, Bretagnolle *et al.* 2008, Watson 2010). In South Africa, the intraspecific disturbance caused by the persistent intrusion of single (unpaired) adult Black Eagles *Aquila verreauxi* into established nesting territories negatively affected nesting attempts and nesting success (Gargett 1975). In Corsica, behavioral interference between breeding and non-breeding Osprey *Pandion haliaetus* resulted in decreased hatching success (Bretagnolle *et al.* 2008). We did not quantify the age structure of the breeding population, size of the non-breeding population, or intraspecific interactions, but we made more frequent observations of Golden Eagles with sub-adult plumage and more aggressive encounters between apparent territory holders and Golden Eagles with sub-adult plumage in and just after the years when Snowshoe Hare were abundant (C. McIntyre unpubl. data). To explore fully the potential relationships between age structure, intraspecific interactions and nesting rates, a detailed assessment of the age structure of the Denali Golden Eagle population (i.e. territorial and non-territorial segments) and the rate of interactions with territorial Eagles and non-territorial Eagles (e.g. floaters) would be necessary.

Changes in body condition of breeders can also influence nesting rates. Nesting rates in southwest Idaho where Golden Eagles are resident were related to winter Jackrabbit *L. californicus* densities and the severity of the winter preceding the nesting season (Steenhof *et al.* 1997). These results suggest that Eagles may experience carry-over effects from one season to the next (Newton 2008, Harrison *et al.* 2011). Resident Golden Eagles remain on or near their nesting grounds year-round, whereas migratory Golden Eagles in North America spend approximately 40% of the year in migration or on their winter ranges, which are often thousands of kilometres to the south of the breeding grounds (Kochert *et al.* 2002, Watson 2010). Identifying carry-over effects in Denali's Golden Eagles will be very challenging because individuals from Denali may use different migration routes and different wintering areas that are spread across a vast area of western North America (McIntyre *et al.* 2008). However, given the rapid loss and alteration of Golden Eagle habitat across western North America (Kochert & Steenhof 2002), we should not ignore the influences of the

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conditions on the wintering areas and migration corridors on the future reproductive success of Golden Eagles in Denali.

We thank the U.S. National Park Service (NPS), specifically Denali National Park and Preserve and the Central Alaska Monitoring Network, for funding this study. We also thank Pam Sousanes for providing summaries of the weather data, all the pilots who flew the aerial surveys, and all the people who helped with this study, especially Michelle Ambrose, Skip Ambrose, Mike Britten, Jane Bryant, Paul Chollet, Christian and Paco Grand, Ray Hander, Gary Koy and Mark Paulson. We greatly appreciate the comments of Michael Collopy, Todd Katzner, Maggie MacCluskie, Fabrizio Sergio, Karen Steenhof, Johann Walker and an anonymous reviewer that greatly improved earlier versions of the manuscript.

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Received 23 May 2011;
revision accepted 2 October 2011.
Associate Editor: Arjun Amar.

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