AN ABSTRACT OF THE DISSERTATION OF

Carol L. McIntyre for the degree of Doctor of Philosophy in Wildlife Science presented on July 8, 2004.

Title: Golden Eagles in Denali National Park and Preserve: Productivity and Survival in Relation to Landscape Characteristics of Nesting Territories.

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Michael W. Collopy

Denali National Park and Preserve (Denali) contains one of the highest densities of nesting Golden Eagles (*Aquila chrysaetos*) in North America. Productivity of this migratory population varies both temporally and spatially. Regardless of prey abundance, more fledglings are consistently produced at some nesting territories than others. In many raptor studies, the areas where the most fledglings are produced are often considered the highest quality nesting territories; however, few studies have examined the relationship between productivity and survival of juvenile Golden Eagles.

I studied the effects of landscape characteristics of nesting territories on the productivity and survival of Golden Eagle in Denali. I quantitatively described the landscape characteristics including land cover composition, elevation, and terrain ruggedness, surrounding 36 Golden Eagle nesting sites and compared the landscape characteristics between 18 low and 18 high production nesting territories. I also instrumented 48 fledgling Golden Eagles with satellite radio transmitters to estimate

the length of the post-fledging dependence period, survival during the post-fledging dependence period, and survival during the first year of independence.

I identified 27 unique land cover types within nesting territories and found a negative relationship between the amount of Upland land cover and productivity; the probability of being a high production nesting territory decreased as the amount of the Upland land cover within a nesting territory increased.

Satellite telemetry was useful for estimating the length of the post-fledging dependence period, fledgling survival, and first-year survival of Golden Eagles. The post-fledging dependence period of Golden Eagles in Denali is shorter than reported for Golden Eagles in temperate latitudes. Fledgling survival during the post-fledging dependence period was high and counts of fledglings made before actual fledging occurs provide realistic estimates of the reproductive success of Golden Eagles in Denali. First-year survival of Golden Eagles from Denali was lower than survival of Golden Eagles from temperature latitudes. By contrasting several models of survival using program MARK, I found evidence that Golden Eagles from single-fledgling broods had a higher first year survival rate than those from two-fledgling broods. Thus, productivity may not be a good predictor of survival of Golden Eagles in Denali.

Golden Eagles in Denali National Park and Preserve: Productivity and Survival in Relation to Landscape Characteristics of Nesting Territories

by

Carol L. McIntyre

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I understand that my dissertation will become part of the permanent collection of Oregon State University libraries. My signature below authorized release of my dissertation to any reader upon request.

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Carol L. McIntyre, Author

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This research developed from a long-term ecological monitoring program of Golden Eagles in Denali. I am grateful for many conversations and discussions about Golden Eagle ecology with Skip Ambrose, John Dalle-Molle, Al Lovaas, Bob Ritchie, Ken Stahlnecker, Ted Swem, and Joe Van Horn that motivated me to develop this project.

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Recovering and identifying the cause of death of the Golden Eagles that suffered mortality in this study was a great example of coordination, collaboration, persistence, and enthusiasm. I am indebted to everyone who helped in the recovery efforts and the post-mortem analysis. I especially thank Gordon Court, Alberta Environmental Protection, for coordinating recovery efforts across Alberta and coordinating post-mortem analyses, Adam James, for his many hours of slogging through deep snow to make three significant recoveries, and Todd Powell, Yukon Renewable Resources, for braving miserable weather conditions to recover Golden Eagles in remote locations in Yukon in two years. I thank the other biologists and field assistants who recovered Golden Eagles and provided habitat information including Perry Abramenko, Layne Adams, Rhys Beaulieu, Jerry Belant, Jane Bryant, John Burch, Aaron Foos, Jim Hawkins, Nancy Hughes, Jonathan Keating, Floyd Kunnas, Rich Lowell, Kim Morton, Keith Mueller, Pat Owen, Phil Schempf, Hank, Jake, and Jeb Timm, Kim Titus, Ed Vorisek, Mark Wayland, and Kerry Wrishko. Many of these people spent many hours, trekking over many miles, often through knee-deep in snow or waist-deep in bogs, to recover an eagle. I thank Trent Bollinger, James Hanson, Robert McClymont, Chris Terzi, Mark Wayland, and G. Wobeser for conducting post-mortem examinations and providing concise summaries.

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CONTRIBUTION OF AUTHORS

This dissertation resulted from a research project requiring cooperation from other subject matter experts. Janet Kidd and Alice Stickney developed the initial land cover map and are co-authors of Chapter 2. Jon Paynter generated the triangular irregular networks and calculated surface area estimates of each land cover type and is a co-author of Chapter 2. Dr. Michael W. Collopy was involved in all aspects of this research and is a co-author on all chapters.

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Olaus Murie,
from Two in the Far North by
Margaret E. Murie

Golden Eagles in Denali National Park and Preserve:
Productivity and survival in relation to landscape characteristics of nesting territories

CHAPTER 1

GENERAL INTRODUCTION

The Golden Eagle (*Aquila chrysaetos*) is a large, long-lived diurnal raptor that has a Holarctic breeding distribution (Kochert et al. 2002). Breeding populations in North America occur mainly in the western portion of the continent, with some of the highest documented breeding densities located in Denali National Park and Preserve, Alaska (Denali) (McIntyre and Adams 1999, Kochert et al. 2002). Golden Eagles in Denali are migratory; territorial breeders usually occupy nesting territories from early March until late September.

Compared to many other species of birds, the breeding season of Golden Eagles is relatively long (Watson 1997, Kochert et al. 2002). Further, the reproductive rates of Golden Eagles fluctuate with prey densities and abundance (Steenhof et al. 1997, Watson 1997, Kochert et al. 2002). Reproductive success of Golden Eagles in interior and northern Alaska is highly variable, presumably because of the short growing season, extreme weather events, low prey diversity, and the cyclic behavior of primary prey species (McIntyre and Adams 1999).

From 1988 to 1997, I monitored the reproductive success of Golden Eagles in Denali (McIntyre and Adams 1999). During this period, I recognized that some nesting territories produced significantly more fledglings than others did (McIntyre 2002). Similar to Golden Eagles in other study areas (Steenhof et al. 1997, Watson

1997), Golden Eagles in Denali respond to changes in prey abundance and many do not breed in years when prey abundance is low (McIntyre and Adams 1999). Regardless of prey abundance, long-term productivity is much higher at some nesting territories (McIntyre 2002). The patterns that I observed in my long-term monitoring project suggested both temporal variation in reproduction, apparently in response to changing prey abundance, but also spatial variation in reproduction.

Territory quality influences long-term productivity of raptors (Newton 1979, 1998). Although many Golden Eagle studies provide measurements of productivity (Kochert et al. 2002), few studies have addressed the role of landscape characteristics of nesting territories on long-term productivity (Watson 1992, Marzluff et al. 1997, Kochert et al. 1999, Whitfield et al. 2001).

I designed the research presented in this dissertation to investigate the role of landscape characteristics of nesting territories on long-term productivity, the duration of the post-fledging dependence period, and survival of juvenile Golden Eagles. Identifying the factors that influence long-term productivity and survival of Golden Eagles in Denali is essential for understanding their population trends. This includes assessing the role of habitat on long-term productivity and survival. For example, identifying features of the landscapes of the nesting territories that produce potential breeders may enable land managers to better understand the specific habitat needs (Warkentin et al. 2004) of Golden Eagles in Denali. Further, measuring long-term productivity and site-specific demography of Golden Eagles, including survival and recruitment, in combination with measuring habitat quality may be useful for identifying the factors affecting long-term population trends in Golden Eagles in

Denali. For example, loss of prey habitat may have influenced the long-term population declines in Golden Eagles in the Snake River Birds of Prey National Conservation Area, southwest Idaho (Kochert et al. 1999).

Survival and recruitment of breeders are important facets of Golden Eagle ecology that are not well described in the literature (Watson 1997, Kochert et al. 2002). Further, many studies use productivity as a measurement of reproductive success (Steenhof et al. 1997, McIntyre and Adams 1999, Kochert et al. 2002). However, few studies measure survival of young after they leave the nest (Watson 1997, Kochert et al. 2002). If survival during the post fledging dependence period were low, estimates of the number of young fledged per nest typically reported in Golden Eagles studies would overestimate reproductive success (Zelenak et al. 1997). Because the long-term ecological study of Golden Eagles in Denali bases measurements of reproductive success on estimates of productivity made from counts of nestlings before actual fledging, an assessment of post-fledging survival was needed.

The core chapters of this dissertation were prepared as journal submissions, each addressing the role of landscape characteristics on productivity and the role of productivity on the length of the post-fledging dependence period and first-year survival of Golden Eagles. Chapter 2 provides the first quantitative description of the landscape characteristics of Golden Eagle nesting territories in Denali and sets the stage for investigating the productivity of Golden Eagles in relation to the landscape characteristics of their nesting territories in Chapter 3. Chapter 4 provides the first quantitative estimates of the length post-fledgling dependence period of Golden

Eagles in the northern latitudes of North America and examines the length of post fledging dependence period in relationship to long-term productivity of the natal territory. Chapters 5 and 6 provide the first estimates of survival during the post-fledging dependence period and the first-year of independence of migratory Golden Eagles from northern latitudes of North America and evaluate survival during these periods in relationship to long-term productivity of the natal territory. Chapter 7 offers concluding remarks and recommendations for future investigations.

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CHAPTER 2

CHARACTERISTICS OF THE LANDSCAPE SURROUNDING GOLDEN EAGLE NEST SITES IN DENALI NATIONAL PARK AND PRESERVE, ALASKA

Carol L. McIntyre, Michael W. Collopy, Janet G. Kidd,
Alice A. Stickney and Jon Paynter

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Abstract

We described the landscape characteristics within a 3-km radius surrounding the geographic center of 36 Golden Eagle nesting territories in Denali National Park and Preserve, Alaska. We measured and calculated the amount of surface area, terrain ruggedness index, and composition of the area by physiographic zones and unique land cover types within each 3-km circular plot. We also calculated diversity measurements including Richness (number of land cover types), Evenness, Shannon's Diversity Index and Simpson's Diversity Index. We delineated 27 land cover types within Golden Eagle nesting territories based on 11 unique types of vegetation cover and structure within 4 terrestrial physiographic zones: Alpine, Upland, Lowland, and Riparian. Our results suggest that Golden Eagle nesting territories in Denali are characterized by rugged terrain, alpine areas, and a mosaic of land cover types dominated by Alpine Low Shrubs, Alpine Barren, Upland Low Shrubs, Riparian Barren, and Riparian Shrubs. Alpine land cover types dominated most Golden Eagle nesting territories. Shrub cover types dominated the area within the 3-km plots (mean = 68.5%, range = 13.6-96.8%, SE = 3.4, 95% CI = 61.2-75.5%) of the area within nesting territories. Our results suggest that Golden Eagle build their nest sites in proximity to open landscapes that may favor detection of prey and enhance hunting success.

Introduction

Breeding Golden Eagles (*Aquila chrysaetos*) are central-place foragers, with much activity centered on the occupied nest site during the breeding season (Watson

1997, Kochert et al. 2002). Across their range, Golden Eagles select nesting sites based on proximity to suitable hunting terrain (Watson 1997). Land cover provides food, shelter and breeding sites for prey and may reflect the amount of potential habitat for prey (Ferrer and Donazar 1996, Knick and Dyer 1997, Kochert et al. 1999), potential foraging habitat for Golden Eagles (Janes 1984, Marzluff et al. 1997), and potential prey availability (Carter and Jones 1999) surrounding nest sites. Land cover, particularly vegetation structure and canopy, may influence prey availability and foraging success of Golden Eagles and other large raptors (Bechard 1982, Tjernberg 1983, Marzluff et al. 1997, McGrady et al. 1997). Open landscapes would favor detection of prey and enhance hunting success of Golden Eagles (Carrete et al. 2000).

Topography also is an important component of the landscape (Forman 1995). Topography may influence distribution and abundance of land cover types (Forman 1995) within nesting territories, as well as the flight dynamics of Golden Eagles within these territories (Cone 1962, Donazar et al. 1993, McLeod et al. 2002). Further, wind direction and speed may interact with terrain to influence how Golden Eagles use their nesting territories (McGrady et al. 1997).

Information on the landscape characteristics of nesting territories and foraging areas of Golden Eagles in Alaska and northwestern Canada is limited to general qualitative descriptions. For example, in Alaska, Golden Eagles breed in habitat dominated by rugged topography or mountainous terrain, near or above timberline, and along riparian areas, often in open landscapes dominated by low tundra vegetation (Kochert et al. 2002). In northwestern Canada, Golden Eagles breed in habitat with high topographic relief dominated by low-arctic tundra (Poole and Bromley 1988) or in areas dominated by tundra, river outwash plains, and alpine and subalpine ecotypes (Hayes and Mossop 1981, Sinclair et al. 2003). There are no quantitative descriptions of the landscape characteristics of nesting territories and potential foraging areas of Golden Eagles in Alaska or northwestern Canada (Kochert et al. 2002).

The impetus for this study was to provide quantitative descriptions of the landscape characteristics surrounding nest sites of Golden Eagles in Denali, so we could test hypotheses regarding the relationship between landscape characteristics and long-term productivity (see Chapter 3). Our results should also be valuable for predicting how Golden Eagles will respond to land cover change in Denali (Steenhof et al. 1999, Kochert et al. 1999), particularly in relation to large-scale perturbations such as climate change.

Methods

Study Area

The 2,100-km^2 study area, centered at 63° 35.8' N, 149° 38.2'W, is in the northern foothills of the Alaska Range in the northeastern portion of Denali in central Alaska. Steep-sided mountains, small streams, large, swift-running glacial rivers, broad glacially carved valleys, and extensive gravel bars dominate the landscape. Broad glacial valleys are interspersed among the foothills. Water, wind, and glacial action shape the terrain in the study area. Golden Eagles build nests exclusively on cliffs and rock outcroppings in the study area.

Delineating Nesting Territories

We delineated unique nesting territories using data on occupancy and breeding activities collected at individual nests from 1987 to 1997. During this period, we used two standardized aerial surveys conducted using a small helicopter to locate nest sites and to determine occupancy and breeding activities at these sites (McIntyre and Adams 1999, McIntyre 2002). Golden Eagles use one nest per year for raising a brood; however, nesting territories often contain multiple nests that belong to one pair (Kochert et al. 2003). In Denali, Golden Eagle nesting territories contain two to eight nests that usually occur in well-defined groups (McIntyre, unpublished data). We grouped clusters of nests (≤1 km apart) used by a single pair of eagles in any given year as unique nesting territories (Steenhof 1987). We calculated the center of each nesting territory (referred to as the nesting centroid) as the average latitude and longitude of all known nests within each nesting territory using methodology described by McGrady et al. (1997) and Kochert et al. (1999). We mapped a circular area around each nesting centroid within a 3-km radius encompassing approximately 2,826 ha. The biological basis for this sampling area in Denali was that the radius of the circular plots approximated one-half the average nearest-neighbor distance (NND) (NND = 6,000-m) between the centers of all know nesting territories in the study area (n = 72). For simplicity, we hereafter refer to the circular plots as the nesting territory (following Kochert et al. 1999).

Developing the Land Cover Map

No reliable, high-resolution land cover map existed for Denali. Therefore, we created the land cover map for this study (Kidd and Stickney 2000). Satellite imagery for the study area was limited to low resolution coverages often obscured by cloud cover. Therefore, we used the most recent color infrared aerial (CIR) photographs (August 1981) (1:63,360 scale) of the study area and field verification of the CIR photographs to develop the land cover map. We delineated the boundaries of individual land cover types on acetates overlaying the CIR photographs using a mirror stereoscope and created digital maps of the land cover types within each nesting territory by digitizing the mapped unit areas on the acetate overlays using ArcView© Geographic Information System version 3.2 (GIS) software (Environmental Systems Research Institute, Redlands, California, USA). We obtained geodetic control by transferring Universal Transverse Mercator (UTM) coordinates from U.S. Geological Survey (USGS) orthoquad photographs of the study area to the CIR aerial photographs. We mapped land cover at a minimum resolution of 0.5 ha, except for distinct landscape features such as lakes, ponds, and barren rock outcroppings, which we mapped at their actual size. The estimated accuracy of the land cover delineations was 85% (J. Kidd, personal communication).

Land Cover Classification Scheme

We used the Alaska Vegetation Classification (AVC) (Viereck et al. 1992) as our land cover classification scheme. The basic elements of the hierarchical AVC are plant communities including their structure and canopy closure (Viereck et al. 1992).

The AVC contains five levels of classification resolution; each AVC level is composed of an increasing number of formations and describes vegetation cover with an increasing degree of complexity. We created the modified AVC Level III using physiographic zone, vegetation structure, and canopy (Table 2.1) as a balance between the coarse descriptions of AVC Levels I-III and the complex descriptions of AVC level IV (n = 77 individual land cover classes in the study area).

We used ARC/INFO© version 8.2 GIS (Environmental Systems Research Institute, Redlands, California, USA) to generate a series of triangular irregular networks (TINS) to incorporate terrain into our estimates of land cover type, providing an estimate of the surface area for each physiographic zone and land cover type within each nesting territory. We created TINS using a 1:63,360-scale digital elevation model (DEM) obtained from the USGS and the GIS land cover type coverages (Kidd and Stickney 2000) as the source for breaklines. We report the amount of each physiographic zone and land cover type in Golden Eagle nesting territories using these surface area estimates.

We selected 50 nesting territories for this study. However, we had to eliminate 14 nesting territories from our analysis because poor aerial photo coverage or snow cover resulted in unknown classification of land cover for $\geq$10% of the area within these nesting territories. Our final data set of 36 nesting territories represented 59% of the 61 nesting territories monitored continuously from 1988 to 1997.

Table 2.1. Habitat classification characteristics for delineating land cover types within Golden Eagle nesting territories, Denali National Park and Preserve, Alaska (Kidd and Stickney 2000).

Classification variable	Description
Physiographic zones	
Alpine	Areas $\geq$800 m above sea level.
Upland	Well-drained slopes, ridges, and inactive flood plains < 800 m above sea level.
Lowland	Poorly drained areas in valley bottoms and on lower slopes of hillsides, and other low-lying floodplain areas.
Riparian	Active flood plain, annual seasonal inundated areas, and river bars.
Rivers/Streams	Permanent rivers and streams.
Lakes/Ponds	Permanent lakes and ponds.
Vegetation type, height and canopy cover class	
Barren	Vegetation cover is < 10%.
Barren partially vegetated	Vegetation cover is 10 to 25%.
Shrub	Vegetation is $\leq$3 m tall.
Forest	Trees > 3 m tall and comprise $\geq$10% of area.
Dwarf	Vegetation is < 0.2 m tall.
Low	Vegetation is $\geq$ 0.2 m and $\leq$ 1.5 m tall.
Tall	Vegetation is > 1.5 m tall.
Open	Canopy cover is 25 to 60%.
Closed	Canopy cover is >60%.

Describing Terrain Ruggedness

The amount of surface area within the 3-km circular plot provided us with an initial indication of the ruggedness of a nesting territory. Intuitively, greater amounts of surface area indicate greater terrain ruggedness. To standardize the measurement of terrain ruggedness, we developed a terrain ruggedness index using the ratio between the surface area and planar area for each nesting territory. The values of the terrain ruggedness index range from 1, indicating no difference between planimetric and surface area estimates, to > 1, indicating a difference between surface area and planar area). Higher terrain ruggedness index values indicate a larger difference between the surface area and planar area, and represent greater terrain ruggedness.

Describing Landscape Characteristics

We measured and/or calculated the amount of surface area, terrain ruggedness index, composition by physiographic zone, composition by land cover type, and four diversity measurements (i.e., number of land cover types, Evenness, Shannon's Diversity Index, and Simpson's Diversity Index) for each nesting territory. We described these landscape characteristics using the mean ($\bar{x}$), standard deviation (SD), standard error (SE), 95% confidence intervals (95% CI), and frequency of occurrence (FO).

Data Analysis

We compared the difference in surface and planar estimates of the amount of hectares made up of each physiographic zone using paired *t*-tests and differences in the amount of hectares of each physiographic zone within nesting territories using two sample *t*-tests. We used linear regression to examine the relationships between the number of land cover types and terrain ruggedness, and the amount of Alpine area (ha) and the elevation of the nesting centroid. We used the square-root transformation for all count data, but report means as untransformed values for clarity. We calculated diversity statistics using PC-ORD statistical software (McCune and Mefford 1999) and conducted all statistical analyses using S-Plus Version 6.0 statistical software (Insightful 2001). We evaluated significance at $P = 0.05$.

Results

Surface Area and Terrain Ruggedness Index

The amount of planimetric area within each nesting territory was 2,826 ha. After accounting for terrain, the amount of surface area within Golden Eagle nesting territories ranged from 3,285 ha to 4,873 ha ($\bar{x} = 4069$, SE = 57.8, 95% CI = 3955-4186). The terrain ruggedness index ranged from 1.17 to 1.73 ($\bar{x} = 1.45$, SE = 0.02, 95% CI = 1.40-1.49).

We based our estimates of land cover within nesting territories using surface area. However, most published raptor habitat studies calculate the amount of land cover within a plot or home range using planimetric methods. In landscapes dominated by rugged topography, planar estimates of land cover may substantially underestimate the amount of area comprised of different land cover types within nesting territories. Our results suggest that differences in the area calculated by planimetric and surface area methods will be greatest in areas with high topographic relief. In our study, we found significant differences between the amount of area calculated using surface and planimetric methods for the Alpine, Upland, Riparian, and Streams/Rivers physiographic zones (Table 2.2).

Physiographic Zones

Golden Eagles in our study area build nests exclusively on cliffs and rock-outcroppings. The elevation of 88.9% of the nesting centroids in our study area was $\geq$800 m. The elevation of nesting centroids ranged from 701 to 1,402 m ($\bar{x}$ = 1,108 m, SE = 27.41, 95% CI = 1,052-1,163). Thirty-two nesting centroids were in the Alpine zone and four were in the Upland zone.

The number of physiographic zones within Golden Eagle nesting territories ranged from three to six (median = 4). The Alpine zone dominated Golden Eagle nesting territories (Table 2.3). The proportion of a nesting territory made up of Alpine increased with the elevation of the nesting centroid ($r^2 = 0.38$, $P < 0.001$). Upland was present in most nesting territories, but nesting territories generally contained less Upland than Alpine ($t = 7.71$ $P = 0.001$; Table 2.3). On average, the area within Golden Eagle nesting territories contained 42 percentage points more Alpine than Upland. Alpine was the dominant physiographic zone in 29 nesting territories; 51-94% of the total area within these nesting territories was Alpine. Upland was the dominant physiographic zone in seven nesting territories; 51-78% of the total area within these nesting territories was Upland. Riparian and Streams/Rivers occurred in all nesting territories (Table 2.3). Nesting territories contained between < 1 to 14%

Table 2.2. Estimates of the mean hectares (with SE) of each of six physiographic zones calculated for planimetric area and surface area within 36 Golden Eagle nesting territories, Denali National Park and Preserve, Alaska.

Physiographic zone	Planimetric estimate	Surface area estimate	*t*	*P*
Alpine	1813 (107)	2788 (164)	2.93[a]	0.006
Upland	794 (109)	1046 (156)	-4.90	0.001
Lowland	19 (13)	20 (14)	-1.25	0.217
Riparian	170 (21)	189 (22)	-8.04	0.001
Rivers/Streams	12 (2)	17 (3)	-7.29	0.001
Lakes/Ponds	2 (1)	2 (1)	-1.29	0.203

[a] paired t-test

Table 2.3. Summary of physiographic zones within Golden Eagle nesting territories (n = 36), Denali National Park and Preserve, Alaska.

Physiographic zone	Percent of territories	Composition (%)		
		Mean	SE	95% CI[a]
Alpine	100	68.23	3.83	60.44 - 76.02
Upland	89	25.94	3.85	18.12 - 33.76
Lowland	31	0.53	0.38	0.00 - 1.30
Riparian	100	4.69	0.56	3.55 - 5.83
River/Streams	100	0.41	0.06	0.27 - 0.54
Lakes/Ponds	33	0.01	0.01	0.00 - 0.01

[a] 95% Confidence Interval

Riparian. Within the Riparian zone, 21 nesting territories contained extensive gravel bars associated with clearwater and glacial rivers.

Lowland and Lakes/Ponds did not occur at high frequency and did not make up a large proportion of the landscape (Table 2.3). Lowland occurred in 11 nesting territories and in all but 1 case, made up < 1% of the total area within these nesting territories. Lakes/Ponds occurred in 12 nesting territories but < 1% of the total area within these nesting territories was made up of Lakes/Ponds.

Land Cover Types

We delineated 27 land cover types within Golden Eagle nesting territories based on 11 unique types of vegetation cover and structure within the four terrestrial physiographic zones (Table 2.4). The Upland and Alpine zones contained 10 and 8 land cover types, respectively. The Lowland zone was the least diverse physiographic zone, containing three land cover types. Barren and Barren Partially Vegetated areas occurred primarily within the Alpine and Riparian zones (Table 2.4). Barren areas within the Alpine zone consisted primarily of cliffs, rock outcroppings, and talus slopes. Barren areas within the Upland zone consisted primarily of river bars associated with streams and rivers.

Dwarf Shrub was limited to the Alpine zone. Low Shrub occurred primarily in Alpine and Upland zones. Closed Low Shrub was the only land cover type to occur in all four physiographic zones. Tall Shrubs were more common in Upland and Riparian zones. Tall Shrubs were limited to riparian zones in the Alpine zone.

Table 2.4. Attributes of the modified Alaska Vegetation Classification Level III land cover types within Golden Eagle nesting territories (n = 36), Denali National Park and Preserve, Alaska. Land cover types in bold type occur in > 50% of the nesting territories.

		Composition (%)		
Modified AVC III land cover type	n	Mean	SE	95% CI
Alpine Barren	34	19.92	3.51	12.79 - 27.05
Alpine Barren Partially Vegetated	35	4.48	0.76	2.94 - 6.02
Alpine Dwarf Shrub	26	3.30	0.91	1.45 - 5.14
Alpine Low Shrub	30	4.41	1.39	1.60 - 7.23
Alpine Open Low Shrub	36	10.87	1.38	8.08 - 13.66
Alpine Closed Low Shrub	35	24.97	2.92	19.04 - 30.91
Alpine Open Tall Shrub	2	0.01	0.01	0.00 - 0.03
Alpine Closed Tall Shrub	6	0.27	0.14	0.00 - 0.56
Lowland Low Shrub	3	0.15	0.13	0.00 -0.42
Lowland Open Low Shrub	9	0.34	0.21	0.00 - 0.78
Lowland Closed Low Shrub	1	0.04	0.04	0.00 - 0.12
Riparian Barren	31	2.17	0.43	1.29 - 3.04
Riparian Barren Partially Vegetated	21	0.79	0.23	0.34 - 1.25
Riparian Closed Low Shrub	2	0.02	0.02	0.00 - 0.06
Riparian Open Tall Shrub	33	0.96	0.15	0.65 - 1.27
Riparian Closed Tall Shrub	30	0.75	0.14	0.47 - 1.04
Riparian Open Broadleaf Forest	1	0.00	0.00	0.00 - 0.01
Upland Barren	5	0.09	0.07	0.00 - 0.23
Upland Barren Partially Vegetated	8	0.16	0.09	0.00 - 0.35
Upland Low Shrub	26	3.47	0.62	2.20 - 4.73
Upland Open Low Shrub	23	3.40	0.97	1.44 - 5.37
Upland Closed Low Shrub	30	8.29	1.28	5.69 - 10.88
Upland Open Tall Shrub	6	0.10	0.05	0.00 - 0.21
Upland Closed Tall Shrub	25	7.18	1.81	3.50 - 10.86
Upland Open Needleleaf Forest	20	3.04	0.95	1.12 - 4.95
Upland Closed Needleleaf Forest	2	0.03	0.02	0.00 - 0.08
Upland Open Broadleaf Forest	4	0.19	0.16	0.13 - 0.51

Needleleaf Forests occurred only in Upland zones and Broadleaf Forests occurred only in Upland and Riparian zones (Table 2.4).

Shrub cover types dominated the landscape in the study area. An average of 68.5% (range = 13.6-96.8%, SE = 3.4, 95% CI = 61.2-75.5%) of the area within the 36 nesting territories was made up of shrub cover. Shrub land cover included many different species of vegetation (Table 2.5). Many species of Golden Eagle prey, including snowshoe hare, willow ptarmigan, arctic ground squirrel, and hoary marmot forage on these plants (Krebs et al. 2001).

Alpine Closed Low Shrub and Alpine Barren were the most common land cover types in Golden Eagle nesting territories (Table 2.4). Alpine Closed Low Shrub consisted primarily of *Betula glandulosa, B. nana*, and *Salix* spp. Alpine Barren consisted primarily of talus slopes, rock outcroppings, and cliffs. An average of 27.6% (range = 2.2- 85.9%, SE = 3.6, 95% CI = 20.3-34.9%) of the area within nesting territories was Barren. An average of 3.3% (range = 0.0-25.4, SE = 1.0, 95% CI = 1.2-5.4%) of the area within nesting territories was Forest.

River bars associated with clearwater or glacial rivers dominated the Riparian Barren land cover type. Riparian Barren Partially Vegetated land cover type included river bars with avens (*Dryas* sp.), soapberry (*Shepardia canadensis*), shrub willows (*Salix* sp.), dwarf fireweed (*Epilobium latifolium*), and vetch (*Hedysarum alpinum*). Riparian Low Shrub consisted primarily of willow, avens, and soapberry. Taller shrub willows and green alder (*Alnus cripsa*) dominated the Riparian Open Tall Shrub and Riparian Closed Tall Shrub land cover types. Willow and green alder dominated Riparian Tall Shrub. Riparian Open Tall Shrub and Riparian Closed Tall Shrub both

Table 2.5. Summary of dominant (D), subdominant (SD), understory (U) and common (P) species found in Dwarf, Low, and Tall Shrub land cover types within Golden Eagle nesting territories, Denali National Park and Preserve, Alaska.

Species	Common name	Dwarf Shrub	Low Shrub	Tall Shrub
Alnus crispa	Green alder	-	-	D
Anemone spp.	Anemone	P	U	-
Arctagrostis latifolia	Polar grass	P	-	U
Arctostaphylos alpina	Alpine bearberry	D	U	U
Arctostaphylos rubra	Red-fruit bearberry	D	U	-
Astragalus alpinus	Vetch	-	U	-
Betula glandulosa	Resin birch	-	D	-
Betula nana	Dwarf birch	-	D	U
Calamagrostis canadensis	Bluejoint grass	-	-	U
Carex bigelowii	Bigelow sedge	P	-	U
Carex spp.	Sedge	P	-	-
Cassiope tetragona	Four-angled cassiope	D	-	-
Dryas spp.	Avens	D	SD	-
Empetrum nigrum	Crowberry	D	U	-
Epilobium angustifolium	Fireweed	-	-	U
Epilobium latifolium	Dwarf fireweed	-	-	U
Eriophorum angustifolium	Cotton grass	-	U	-
Fescue altaica	Fescue grass	-	-	U
Hedysarum spp.	Vetch	-	U	-
Ledum decumbens	Labrador tea	-	U	U
Mertensia paniculata	Bluebell	-	-	U
Polygonum bistorta	Bistort	-	-	U
Potentilla fruticosa	Bush cinquefoil	-	U	U
Salix alaxensis	Feltleaf willow	-	-	D
Salix arbusculoides	Littletree willow	-	-	D
Salix arctica	Arctic willow	SD	-	-
Salix brachycarpa	Barren ground willow	-	D	-
Salix glauca	Grayleaf willow	-	D	D
Salix lanata	Richardson willow	-	D	D
Salix planifolia	Diamondleaf Willow	-	D	D
Salix reticulata	Netleaf willow	SD	-	-
Shepardia canadensis	Soapberry	-	-	U
Vaccinium uliginosum	Bog blueberry	D	U	U
Vaccinium vitis-idaea	Mountain cranberry	D	U	-

occurred in > 83% of the nesting territories; but combined, these land cover types made up < 1.7 % of the land cover within these territories (Table 2.4). Both Riparian Open Tall Shrub and Riparian Closed Tall Shrub were limited to linear riparian areas. Green alder, with a mixture of shrub birch and willow were the primary vegetation types in Upland Closed Tall Shrub. White spruce (*Picea glauca*) was the only tree species in Needleleaf Forest. Broadleaf Forest contained paper birch (*Betula papyrifera*) and balsam poplar (*Populus balsamifera*).

We detected a bimodal distribution in the frequency of occurrence of land cover types. Twelve land cover types occurred in $\leq$25% of the nesting territories (Table 2.3) and totaled $\leq$3% of the area within these nesting territories. The remaining 15 land cover types occurred in $\geq$ 56% of the nesting territories.

Landscape Diversity

The number of land cover types within individual nesting territories ranged from 8 to 19 ($\bar{x}$ = 13.44, SE = 0.50, 95% CI = 12.42-14.46). The number of land cover types was not related to terrain ruggedness index (r^2 = 0.007, P = 0.62). Evenness ranged from 0.38 to 0.87 ($\bar{x}$ = 0.68, SE = 0.02, 95% CI = 0.64-0.72). Shannon's Diversity Index ranged from 0.91 to 2.42 ($\bar{x}$ = 1.7, SE = 0.06, 95% CI = 1.63-1.88) and Simpson's Diversity Index ranged from 0.38 to 0.89 ($\bar{x}$ = 0.74, SE = 0.02, 95% CI = 0.71-0.78).

Alpine Closed Low Shrub, Alpine Barren and Alpine Open Low Shrub were the most common dominant land cover types. The proportion of an individual nesting territory dominated by a single land cover type ranged from 0.16-0.78 ($\bar{x}$ = 0.39, SE = 0.02, 95% CI = 0.34-0.44). A single land cover type dominated ≥50% of the area within 10 of 36 nesting territories.

Discussion

Golden Eagles traditionally hunt in open country (Brown and Watson 1964, Watson 1992, Kochert et al. 2002). Our results suggest that Golden Eagles in Denali build their nesting sites in open landscapes that may favor detection of prey and perhaps enhance hunting success (Tjernberg 1983, Marzluff et al. 1997, McGrady et al. 1997, Carrette et al. 2000). Most nesting centroids of Golden Eagles in our study area occurred in the Alpine zone where bare rock, and dwarf and low alpine vegetation dominate the landscape. Alpine was the dominant physiographic zone within most Golden Eagle nesting territories. We did not measure prey availability or prey abundance in this study. However, 21 of the 27 land cover types occurring within nesting territories potentially support one or more of the primary prey species of breeding Golden Eagles in Denali including snowshoe hare, Willow Ptarmigan and arctic ground squirrel (*Spermophylis paryii*) (Dixon 1938, Murie 1964).

Riparian Barren and Riparian Open Tall Shrub land cover types and the physiographic zone Rivers/Streams occurred in nearly every nesting territory. Although these linear landscape features are not abundant in relation to percent cover, they are common features in Golden Eagle nesting territories in Denali. Although it is generally assumed that Golden Eagles acquire all the liquid they need from their prey (Watson 1997), clearwater streams provide water for drinking, bathing, and preening

(Charlet and Rust 1991, Kochert et al. 2002). Further, riparian vegetation also provides food and shelter for snowshoe hare and willow ptarmigan during late winter and early spring (Weeden 1958, Murie 1964). These two species are important food resources for Golden Eagles before and during incubation (McIntyre and Adams 1999).

High mean values of Evenness, Shannon's Diversity Index and Simpson's Diversity Index suggest high landscape diversity in relation to land cover types within nesting territories. Evenness is a measure of the relative abundance of the different land cover types comprising a nesting territory (McCune and Grace 2002). The high mean value of Evenness suggests a relatively even distribution of different land cover types within most nesting territories. Similarly, high mean values of Simpson's Diversity Index suggest that the proportional distribution of area among land cover types within most nesting territories is relatively equitable (McCune and Grace 2002). All four measures of diversity were lower in nesting territories where a single land cover comprised > 50% of the area within the nesting territory.

We hypothesized that greater topographic complexity would result in a greater number of land cover types within nesting territories because topographic complexity often results in greater vegetation diversity (Rosenzweig 1995). However, we failed to detect a relationship between the terrain ruggedness index and the number of land cover types in Golden Eagle nesting territories. This lack of association may have resulted from using a land cover scheme with a relatively coarse-scale resolution.

Our results suggest that rugged terrain is a common feature of most Golden Eagle nesting territories in Denali. Topography can influence flight dynamics (Cone

1962) and may potentially influence territory quality (Donazar et al. 1993). Golden Eagles nesting and foraging in areas with favorable flight dynamics would presumably maximize their net rate of energetic gain (Pyke 1984, McGrady et al. 1997) and use less energy for foraging and delivering prey to the nest.

Although many raptors nest in mountainous or rugged terrain, few raptor studies include estimates or measurements of topography and terrain ruggedness (although see Janes 1984, Donazar et al. 1993, Whitfield et al. 2001, Boal et al. 2003). Ignoring the effect of topography on habitat quality may lead to a misunderstanding of the ecology of the animals that live in mountainous terrain (Powell and Mitchell 1998, Rolando et al. 2000). Our terrain ruggedness index provided a measure of topographic complexity. When applicable, and when reliable digital elevation maps are available, we suggest that wildlife habitat studies incorporate measures of terrain ruggedness and surface area.

Throughout much of their Holarctic range, Golden Eagles live in landscapes where human activities directly modify habitats (Watson 1997, Kochert et al. 2002). Two long-term studies in the Snake River Birds of Prey National Conservation Area in southwest Idaho illustrate the importance of measuring attributes of the landscape and measuring the response of nesting raptors to habitat change over time (Kochert et al. 1999, Steenhof et al. 1999). Because our study area is in a National Park, and mostly within a federally protected wilderness area, we do not expect the landscapes within Golden Eagle nesting territories in Denali to change due to direct modification by humans. Rather, we expect that large-scale perturbations including climate change are more likely to shape the future landscapes in Denali. Paleoclimatic records indicate that the Arctic regions of Earth are now warmer than any time in the past 400 years (Overpeck et al. 1997). Climatic models project that rapid Arctic warming will continue, with Alaska warming by 5-12° F by 2100 (Payton et al. 2000). The effects of this warming could cause large-scale changes in vegetation patterns (Rupp et al. 2000, Sturm et al. 2001) that could potentially affect prey abundance and foraging success of Golden Eagles. Our study provides the first quantitative descriptions of the landscape characteristics of nesting territories of Golden Eagles in Denali. In conjunction with productivity and demographic information, our results should be valuable for measuring habitat change and quantifying how Golden Eagles respond to these changes in Denali.

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CHAPTER 3

EFFECTS OF LANDSCAPE CHARACTERISTICS ON PRODUCTIVITY OF GOLDEN EAGLES IN DENALI NATIONAL PARK AND PRESERVE, ALASKA

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Abstract

We investigated the relationships between landscape characteristics and productivity of Golden Eagles in Denali National Park and Preserve, Alaska. We tested the null hypothesis that landscape characteristics including surface area, terrain ruggedness, land cover composition and a suite of diversity measurements did not differ between 18 low production nesting territories (mean productivity = 0.29, SE = 0.20, 95% CI = 0.24- 0.35) and 18 high production nesting territories (mean productivity = 0.93, SE = 0.18, 95% CI = 0.89- 0.98). The mean elevation of the nesting centroid of low production nesting territories was significantly lower than high production nesting territories. Low production nesting territories had more Upland land cover than high production nesting territories. The probability of a nesting territory being high production decreased significantly as the proportion of the nesting territory composed of Upland land cover increased.

Introduction

Producing recruits for breeding populations may depend upon choice of mates and the quality of nesting territories (Newton 1986), and securing a good nesting territory is apparently important for improving or maintaining fitness (Newton 1979). Many species of long-lived raptors, including Golden Eagles (*Aquila chrysaetos*), are territorial in the breeding season (Newton 1979). Golden Eagles apparently occupy the same nesting territory for many consecutive years, despite fluctuations in prey abundance (Marzluff et al. 1997, Watson 1997, Kochert et al. 2002), suggesting that obtaining and maintaining a good territory is important.

Few studies have quantitatively examined the relationship between the landscape characteristics of nesting territories and the long-term productivity of Golden Eagles. In southwestern Idaho, Golden Eagles foraged in habitats that had the potential to contain their primary prey, black-tailed jackrabbits (*Lepus californicus*), but territories in poor jackrabbit habitats had similar productivity compared to those in good jackrabbit habitats (Marzluff et al. 1997). Golden Eagle productivity on the Isle of Mull, in western Scotland, was not related to range size, mean elevation, variation in elevation, terrain ruggedness, or mean cover of closed canopy forest (Whitfield et al. 2001). However, in Argyll in southwest Scotland, breeding success of Golden Eagles was negatively correlated with the extent of closed canopy forest (Watson 1992). Results of these studies suggest that the relationship between landscape characteristics of nesting territories and productivity of Golden Eagle is not clear. The contrasting results of these studies are consistent with Marzluff et al. (1997) who suggested that habitat quality may "come under a variety of guises depending upon habitat availability and eagle prey selection."

Identifying features of the surrounding landscapes that are associated with highly productive nesting territories may enable land managers to better identify specific habitat needs (Warkentin et al. 2004) and factors that influence the reproductive success of Golden Eagles. Highly productive pairs of raptors often occupy territories with a higher abundance of prey (Watson 1997), more or higher quality foraging areas (Newton 1979), regularly dispersed hunting perches (Janes 1984), or vegetative cover that enhances foraging opportunities and/or prey availability (Bechard 1982) compared to lower producing pairs. In this study, we investigated whether landscape characteristics affect productivity of Golden Eagles in Denali. Specifically, we asked if elevation, terrain ruggedness, land cover composition and vegetation structure differ between low production versus high production Golden Eagle nesting territories and if these landscape characteristics are good indicators of the productivity of a nesting territory.

Methods

Study area

The 2,100 km^2 study area, centered at 63° 35.8'N, 149° 38.2'W, is in the northern foothills of the Alaska Range in the northeastern portion of Denali in central Alaska. Elevations in the study area range from 427 m in the lowlands and river bottoms to 2,590 m. Elevations of the foothill summits range from 607 to 1,372 m. Broad glacial valleys and upland areas are interspersed among the foothills. Glacial action, erosion, water, and wind are the primary forces shaping the landscape.

Defining Low and High Production Nesting Territories

We defined low and high production nesting territories using data collected at the same 61 nesting territories monitored for 10 consecutive years from 1988 to 1997. We documented occupancy, breeding activities, and breeding success annually using two standardized aerial surveys (McIntyre and Adams 1999). Each year we documented the number of fledglings produced at occupied nesting territories and calculated the average productivity (number of fledglings per occupied year) for each nesting territory for the 10-year period. We defined the number of fledglings as the number of young observed in the nest that were ≥ 56 days old (80% of the estimated age at fledging) (Steenhof 1987). We assumed that very little mortality occurred in the nest after nestlings were ≥51 days old.

Because we wanted to determine if landscape characteristics differed between highly productivity and poorly productive nesting territories, we specifically selected the nesting territories for this study that exhibited the highest and the lowest productivity within the study area. This sample of nesting territories could be separated into two production categories to establish a binomial high-low productivity variable. There was a significant difference in mean productivity between the two production classes ($t = -10.09$; $P < 0.0001$). We categorized nesting territories with an average productivity of > 0.70 as high production nesting territories and nesting territories with an average productivity of < 0.50 as low production nesting territories. Our final sample included 18 high production nesting territories with a mean productivity of 0.93 (SE = 0.18, 95% CI = 0.89 - 0.98) and 18 low production nesting territories with a mean productivity of 0.29 (SE = 0.20, 95% CI = 0.24 - 0.35).

Landscape Characteristics

We measured landscape characteristics (terrain ruggedness, physiographic zones, and land cover types) within a 3-km circle surrounding the nesting centroid (McGrady et al. 1997, Kochert et al. 1999) of 18 low production and 18 high production Golden Eagle nesting territories (see Chapter 2 for details). The biological basis for this sampling area was that the radius of the circular plots approximated one-half the average nearest-neighbor distance (radius = ½ NND or 3000-m) between the centers of all known nesting territories (n = 72). For simplicity, we refer to these circular plots hereafter as the nesting territory (following Kochert et al. 1999).

We used the Alaska Vegetation Classification (AVC) (Viereck et al. 1992) as our land cover classification scheme. Chapter 2 contains a detailed description of how we developed the land cover map for this project. The modified AVC Level III vegetation classification included 27 unique land cover types that incorporated physiographic zone (Alpine, Upland, Lowland, Riparian, Streams/Rivers, and Lakes/Ponds), vegetation structure (Dwarf, Low, Tall), vegetation type (Barren, Partially Vegetated, Shrub, Forest) and canopy (Open, Closed) (Table 2.1). We used the modified AVC Level III to provide a reasonable balance between the broad descriptions of AVC Levels I and II and the complex descriptions of AVC level IV for comparing the land cover composition of low and high production Golden Eagle nesting territories.

Comparing Landscape Characteristics

We measured the amount of surface area (ha), terrain ruggedness index (ratio of surface area to planar area), composition by physiographic zone (ha, % composition, frequency of occurrence), composition by land cover type (ha, % composition, frequency of occurrence), and elevation of the nesting centroid for each nesting territory. We also calculated a suite of diversity measurements based on land cover for each nesting territory and for pooled samples of low and high production nesting territories including the number of land cover types, Evenness, Shannon's Diversity Index, Simpson's Diversity Index, and the dominant land cover type. We used descriptive statistics including mean ($\bar{x}$), standard deviation (SD), standard error (SE), 95% confidence intervals (95% CI), and frequency of occurrence (FO) to describe landscape characteristics and diversity measurements.

Data Analysis

We tested the null hypothesis that landscape variables measured at low production nesting territories did not differ from variables measured at high production nesting territories. We examined the relative differences between low and high production nesting territories for each landscape variable using box and whisker plots (following Finn et al. 2002). We used box and whisker plots instead of simultaneous univariate tests to avoid making Type I errors (Finn et al. 2002). We examined the box and whisker plots and identified variables with central tendencies that varied with production (Finn et al. 2002). We used Mann-Whitney tests to test for significant differences in these variables between low and high production nesting territories, and logistic regression to evaluate their usefulness as indicators of productivity of Golden Eagle nesting territories. We used logistic regression to assess the relationship of broad-scale landscape characteristics including physiographic zone, elevation of the nesting centroid, and terrain ruggedness index (explanatory variables) and the production history of Golden Eagle nesting territories (a binary response variable: 1= high production, 0 = low production), using each nesting territory as an observation. Before running the regressions, however, we explored the selection of explanatory variables using scatterplot matrices and correlation coefficients to identify possible transformations and to identify any highly correlated explanatory variables to minimize multicollinearity in our models (Ramsey and Shafer 1997). After examining the scatterplots, we eliminated variables that were highly correlated from consideration in the regression models. To select the model from which we drew inference, we used Mallow's Cp values to contrast all possible combinations of explanatory variables. This model selection method uses the principal of parsimony to determine which model is best fit by the data (Burnham and Anderson 1998), avoiding assumptions and biases of traditional stepping model selection procedures (Flack and Chang 1997). The model with the lowest Cp value is the one best supported by the data and provides the strongest inference (Esler et al. 2000).

We examined the data for departures from normality using probability plots before conducting statistical tests. Since the data did not satisfy the assumptions of parametric statistical tests, we used the Mann-Whitney test in our analyses. We calculated diversity statistics using PC-ORD statistical software (McCune and Mefford 1999) and conducted all statistical analyses using S-Plus Version 6.0 statistical software (Insightful 2001). We evaluated significance at $P = 0.05$.

Results

Surface area, terrain ruggedness, and elevation

Terrain ruggedness index did not differ significantly different between low and high production nesting territories ($Z = -1.31$, $P = 0.18$; Table 3.1). The mean elevation of the nesting centroid of high production nesting territories was significantly higher than low production nesting territories ($Z = 2.06$, $P = 0.04$).

Table 3.1. Surface area, terrain ruggedness index and elevation of nesting centroids for low (n = 18) and high (n = 18) production Golden Eagle nesting territories, Denali National Park and Preserve, Alaska. Data shown are mean, standard error (SE) and 95% confidence interval (95% CI).

	Low production			High production		
	Mean	SE	95% CI	Mean	SE	95% CI
Surface area (ha)	4164	92.27	3969 - 4358	3974	64.77	3837 - 4110
TRI[1]	1.47	0.03	1.41 - 1.55	1.41	0.02	1.36 - 1.46
Elevation[2] (m)	1053	45.85	957 - 1150	1163	25.31	1109 - 1216

[1]Terrain ruggedness index (ratio of surface area to planar area).
[2]Elevation of nesting centroid.

Physiographic zones

We delineated six distinct physiographic zones within nesting territories (Table 3.2). Alpine was the most common physiographic zone in most low and high production nesting territories. Upland made up a higher proportion of the area within low production nesting territories than high production nesting territories ($Z = 2.20$, $P = 0.03$). Riparian areas made up a similar proportion of the landscape within low and high production nesting territories ($Z = 1.59$, $P = 0.09$). Lowland was the rarest physiographic zone, occurring in only 11 nesting territories and making up < 3% of the area within nesting territories. Rivers/Streams and Lakes/Ponds were rare, comprising < 1% of the area within low and high production nesting territories.

Land Cover

We delineated 27 land cover types in low production nesting territories and 22 land cover types in high production nesting territories (Table 3.3). Overall, the landcover composition of nesting territories was similar (Table 3.3). Shrub land cover types dominated both low and high production nesting territories (Table 3.3). An average of 69% (range = 38.9-71.0%, SE = 4.5, 95% CI = 58.7-77.5%) of the area within low production nesting territories was shrub cover and an average of 70% (range = 13.6-96.8%, SE = 5.3, 95% CI = 57.7-80.1%) of the area within high production nesting territories was shrub cover. An average of 25.8% (range = 3.1-59.9%, SE = 4.8, 95% CI = 15.6-35.9%) of the area within low production nesting territories and an average of 29.4% (range = 2.2-85.9%, SE = 5.5, 95% CI = 17.8-40.9%) of the area within high production nesting territories was Barren land cover

Table 3.2. Composition of low (n = 18) and high (n = 18) production Golden Eagle nesting territories, Denali National Park and Preserve, Alaska, by physiographic zone.

Physiographic	Low production				High production			
zone	n[a]	Mean	SE	95% CI	n	Mean	SE	95% CI
Alpine	18	60.51	6.18	47.46 - 73.55	18	76.95	3.91	67.77 - 84.21
Upland	18	34.34	5.82	22.04 - 46.63	13	17.54	4.33	8.39 - 26.69
Lowland	6	0.86	0.75	0.00 - 2.46	5	0.02	0.09	0.00 - 0.36
Riparian	18	3.55	0.67	2.12 - 4.98	18	5.84	0.82	4.08 - 7.59
Rivers/Streams	18	0.43	0.10	0.22 - 0.64	18	0.39	0.09	0.19 - 0.59
Lakes/Ponds	6	0.08	0.05	0.00 - 0.19	6	0.02	0.01	0.00 - 0.05

[a] n = number of territories with physiographic zone.

Table 3.3. Composition of low (n = 18) and high (n = 18) production Golden Eagle nesting territories, Denali National Park and Preserve, Alaska, using the modified Alaska Vegetation Classification Level III land cover types within, 1988 - 1997.

	Low production				High production			
Modified AVC III land cover type	n[a]	Mean	SE	95% CI	n	Mean	SE	95% CI
Alpine Barren	16	19.12	4.81	8.97 - 29.28	18	20.71	5.24	9.63 - 31.78
Alpine Barren Partially Vegetated	17	3.97	1.08	1.69 - 6.25	18	4.98	1.08	2.70 - 7.26
Alpine Dwarf Shrub	14	2.36	0.71	0.86 - 3.86	12	4.23	1.66	0.71 - 7.75
Alpine Low Shrub	15	4.22	2.40	0.00 - 9.29	15	4.60	1.46	1.51 - 7.68
Alpine Open Low Shrub	18	9.69	1.87	5.73 - 13.65	18	12.04	2.03	7.77 - 16.32
Alpine Closed Low Shrub	17	20.85	3.98	12.44 - 29.26	18	29.09	4.16	20.31 - 37.88
Alpine Open Tall Shrub	1	0.02	0.02	0.00 - 0.06	1	< 0.01	<0.01	<0.01 - <0.01
Alpine Closed Tall Shrub	3	0.25	0.17	0.00 - 0.61	3	0.29	0.23	0.00 - 0.77
Lowland Low Shrub	3	0.30	0.26	0.00 - 0.85	0	-	-	-
Lowland Open Low Shrub	4	0.48	0.42	0.00 - 1.37	5	0.20	0.09	<0.01 - 0.39
Lowland Closed Low Shrub	1	0.07	0.07	0.00 - 0.24	0	-	-	-
Riparian Barren	15	1.48	0.50	0.42 - 2.53	16	2.85	0.67	1.42 - 4.28
Riparian Barren Partially Vegetated	8	0.73	0.35	0.00 - 1.48	13	0.85	0.29	0.25 - 1.46
Riparian Closed Low Shrub	1	0.02	0.02	0.00 - 0.06	1	0.02	0.02	0.00 - 0.08
Riparian Open Tall Shrub	16	0.83	0.22	0.36 – 1.29	17	1.08	0.21	0.63 - 1.53
Riparian Closed Tall Shrub	14	0.48	0.15	0.17 - 0.80	16	1.02	0.02	0.54 - 1.50
Riparian Open Broadleaf Forest	1	<0.01	<0.01	0.00 - 0.02	0	-	-	-

[a] n = number of nesting territories containing land cover type.

Table 3.3 (cont'd).

Modified AVC III land cover type	Low production n	Mean	SE	95% CI	High production n	Mean	SE	95% CI
Upland Barren	5	0.18	0.14	0.00 - 0.47	0	-	-	-
Upland Barren Partially Vegetated	7	0.31	0.18	0.00 - 0.69	1	<0.01	<0.01	<0.01 - 0.01
Upland Low Shrub	13	3.73	0.87	1.88 - 5.56	13	3.20	0.91	1.29 – 5.13
Upland Open Low Shrub	13	5.17	1.73	1.51 - 8.84	10	1.65	0.67	0.21 – 3.06
Upland Closed Low Shrub	17	8.31	1.43	5.30 - 11.32	13	8.26	2.17	3.69 - 12.83
Upland Open Tall Shrub	5	0.17	0.10	0.00 - 0.39	1	0.03	0.03	0.00 – 0.09
Upland Closed Tall Shrub	15	11.11	3.06	4.64 - 17.55	10	3.26	1.54	0.01 – 6.50
Upland Open Needleleaf Forest	12	4.92	1.64	1.45 - 8.39	8	1.15	0.74	0.00 – 2.71
Upland Closed Needleleaf Forest	2	0.06	0.04	0.00 - 0.15	0	-	-	-
Upland Open Broadleaf Forest	3	0.38	0.31	0.00 - 1.03	1	<0.01	<0.01	<0.01 - 0.02

types. Forest was the least common and least abundant land cover type in both low and high production nesting territories. An average of 5.4% (range = 0.0-11.6%, SE = 1.8, 95% CI = 1.5-9.5%) of the area within low production nesting territories and an average of 1.2% (range = 0.0-12.9%, SE = 0.8, 95% CI = 0.0-2.7%) of the area within high production nesting territories was made up of Forest.

Alpine Closed Low Shrub and Alpine Barren were the most abundant land cover types in low and high production nesting territories (Table 3.3). Birch (*Betula* spp.) and willows (*Salix* spp.) dominated the Alpine Closed Low Shrub land cover type. Alpine Closed Low Shrub also contained a mixture of other shrubs and herbaceous plants including bearberry (*Arctostaphylos* spp.), crowberry (*Empetrum nigrum*), blueberry (*Vaccinium uliginosum*), cranberry (*Vaccinium vitis-idaea*), avens (*Dryas* spp.) and cassiope (*Cassiope tetragona*). Talus slopes, cliffs, and rock-outcroppings dominated the Alpine Barren land cover type. Alpine Open Tall Shrub and Alpine Closed Tall Shrub were the least common and least abundant Alpine land cover types in both low and high production nesting territories. Lowland land cover was uncommon in most nesting territories (Table 3.3). Four of the six Riparian land cover types occurred frequently, but not in great amounts, in both low and high production nesting territories (Table 3.3). The most pronounced differences in the composition of land cover within low and high production nesting territories were the amounts of Upland Open Low Shrub, Upland Closed Tall Shrub, and Upland Open Needleleaf Forest (Figure 3.1). Low production nesting territories contained significantly more Upland Closed Tall Shrub and Upland Closed Forest land cover types than high production nesting territories ($Z = 2.42$, $P = 0.01$). The amount of

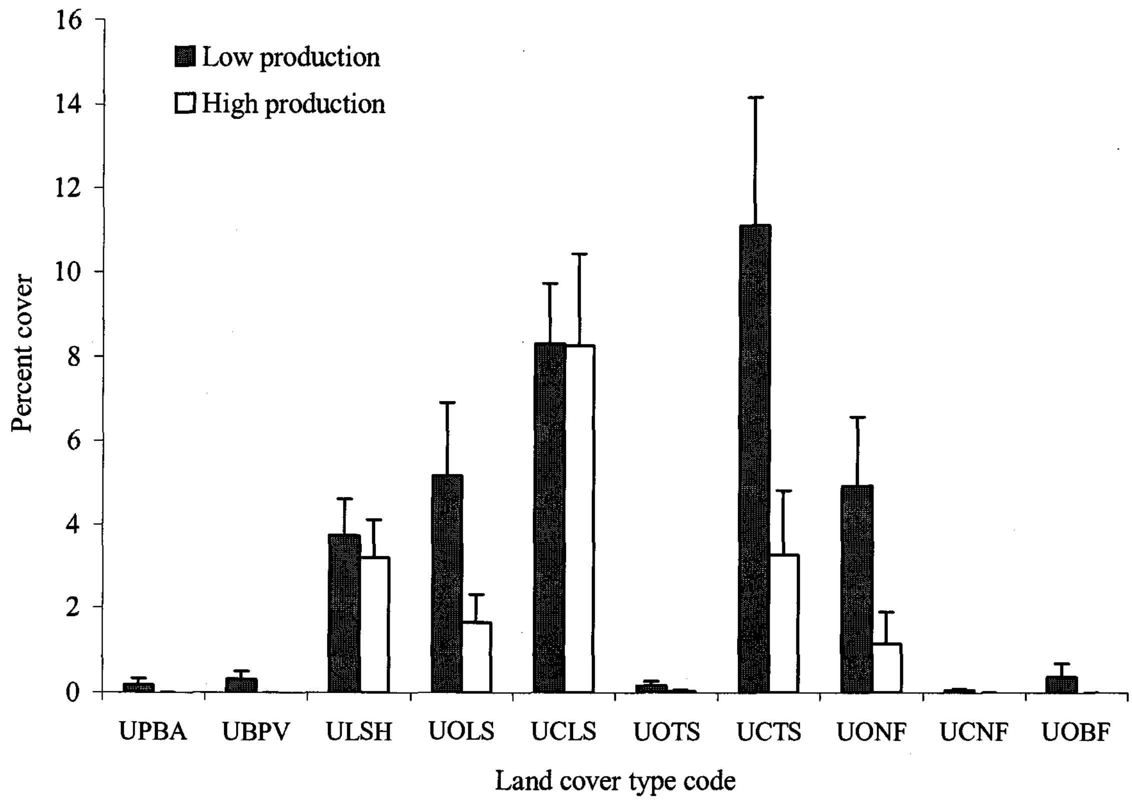

Figure 3.1. Upland land cover types within low (n = 18) and high (n = 18) production Golden Eagle nesting territories, Denali National Park and Preserve. Data shown are mean percent cover and standard error of land cover types. Land cover type codes are: UPBA = Upland Barren, UPBV = Upland Barren Partially Vegetated, ULSH = Upland Low Shrub, UOLS = Upland Open Low Shrub, UCLS = Upland Closed Low Shrub, UOTS = Upland Open Tall Shrub, UCTS = Upland Closed Tall Shrub, UONF = Upland Needleleaf Forest, UCNF = Upland Closed Needleleaf Forest, and UOBF = Upland Open Broadleaf Forest.

Upland land cover within a nesting territory was inversely related to the elevation of the nesting centroid ($r^2 = 0.39$, $P < 0.001$).

Landscape Diversity

The number of land cover types (richness) within a nesting territory ranged from 8 to 19 in low production nesting territories and from 8 to 16 in high production nesting territories (Table 3.4). The number of land cover types within low and high production nesting was not significantly different ($Z = -1.24$, $P = 0.21$). All diversity measurements were similar between low and high production nesting territories. Evenness ranged from 0.56 to 0.84 for low production nesting territories and from 0.38 to 0.87 for high production nesting territories (Table 3.4). and did not differ between low and high production nesting territories ($Z = 0.13$, $P = 0.89$). Shannon's Diversity Index ranged from 1.24 to 2.42 for low production nesting territories and from 0.91 to 2.14 for high production nesting territories (Table 3.4) and did not differ between low and high production nesting territories ($Z = -0.77$, $P = 0.44$). Simpson's Diversity Index ranged from 0.62 to 0.89 for low production nesting territories and from 0.38 to 0.85 for high production nesting territories and did not differ between low and high production nesting territories (Z=-0.81, $P = 0.42$). A single land cover type (dominant) comprised an average of 37% of the area within low production nesting territories and an average of 41% of the area within high production nesting territories (Table 3.4). Alpine Barren (n = 6), Alpine Closed Low Shrub (n = 3) and Upland Closed Low Shrub (n = 3) were the most common dominant land cover types in low production nesting territories.

Table 3.4. Attributes of diversity measurements for land cover types within low (n = 18) and high (n = 18) production Golden Eagle nesting territories, Denali National Park and Preserve, Alaska, 1988 - 1997.

Diversity measurement	Low production			High production		
	Mean	SE	95% CI	Mean	SE	95% CI
Richness[1]	14.22	0.83	12.45 - 15.99	12.67	0.52	11.57 - 13.76
Evenness[2]	0.68	0.03	0.63 - 0.73	0.67	0.03	0.61 - 0.73
SHDI[3]	1.81	0.09	1.62 - 1.99	1.70	0.07	1.54 - 1.87
SIDI[4]	0.76	0.02	0.71 - 0.81	0.73	0.03	0.67 - 0.79
Dominant[5]	0.37	0.03	0.31 - 0.44	0.41	0.04	0.34 - 0.49

[1] Richness is the number of land cover types within each nesting territory. (The mean number of land cover types is also referred to as Alpha Diversity).
[2] Evenness is a measure of the relative abundance of the different land covers within a nesting territory.
[3] SHDI (Shannon's Diversity Index) is a measure of diversity of the landscape, determined both by the number of land cover types and by the proportional distribution of land covers within the nesting territory.
[4] SIDI (Simpson's Diversity Index) is measure of diversity that gives the probability that any two individual samples drawn at random from a nesting territory are different land cover types.
[5] Dominant is the proportion of a nesting territory comprised of the dominant (most abundant) land cover type

Alpine Closed Low Shrub (n = 9) and Alpine Barren (n = 5) were the most common dominant land cover types in high production nesting territories. The proportion of area within low and high production nesting territories made up of a single land cover type was not significantly different ($Z = 0.68$, $P = 0.49$).

Predicting Productivity

We developed a logistic regression model for predicting production class (low or high) of a nesting territory based on landscape characteristics. The logistic regression model contained five explanatory variables; percent of Upland, Lowland, and Riparian land cover types, elevation of nesting centroid, and terrain ruggedness. Percent of Upland land cover was the only variable that significantly predicted high production nesting territories (logit (π) = 0.92 – 3.59*Upland*). We observed a significant relationship between the percent of a nesting territory composed of Upland land cover and production class (drop-in-deviance test, $P = 0.02$). The probability of being a high production nesting territory significantly decreased as the percent of Upland land cover increased (Figure 3.2). Further, 61% of low production nesting territories consisted of $\geq$ 25% Upland land cover, whereas, only 11% of high production nesting territories consisted of $\geq$ 25% Upland land cover (Fisher's Exact test, $P = 0.04$).

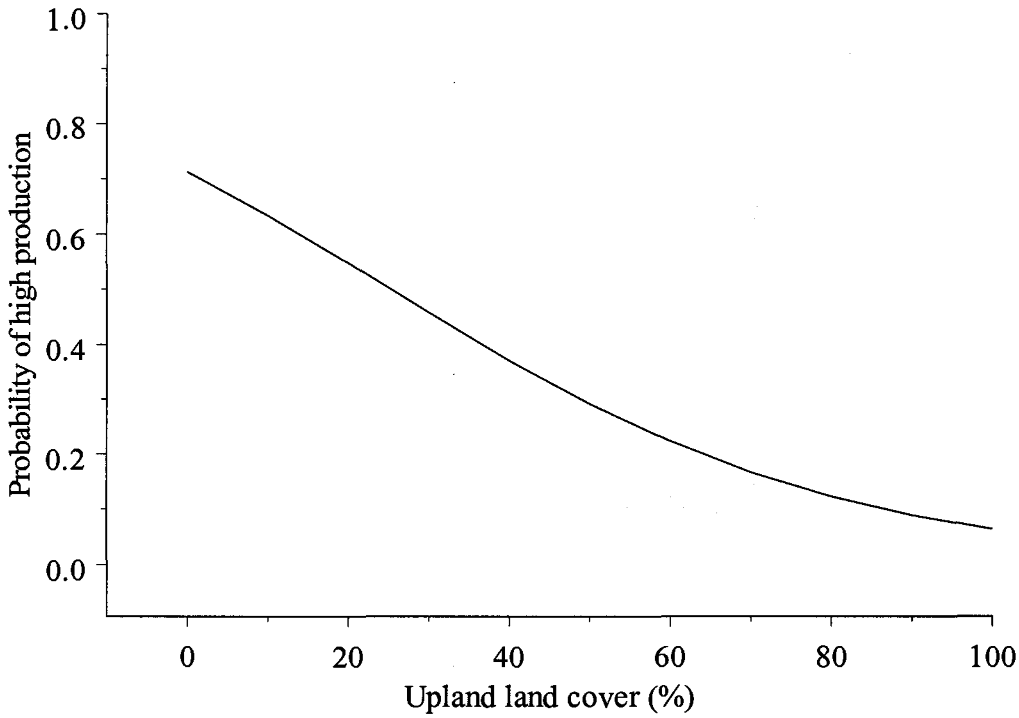

Figure 3.2. Relation between Golden Eagle productivity and the percent of Upland land cover within a nesting territory. The function was created using logistic regression of landscape variables within a 3-km radius plot around the nesting centroid of 18 low production and 18 high production nesting territories, Denali National Park and Preserve, Alaska, 1988-1997.

Discussion

We tested the null hypothesis that landscape characteristics including land cover composition, terrain ruggedness, and elevation of the nesting centroid would not differ between low and high production nesting territories. We found that the terrain ruggedness index for low and high production nesting territories was similar and that most of the area within both low and high production nesting territories consisted of Alpine land cover types. However, the mean elevation of nesting centroids for low production nesting territories was significantly lower than high production nesting territories. Further, low production nesting territories contained more Upland land cover types, including more Upland Closed Tall Shrub and Upland Closed Forest land cover types than high production nesting territories. A logistic regression model predicted that a nesting territory was more likely to be a low production nesting territory as the percentage of the area made up of Upland land cover types increased.

Golden Eagles usually hunt in open landscapes (Watson 1997, Kochert et al. 2002). Nesting territories dominated by open landscapes may potentially provide more foraging areas for Golden Eagles (Watson 1997). We did not measure prey availability, prey abundance, or foraging behavior in this study; however, we hypothesize that closed-canopy tall shrubs and closed-canopy forested areas may conceal prey (Bechard 1982), thereby reducing prey availability, limiting foraging success, and consequently decreasing long-term productivity of Golden Eagles in Denali. Based on our findings, we hypothesize that increases in closed-canopy land cover within nesting territories (a more closed-landscape) could negatively affect the long-term productivity Golden Eagles in Denali by decreasing foraging success.

There is some evidence that shrub and forest cover are increasing in the Arctic regions of Alaska (Rupp et al. 2000, Sturm et al. 2001). Similar increases in shrub and forest cover in Denali could potentially affect prey abundance and foraging success of Golden Eagles.

We found evidence that some broad-scale variables of the landscape around the nesting centroids of low and high production Golden Eagles nesting territories in Denali may differ. However, we regard the value of our results as a foundation for developing additional hypotheses for identifying other factors affecting long-term productivity of Golden Eagles in Denali for several reasons. First, we based our study entirely on a suite of landscape characteristics and did not address the affects of prey abundance, prey availability, or climate on long-term productivity. Based on findings by Steenhof et al. (1997) for Golden Eagles and Franklin et al. (2000) for Northern Spotted Owls (*Strix occidentalis caurina*), we suggest that future studies relating Golden Eagle productivity in Denali to habitat include quantitative and realistic measurements of prey availability, prey abundance and climate. Second, our sampling area was a 3-km radius circle surrounding the nesting centroid and not the actual nesting territory. We have no qualitative or empirical data to describe the shape or size of a Golden Eagle nesting territory in Denali. Future studies investigating long-term productivity and landscape characteristics should include descriptions of the actual size and shape of the nesting territories and measurements of core use areas (Marzluff et al. 1987).

We agree with Kochert et al. (1999) that long-term productivity of Golden Eagles depends on both the quality of the individual Golden Eagle (intrinsic factors) and the quality of the nesting territory that it inhabits (extrinsic factors). However, we know of no published study that has tested the hypotheses proposed by Kochert et al. (1999) for Golden Eagles. Many challenges are associated with sustaining long-term demographic and habitat studies of Golden Eagles in North America. Understanding the intrinsic and extrinsic factors that affect long-term productivity of Golden Eagles in North America will require more detailed knowledge of: (1) variation in long-term production of individuals, including correlates of age and reproduction (Newton 1986, Franklin et al. 2000, Ferrer and Bisson 2003); (2) spatial and temporal variation in habitat quality in relation to weather, prey abundance, and prey availability (Korpimäki 1992, Hakkarainen et al. 1997, Lõhmus 2003); (3) relationships between environmental variation and age-related differences in reproduction (Laaksonen et al. 2002); (4) composition and configuration of nesting territories (Marzluff et al. 1997); (5) resource selection during the breeding and non-breeding seasons (Marzluff et al. 1997); and, (6) differences in habitat and life history traits of resident and migratory populations (McIntyre and Adams 1999). Making inferences to populations will require well-designed sampling methods and relatively large sample sizes (Franklin et al. 2000). Sustaining long-term studies will require adequate and secure funding. Kochert et al. (2002) and Kochert and Steenhof (2002) summarize the status, trends, and conservation issues of Golden Eagles in the United States and Canada and offer suggestions for future monitoring projects. We suggest that future studies of Golden Eagles also include assessments of long-term productivity and the factors that influence it.

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CHAPTER 4

DURATION OF THE POST-FLEDGING DEPENDENCE PERIOD OF GOLDEN EAGLES IN DENALI NATIONAL PARK AND PRESERVE, ALASKA.

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Abstract

We calculated the duration of the post-fledging dependence period for migratory Golden Eagles using satellite telemetry over three consecutive years, 1997-1999. The post-fledging dependence period averaged 49.8 days (SD = 6.1 days, n = 41). The post fledging dependence period was longer for eagles that hatched earlier, but hatch date did not influence date of departure from the natal nesting territory. Fledgling Golden Eagles departed their natal areas over a 3-week period from 17 Sept. to 5 Oct. (mean = 26 Sept., SD = 4.9 days), 32 to 62 days after fledging. Siblings usually departed their natal areas > 2 days apart. The post-fledging dependence period of migratory Golden Eagles in Denali is shorter than those reported for non-migratory populations of this species.

Introduction

For fledglings of many raptor species, the post-fledging dependence period is important for acquiring adequate food reserves before migration (Wood et al. 1998), improving flight skills (Bustamente and Hiraldo 1989), or developing hunting skills (Newton 1979, Weathers and Sullivan 1989, Bustamente 1993). The post-fledging dependence period also may be a time when fledglings can learn the essential skills for survival without the additional pressures of having to secure food to survive (Amar et al. 2000).

There are few published accounts on the length of the post-fledging dependence period for Golden Eagles across their Holarctic range (Watson 1997, Kochert et al. 2002). The reported estimates of the length of the post-fledging dependence period of Golden Eagles in temperate regions of North America and Europe may not apply to northern breeding populations in North America. Golden Eagles breeding at northern latitudes in North America are usually migratory, with adults, subadults and juveniles making round trip migrations each year that often exceed 8,000 km (Brodeur et al. 1996, McIntyre, unpublished data). Further, the breeding season in the northern latitudes of North America may be shorter than the breeding season in temperate areas. In contrast to fledglings in temperate areas, fledglings raised in northern latitudes do not have the option to linger in their natal nesting territories until the start of the next breeding season. Based on field observations, Kessel (1989) suggested that the length of the post-fledging dependence period of Golden Eagles at the northern end of their range in the Brooks Range and on the Seward Peninsula, Alaska is probably ≤ 2 months.

In this paper, we describe the duration of the post-fledging dependence period of migratory juvenile Golden Eagles in Denali National Park and Preserve, Alaska. We tested the null hypotheses that the duration of the post-fledging dependence period did not vary by year, sex, brood size, or history of productivity of the nesting territory.

Methods

Study area

We radio-marked 48 nearly-fledged Golden Eagles in the northeastern portion of Denali National Park and Preserve, Alaska, (hereafter referred to as Denali). Our study area, centered at approximately 63° 35.8'N, 149° 38.2'W, is in the northern foothills of the Alaska Range in the northeastern portion of Denali in central Alaska.

Radio-Marking Procedures

We radio-marked 48 nestlings that were ≥ 56 days of age and in good physical condition from late July to early August 1997 and 1999 with 95 g satellite transmitters (PTTs). We estimated the age of radio-marked fledglings (±5 d) based on their size and feather development using photographic aging guides (Hoechlin 1976, McIntyre, unpubl. data). We categorized radio-marked fledglings as either male or female based on their weight and footpad length (Edwards and Kochert 1986). We only radio-marked males weighing ≥ 3,300 g and females weighing ≥ 3,800 g. We attempted to radio-mark an equal number of fledglings in nesting territories with low and high productivity histories and an equal number of males and females. However, we were obligated to visit nests where the likelihood of injury or loss from premature fledging was presumed low. We assumed that estimates of survival rates of birds that we radio-marked were representative of those in the study area.

We entered nests using standard rock climbing techniques. Upon reaching the nest we secured the fledglings using an Aba (Maechtle 1998), placed a leather falconer's hood over their head to calm them, and put cordura booties on their feet to protect them from injury. When possible, we processed and radio-marked the fledglings in the nest. When this was not possible, we transported the fledglings to a more suitable location near the nest.

We banded all fledglings with U.S. Fish and Wildlife Service, serially numbered, pop-rivet aluminum leg bands and recorded a series of morphological characteristics including hallux length, tarsus width, culmen length, footpad length (all within 5 mm) and weight (within 5 g). We also noted the external physical condition of fledglings and estimated the fullness of their crop as empty, 25%, 50% or 100%. We categorized fledglings as either male or female based on their weight and footpad length (Edwards and Kochert 1986).

We radio-marked fledglings using a body harness (Dunstan 1972) constructed from 1.3-mm Teflon ribbon (Bally Ribbon, Bally, Pennsylvania). We used biodegradable, waxed-cotton embroidery thread to stitch the four strands of the body harness together near the carnia of the sternum. We incorporated a 3 mm x 3 mm soft leather patch into the harness to cover the carnia to prevent abrasion. The harness was designed to fall off when the cotton embroidery thread decomposed. The harness and radio transmitters weighed ~3% of the total body weight of the fledgling at deployment and were within conventional guidelines for telemetric studies of birds (Caccamise and Hedin 1985). The Institutional Animal Care and Use Committee at Oregon State University reviewed and approved our capture, handling, and attachment protocols.

We used 95-g satellite radio telemetry units (platform transmitter terminals or PTTs) built by Microwave Telemetry, Inc. of Columbia, Maryland, USA. The rectangular PTTs measured 94 mm long x 33 mm wide x 30 mm high, with a 180 mm long antennae made of flexible stranded marine grade stainless steel with a hard nylon coating. The antenna protruded from the back edge of the PTT at a 45-degree angle to the bottom face. PTTs were powered with Lithium batteries and pre-programmed to transmit (active mode) for an 8-hour period every 48 hours during the migration periods and an 8-hour period every 72 hours during winter and summer. A PTT in active mode transmitted a 32-bit message over 360 milliseconds, with a repetition interval of 70 seconds. Each message contained calibrated indices to the internal temperature of the PTT, motion, and battery voltage. Estimated battery life of the PTTs was 2.5-4 years (P. Howey, personal communication).

We attached a 9-g conventional radio transmitter (CRT) (model 3PN) built by Advanced Telemetry Systems, Isanti, Minnesota, USA, to the side of each PTT to aid in finding mortalities. The 10 x 18 mm CRTs were pre-programmed to transmit only after the PTT remained motionless for 48 hours. The CRTs had a pulse of 59-beats per minute and an expected battery life of 60 days. We secured the CRT antenna to the shoulder strap of the body harness using dental thread, making sure that the CRT and PTT antennas did not interfere with one another. The entire radio-package, including harness weighed 106 g.

Collecting Satellite Telemetry Data

We determined the status (alive or dead) and the location of each radio-marked eagle using National Oceanic and Atmospheric Administration (NOAA) polar orbiting satellites with onboard tracking equipment operated by Service Argos (ARGOS) (Landover, Maryland). Within 24 hr of satellite contact with a radio-marked eagle, we received information on their location (latitude and longitude), location quality, temperature, activity, and battery voltage from ARGOS. We categorized the status of each radio-marked fledgling as alive, dead or radio-failure using data from the on-board sensors. We categorized a PTT as a failure if we lost complete contact with it within the expected life span of its power source and a PTT as a mortality if it remained motionless and inactive for >2 duty cycles (~ 5 days).

Determining the Length of the Post-Fledging Dependence Period

We defined the date of departure from the natal nesting territory as the mid-point between the last date that the radio-marked fledgling was within its natal territory and the first date that it was not within its natal territory. We defined the post-fledging dependence period as the time between the estimated date of fledging and the measured date of departure from the natal area (Newton 1979, Rohner and Hunter 1996). Our radio-tracking data indicated that radio-marked fledglings did not leave their natal nesting territories until they initiated migration. Therefore, we assumed that independence corresponded with departure from the natal nesting territory (Newton 1979) and used the date of the start of migration to mark the end of the post-fledging dependence period. We calculated the duration of the post-fledging dependence period as the number of days between the estimated fledging date and measured date of departure from the natal nesting territory.

Data Analysis

We analyzed data from 37 fledglings radio-marked in 1997 and 1999 at nesting territories where we knew the long-term productivity history of the territory. We did not used data from five fledglings radio-marked in 1998 because the low sample size may not be representative of the larger population. We used the square-root transformation for all count data, but report means as untransformed values for clarity. We used Mann-Whitney tests to compare the length of the post-fledging dependence period (number of days) and date of departure (calendar day) from the natal nesting territory between years, sexes, brood size (one or two fledglings), and production class (low or high) of the nesting territory. We used simple linear regression to examine the length of the post-fledging dependence period and the date of departure from natal nesting territory in relation to estimated hatch dates.

We used S-Plus Version 6.0 software (Insightful 2001) for all statistical analyses. Unless otherwise noted, we report variation around the mean as standard error (SE) and standard deviation (SD). For all tests we used $\alpha = 0.05$ as the level of significance.

Results

Duration of the Post-Fledging Dependence Period

The duration of the post-fledging dependence period ranged from 38 to 62 d ($\bar{x} = 49.8$ d, 95% CI = 47.9-51.9 d; Table 4.1). The length of the post-fledging dependence period did not differ between years, sexes, brood size, or productivity class of the nesting territory (Table 4.1). The estimated length of the post-fledging dependence period of Golden Eagles in Denali, ranging from 32 to 62 d, is shorter than those reported for Golden Eagles breeding at temperate latitudes (Table 4.2)

Radio-marked fledglings that hatched earlier had longer post-fledging dependence periods ($F = 38.64$, $P < 0.001$; Figure 4.1). However, estimated hatch date did not influence date of departure from the natal nesting territory ($F = 0.48$, $P = 0.49$).

Table 4.1. Length of the post-fledging dependence period (days) of radio-marked Golden Eagles in Denali National Park and Preserve, Alaska, 1997 and 1999. The *Z*-statistics and related *P*-values are for Mann-Whitney tests for year, sex, brood size, and territory productivity comparisons.

	n	$\bar{x}$	SE	Min	Max	*Z*	*P*
Year							
1997	19	48.2	1.3	38	55	-1.24	0.22
1999	18	51.7	1.6	42	62		
Sex							
Female	22	50.5	1.3	42	62	0.57	0.56
Male	15	49.0	1.7	38	62		
Number of fledglings							
One	11	48.8	1.9	38	60	-0.66	0.50
Two or three	26	50.4	1.3	39	62		
History of territory							
Low production	8	47.8	2.2	38	56	-0.72	0.47
High production	29	50.5	1.2	39	62		
Total	37	49.9	1.1	38	62		

Table 4.2. Estimated length (days) of post-fledging dependence period for Golden Eagles.

Study area	Length of post-fledging dependence period (days)	n	Sources
Nearctic			
North Dakota	135	28	O'Toole 1997
Southwest Idaho	30 to 180	2[a]	Kochert et al. 2002
Central Alaska	32 to 62	48	This study
Palearctic			
Southern England	75 to 85	3	Walker 1987
Israel	176	2	Bahat 1992
Western Scotland	180	2	Grant and McGrady 1999

[a] M. Kochert, personal communication.

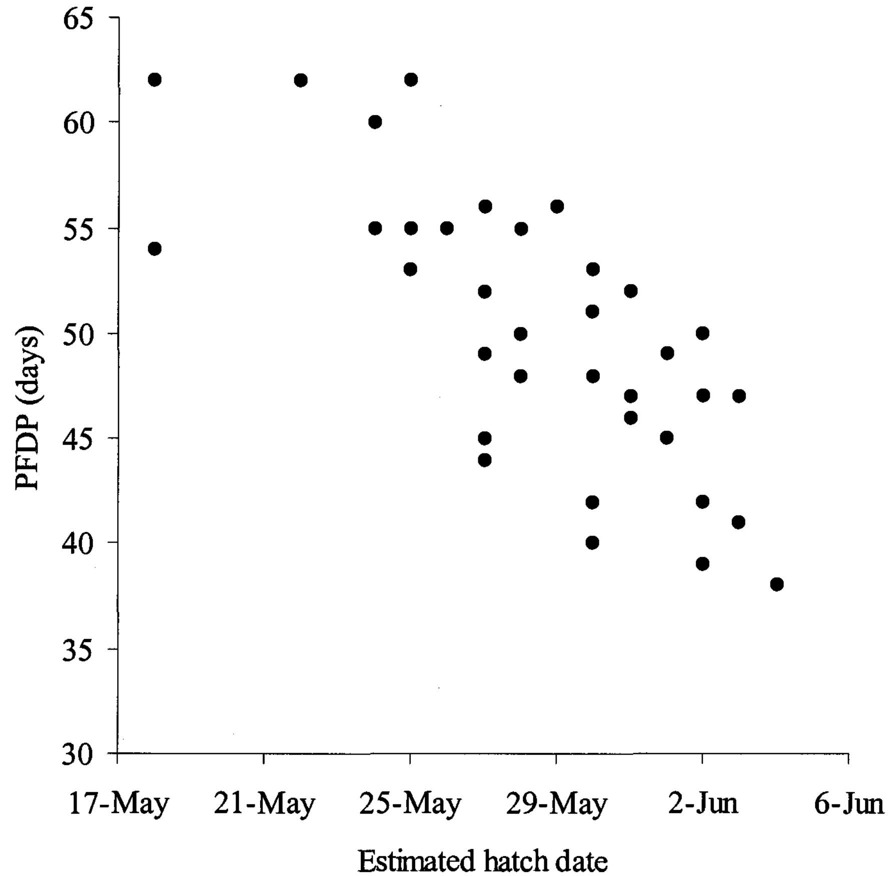

Figure 4.1. Relationship between estimated hatch date and length of the post-fledging dependence period (PFDP) for Golden Eagles, Denali National Park and Preserve, Alaska, 1997-1999 (F = 38.6, P <0.001, r^2 = 0.52).

Departing Natal Areas

All radio-marked fledglings departed their natal areas and started autumn migration between 17 Sep and 4 Oct ($\bar{x}$ = 25 Sept, SD = 4.4 d; Table 4.3). We found no differences in departure dates between years, sexes, brood size, or production history of nesting territory (Table 4.3).

We monitored 12 radio-marked sibling groups throughout the post-fledging dependence period (7 groups with 1 female and 1 male; 3 groups with 2 females; and, 2 groups with 2 males). One sibling group (both males) departed their natal area on the same day. The difference in departure dates for other siblings groups ranged from 1 to 15 d ($\bar{x}$ = 5.3 d, SE = 1.25, 95% CI = 2.85-7.75).

Discussion

Our results are consistent with Kessel's (1989) suggestion that the duration of the post-fledging dependence period of Golden Eagles in western and northern Alaska is $\leq$ 2 months. For the most part, the post-fledging dependence period of migratory Golden Eagles in Denali is shorter than those reported for non-migratory Golden Eagles breeding in temperate latitudes. We acknowledge that basing our calculations of the post-fledging dependence period on estimates of hatch and fledge date may have masked some of the individual variation. Actual fledging events may have occurred slightly before or after 70 d post hatch. However, we believe our results provide important insight into the length of the post-fledging dependence period of migratory Golden Eagles from Denali.

Table 4.3. Dates of departure from natal nesting territories (initiation of autumn migration) of juvenile radio-marked Golden Eagles in Denali National Park and Preserve, Alaska, 1997 and 1999. The *Z*-statistics and related *P*-values are for Mann-Whitney tests for year, sex, brood size, and territory productivity comparisons.

	n	$\bar{x}$	SE	Min	Max	*Z*	*P*
Year							
1997	19	25-Sep	0.9	17-Sep	30-Sep	-0.95	0.34
1999	18	26-Sep	1.1	18-Sep	4-Oct		
Sex							
Female	22	26-Sep	0.9	18-Sep	2-Oct	0.65	0.51
Male	15	25-Sep	1.3	17-Sep	4-Oct		
Number of fledglings							
One	11	18-Sep	1.3	18-Sep	1-Oct	0.71	0.48
Two or three	26	25-Sep	0.9	17-Sep	4-Oct		
History of territory							
Low production	8	26-Sep	1.8	18-Sep	30-Sep	0.37	0.71
High production	29	25-Sep	0.8	17-Sep	4-Oct		
Total	37	25-Sep	0.7	17-Sep	4-Oct		

The factors regulating the post-fledging dependence period in raptors vary across species. Adults may control the length of the dependence period by reducing food provisioning (Watson 1997) or by exhibiting aggressive behavior toward the fledglings (Alonso et al. 1987). In contrast, fledglings may lose interest in the adults once they are able to fend for themselves (Brown 1966) or may leave the natal area in response to changes in food supply (McCollough 1986). The physical condition of fledglings may influence the timing of their departure from the natal area, with fledglings in better physical condition leaving first to secure better feeding areas (Ferrer 1992, Watson 1997). Fledglings may become independent when they start migration (Bustamante and Hiraldo 1989).

In Denali, the lack of a relationship between hatch date and departure date, and the compressed time period within which most fledglings depart their natal nesting territories, suggests that extrinsic factors such as departure of parents, weather conditions, and decreasing food abundance and availability may be the primary cues for initiating migration, thereby ending the post-fledging dependence period. Further, we found that the radio-marked Golden Eagles exhibited little variation in the duration of the post-fledging dependence period, probably because of the short breeding season in Denali tends to synchronize breeding.

Most fledgling Golden Eagles from Denali initiate autumn migration ≤50 d of fledging and often migrate ≥100 km within 2 days of initiating autumn migration (McIntyre, unpublished data). Further, fledgling Golden Eagles from Denali often migrate >2,000 km from their natal nesting territory ≤90 d of fledging (McIntyre, unpublished data). In contrast, fledgling non-migratory Golden Eagles in North

Dakota did not move >10 km from their natal nest until >98 d after fledging (O'Toole 1997); non-migratory fledglings in the Negev Desert, Israel, did not achieve sustained flights of 30 min and 52 min until 62 and 119 d after fledging, respectively (Bahat 1992).

The post-fledging dependence period in raptors is important for developing hunting skills (Newton 1979, Weathers and Sullivan 1989, Bustamente 1995). However, fledglings of some large-bodied vultures and Bald Eagles depend on their parents for food during the post-fledging dependence period (Donazar and Ceballos 1990, Hunt et al. 1992, Wood et al. 1998), and Bald Eagle fledglings do not hunt during the initial stages of migration (Hunt et al. 1992, Wood et al. 1998). Fledgling Golden Eagles did not begin to hunt until 68 d after fledging in the Negev Desert, Israel (Bahat 1992) and until 58 d after fledging in the United Kingdom (Walker 1987). We do not know if Golden Eagle fledglings in Denali hunt during the post-fledging dependence period. However, hunting behavior of fledglings during the post-fledging dependence period in Denali is seldom witnessed (McIntyre, unpublished data). Additionally, the post-fledging dependence period in Denali coincides with the onset of rainy season that may further constrict the time available for developing flight skills. We hypothesize that time during the post-fledging dependence period for Golden Eagles in Denali is used for improving flight skills (Bustamente and Hiraldo 1989) and building up reserves needed to survive their first migration (*sensu* Bustamente and Hiraldo 1989, Wood et al. 1998). Good flight skills and good reserves would be advantageous for fledglings during the early part of their migratory journeys (Robertson 1985).

The post-fledging dependence period is a critical period in the life of long-lived, long-distance migratory birds. Yet, it is one of the least studied times of the life of many raptors. We suggest that future research efforts focus on describing the post-fledging dependence period for Golden Eagles in other parts of their range and for other raptors. We also recommend that new tracking technology such as satellite telemetry and Global Position Telemetry will benefit future studies, especially for migratory populations.

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CHAPTER 5

SURVIVAL OF FLEDGLING GOLDEN EAGLES DURING THE POST-FLEDGING DEPENDENCE PERIOD IN DENALI NATIONAL PARK AND PRESERVE, ALASKA

Carol L. McIntyre and Michael W. Collopy

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Abstract

The reproductive success of many species of raptors is reported as mean brood size or productivity. Mean brood size, the number of fledglings per successful pair, and productivity, the number of fledglings raised per territorial pair, is often estimated based on counts of nestlings during the later part of the nestling period, often when they are > 80% of their age at fledging. However, survival of fledglings during the post fledging dependence period is rarely estimated. If survival during the post-fledging dependence period were low, then reproductive success based on measures of productivity would be overestimated. We monitored the survival of 48 radio-marked fledgling Golden Eagles (*Aquila chrysaetos*) using satellite telemetry during the post-fledging dependence period in Denali National Park and Preserve, Alaska. The estimated survival rate during the fledging dependence period was 0.98 (95% C.I. = 0.92 to 1.00, n = 45). Survival did not differ between males and females ($P = 0.45$) or between fledglings from nesting territories with low and high reproductive histories ($P = 0.13$). In two out of three years, we found 100% agreement between pre-fledging and post-fledging survival; and in one year with a very limited sample size, we found 75% agreement. Our results suggest that reproductive success of Golden Eagles in Denali, based on counts of nestlings when they are > 80% of their age at fledging, is not overestimated.

Introduction

Numerous studies of the nesting ecology of Golden Eagles across western North America provide information on nesting phenology, reproductive success, and fledgling production (Kochert et al. 2002). Many of these studies use estimates of productivity based on counts of nestlings that reach 80% of their fledging age as a measure of reproductive success (Steenhof et al. 1997, McIntyre and Adams 1999, Kochert et al. 2002). However, there are few published accounts of survival of fledglings after they leave the nest (Watson 1997, Kochert et al. 2002).

Estimating productivity of raptors before fledging is relatively straightforward; field biologists count the number of nestlings that reach 80% of their fledging age and calculate productivity as the number of fledglings produced per occupied nesting territory (Steenhof 1987). Little research, however, has been conducted on mortality beyond the nestling stage because of the difficulties associated with monitoring fledglings after they leave the nest (McFadzen and Marzluff 1996, Wood et al. 1998). Estimating survival after fledging and during the post-fledging dependence period, requires identifying individual animals, which usually requires marking and relocating individuals.

If survival during the post-fledging dependence period is low, estimates of reproductive success based on counts of nestlings before fledging will be overestimated (McFadzen and Marzluff 1996, Zelenak et al. 1997). Overestimating reproductive success can lead to erroneous conclusions about population trends of individual populations over time. Therefore, estimating survival during the post-fledging dependence period is essential for more accurately assessing estimates of reproductive success (McFadzen and Marzluff 1996, Zelanak et al 1997, Keedwell 2003) and understanding population dynamics.

In this paper, we describe the survival rates of fledgling Golden Eagles during the post fledging dependence period as determined by satellite telemetry. We tested the null hypothesis that survival of fledglings did not differ by sex or productivity history of their nesting territories.

Methods

Study Area

Our study area, centered at approximately 63° 35.8'N, 149° 38.2'W, is in the northern foothills of the Alaska Range in the northeastern portion of Denali National Park and Preserve, Alaska (hereafter referred to as Denali).

Field Procedures

We radio-marked 48 nestlings that were ≥ 56 days of age and in good physical condition from late July to early August 1997 and 1999 with 95 g satellite transmitters (PTTs). We estimated the age of radio-marked fledglings (±5 d) based on their size and feather development using photographic aging guides (Hoechlin 1976, McIntyre, unpubl. data). We categorized radio-marked fledglings as either male or female based on their weight and footpad length (Edwards and Kochert 1986). We only radio-marked males weighing ≥ 3,300 g and females weighing ≥ 3,800 g. We attempted to radio-mark an equal number of fledglings in nesting territories with low and high productivity histories and an equal number of males and females. However, we were obligated to visit nests where the likelihood of injury or loss from premature fledging was presumed low. We assumed that estimates of survival rates of birds that we radio-marked were representative of those in the study area.

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National Oceanic and Atmospheric Administration (NOAA) polar orbiting satellites with onboard tracking equipment operated by Service Argos (ARGOS) (Landover, Maryland) determined locations of the radio-marked fledglings. We received a series of data including location (latitude and longitude), date, time, location quality, temperature, activity, and battery voltage from ARGOS within 24 hr of satellite contact with a radio-marked fledgling. We categorized the status of each radio-marked fledgling as alive, dead or radio-failure using data from the on-board sensors. We categorized a PTT as a failure if we lost complete contact with it within the expected life span of its power source and a PTT as a mortality if it remained motionless and inactive for >2 duty cycles (~ 5 days).

Determining Date, Location and Cause of Mortality

We monitored the status of radio-marked fledglings each duty cycle and used location and sensor data to determine the date of each mortality and PTT failure. We defined the date of mortality as the last date when the PTT censors indicated movement and stable temperatures. After we categorized a PTT as a mortality, we used ARGOS location data to identify the general geographic position of the radio-marked juvenile and used conventional radio tracking techniques (Mech 1983) to locate the transmitter. We traveled to recovery locations by helicopter and foot. At the mortality site, we physically examined the carcass and noted any apparent sign of the cause of mortality and any sign of scavengers.

Data Analysis

We defined the post-fledging dependence period as the time between fledging and departure from the natal area (Newton 1979, Rohner and Hunter 1996). We used the binomial method (White and Garrott 1990) to estimate the finite rate of survival and the variance of this estimate during the post-fledging dependence period. We assumed that fates of all radio-marked fledglings were independent.

We used Fisher's exact test (Ramsey and Shafer 1997) to test for equal probability of survival between sexes and fledglings from nesting territories with low and high productivity histories. We present estimates of survival rates as proportions with 95% confidence intervals. We used S-Plus Version 6.0 software (Insightful 2001) for all statistical analyses. For all tests we used $\alpha = 0.05$ as the level of significance.

Results

We radio-marked 48 fledgling Golden Eagles from 1997 to 1999 (Table 5.1). We could not radio-mark an equal number of fledglings in all three years due to low productivity and poor physical condition of many nestlings in 1998, field logistics, and nest accessibility. We directly observed all radio-marked fledglings one or more times before and after fledging to monitor their behavior. All radio-marked fledglings fledged, moved freely about their natal nesting territory, and showed no outward sign of increased stress due to radio-marking.

We censored three PTTs from our data set due to PTT failure, harness failure, and unknown fate. Estimated survival rate for all radio-marked fledglings during the

Table 5.1. Attributes of radio-marked fledgling Golden Eagles, Denali National Park and Preserve, Alaska, 1997 to 1999.

	Number of radio-marked fledglings			
Group	1997	1998	1999	Total
Sex				
Female	12	4	13	29
Male	10	1	8	19
Nesting Territory History				
Low productivity	2	3	6	11
High productivity	18	2	12	32
Unknown	2	0	3	5
Total radio-marked fledglings	22	5	21	48
Nesting territories sampled	14	3	16	33

post-fledging dependence period was 0.98 (95% CI = 0.94 to 1.00). The estimated survival rate for females (0.96, 95% C.I. = 0.89 to 1.00) and males (1.00) did not differ ($P = 0.45$). The estimated survival rates of fledglings from high (1.00) and low production (0.90, 95% CI = 0.74 to 1.00) nesting territories did not differ ($P = 0.13$). Survival rates were identical in 1997 and 1999 (1.00), but were lower in 1998 (0.75, 95% CI = 0.33 to 1.00). Estimates of survival in 1998, however, are based on four radio-marked fledglings. We documented one mortality during the post-fledging dependence period. A female fledgling radio-marked in 1998 died ~ 5 weeks after fledging. We found the carcass of this eagle ~ 1,500 m from its natal nest, but the carcass was heavily scavenged and we could not determine the cause of death.

Discussion

Survival of radio-marked Golden Eagles during the post fledging dependence period was high. Our results suggest that most fledglings survive to depart their natal territories. Further, these results suggest that on average, counts of Golden Eagle nestlings made before actual fledging do not overestimated reproductive success. However, the estimated survival rate of fledgling Golden Eagles in 1998, based on a small sample size (n = 3), was 0.75, suggesting that survival during the post-fledging dependence may among years.

There are few other empirically derived survival estimates of fledgling Golden Eagles during the post-fledging dependence period with which to compare our results (Watson 1997, Kochert et al. 2002). In the Altamont Pass Wind Resource Area in central California, 7 of 69 radio-marked fledglings died soon after fledging, apparently within the post-fledging dependence period, from electrocution, collision with fences and starvation (Hunt et al. 1996). Estimates of survival for other large raptors during the post-fledging dependence period are limited to a few studies. The survival rate for 27 radio-marked fledgling Ferruginous Hawks (*Buteo regalis*) was high during the 3 weeks after fledging (mean = 0.86, SE = 0.02) (Zelenak et al. 1997).

Our study occurred over a relatively short time when primary prey sources including snowshoe hare (*Lepus americanus*) and Willow Ptarmigan (*Lagopus lagopus*) were abundant (McIntyre and Adams 1999). Similar to many other northern carnivores, the breeding success of Golden Eagles in Denali is affected by the abundance of snowshoe hare and Willow Ptarmigan (McIntyre and Adams 1999). Survival of juvenile and adult Northern Goshawks (*Accipiter gentilis*) and Great Horned Owls (*Bubo virginianus*), in southwest Yukon, Canada, declined in years when snowshoe hare populations declined (Doyle and Smith 1994, Rohner and Hunter 1996). Similarly, post-fledging survival of Tawny Owls (*Strix aluco*) in Agyll, Scotland, declined in relation to a decline in their main food supply (Petty and Thirgood 1989). Additionally, under conditions of food shortage, factors such as mass at fledging and brood size were expected to influence survival of Sparrowhawks (*Accipiter nisus*) in the post-fledging dependence period (Newton and Moss 1986). Based on these findings, we hypothesize that survival of fledgling Golden Eagles in Denali may vary in relation to food supply and weather, and that estimates of survival should be conducted in years when prey resources are not abundant.

We were unable to determine the cause of death for the single mortality recorded in our study because we found only remnants of the carcass. We assume that the mortality was not a result of impact with a human-made object or human-related disturbance as it occurred >5 km from the nearest road on a windswept ridge free of human-made structures. There are few human-made obstructions in Denali (i.e., no fences, few roads, few power poles, etc). Mortality of fledglings during the fledging-dependence period in Denali probably results from non-human causes including starvation, predation, and interactions with other predators.

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CHAPTER 6

FIRST-YEAR SURVIVAL OF MIGRATORY GOLDEN EAGLES AS DETERMINED BY SATELLITE TELEMETRY

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Prepared for submission to the *Ibis*

Abstract

We estimated first-year survival for 35 migratory Golden Eagles (*Aquila chrysaetos*) raised in Denali National Park and Preserve, Alaska, through their first year of independence using satellite radio telemetry. The estimated survival rate, derived using Kaplan-Meier estimates, was 0.24 (95% C.I. = 0.09 to 0.39. Estimated survival decreased from 1.00 at two weeks after independence to 0.47 (95% CI = 0.32-0.63) at 16 weeks after independence. Golden Eagles were at the greatest risk of mortality within the first 16 weeks after independence during autumn migration and early winter. We contrasted eight different models and used AIC_c scores to select the model that best fit the data. In the best-fitting model, brood size had an effect on survival. The estimated survival of radio-marked eagles from single fledgling broods was 0.41 (SE = 0.17, 95% CI = 0.15-0.74) and from two fledgling broods was 0.13 (SE =0.07, 95% CI = 0.04-0.33). Causes of mortality included starvation, electrocution, and poaching.

Introduction

The time between gaining independence and entering a breeding population is one of the least understood parts of the life history of Golden Eagles (*Aquila chrysaetos*) (Watson 1997, Kochert et al. 2002). Entering a breeding population ultimately depends on surviving to breeding age, but there are few empirically derived estimates of survival of Golden Eagles throughout their Holarctic range (Watson 1997, Kochert et al. 2002). Most Golden Eagle studies use productivity estimates calculated from counts of nestlings before fledging as indices of reproductive success (Steenhof

1987). However, survival rates of adult and immature Bald Eagles (*Haliaeetus leucocephalus*) have a greater effect on population stability and population growth than productivity (Grier 1980, Buehler et al. 1991, Bowman et al. 1995). Similarly, survival of adult females was recognized as the most important factor effecting population trends of Northern Spotted Owls (*Strix occidentalis caurina*) (Burnham et al. 1996, Raphael et al. 1996). Despite the importance of demographic parameters for understanding population status and predicting population trends, no Golden Eagle studies have estimated survival or examined the relationship between productivity and survival (Watson 1997, Kochert et al. 2002).

For many bird species, mortality rates are higher during the first year of life than in subsequent years (Lack 1954, Newton 1979). Higher mortality is attributed to increased risk when young become independent and disperse (Rohner and Hunter 1996, Morrison 2003). Survival rates of first-year (juvenile) raptors are usually much lower than for adults (Newton 1979, Watson 1997). In 26 analyses of raptor banding recoveries, the highest estimate of first-year survival rate was 0.50; 17 estimates of first year survival were less than 0.40 (Newton 1979). Recent studies using radio-telemetry also suggest that survival rates of juvenile and immature raptors are lower than those for adults (Burnham et al. 1996, Kenward et al. 1999).

Survival estimates for Golden Eagles in North America are limited to two studies. The contrasting results of these studies suggest that there may be large differences in survival among different populations of Golden Eagles in North America. Using conventional radio telemetry, Hunt et al. (1996) estimated first-year survival rate for Golden Eagles in a resident population in western California as 0.92

(95% C.I. = 0.85-0.99). Using band recovery data, Harmata (2002) suggested that there was 50% mortality by age three and that 25% of Golden Eagles in the Rocky Mountain West lived to just over age six. Both studies occurred in temperate latitudes where Golden Eagles are not long distance migrants.

Causes of Golden Eagle mortality in North America include starvation, electrocution, collisions, lead poisoning, and illegal poisoning, trapping, and shooting (Kochert et al. 2002). However, knowledge of age-specific mortality of Golden Eagles in North America is lacking. Further, causes of mortality determined from band recovery studies are biased toward deaths resulting from human-caused factors. Reports of natural mortality in free-flying eagles are few and mainly anecdotal (Watson 1997).

In this paper, we determine first-year survival, compare first-year survival in relation to productivity of the natal nesting territory, and identify the causes of mortality of radio-marked migratory juvenile Golden Eagles.

Methods

Telemetry

We radio-marked 48 nearly-fledged Golden Eagles at selected nest sites within the northeastern portion of Denali National Park and Preserve, Alaska. Our radio-package included a 95 g satellite radio transmitter (PTT) and a 9 g conventional radio transmitter (CRT). We used the CRTs to aid in locating mortalities; CRTs were activated only when the eagle remained motionless for > 48 hours. Our field and radio-marking procedures are presented in detail in Chapter 4. We monitored the movements and status of radio-marked Golden Eagles using data collected by National Oceanic and Atmospheric Administration (NOAA) polar orbiting satellites with onboard tracking equipment operated by Service Argos (ARGOS) (Landover, Maryland). For each PTT, we received a series of data including location (latitude and longitude), date, time, location quality, temperature, activity, and battery voltage from ARGOS within 24 hr of satellite contact. We categorized the status of each radio-marked Golden Eagle as alive, dead, or PTT-failure using data from the PTT sensors. We categorized a PTT as a failure if we lost complete contact with it within the expected life span of its power source. We categorized a PTT as a mortality if it remained in the same location and inactive (no movement) for at least two duty cycles (~ 5 days).

Determining Location and Cause of Mortality

We used ARGOS location data to identify the general location of the mortality and used conventional radio tracking techniques (Mech 1983) to locate the PTT. We attempted to recovery all mortalities within two weeks of their occurrence. Travel to recovery areas included airplane, helicopter, all-terrain vehicles, snowmobiles, and foot travel including hiking, cross-country skiing, and snowshoeing.

At each mortality site, we examined the carcass and noted any apparent signs of the cause of mortality. We also noted the general habitat features of the area and any sign of scavengers. All carcasses were stored frozen until we conducted post-mortem examinations. Research wildlife pathologists at the University of Alaska-Fairbanks, the Animal Health Laboratories, Alberta Agriculture, Food and Rural

Development, and the Western College of Veterinary Sciences, University of Saskatchewan performed post-mortem examinations. During all post-mortem examinations, pathologists noted and evaluated any physical signs of abrasions or other injuries potentially caused by the radio package and harness. Pathologists also collected samples of tissues to test for lead.

Data Analysis

For our survival analysis, we assumed that survival times of individuals were independent; that juveniles tracked were representative of the population; and that handling and radio-marking did not influence survival probability. We used known-fate models to estimate first year survival. This analysis is appropriate for data derived from radio-tracking studies and assumes that there are no nuisance parameters involved with animal captures or resightings, and that the probability of resighting the radio-marked animal is 1. With the known-fate model, the survival parameter is a true estimate of survival because the fate of each radio-marked individual is known. Our final data set consisted of 35 radio-marked juvenile Golden Eagles that survived the post-fledging dependence period from nesting territories where we had measurements of long-term productivity. Our preliminary survival analyses indicated no difference in survival between sexes, so we combined data on both sexes to increase our sample size.

Survival estimates and variances were calculated by iterative solution of the likelihood program MARK (White and Burnham 1998). A key feature of modeling survival using program MARK is that it allows the relationship between survival and individual covariates to be derived directly from the data in a way which is both biologically and statistically significant (Hall et al. 2001). We estimated first-year survival during four encounter periods. We defined these periods as first autumn migration, winter, first spring migration, and summer. We defined the end of the summer season as the date when the radio-marked eagle initiated its second autumn migration. Our most general survival model contained 52 intervals (i.e., 1 for each week) and corresponded to the Kaplan-Meier method (Pollock et al. 1989) of computing binomial estimates of survival. Variance estimates for this model were calculated using Greenwood's formula (Pollack et al. 1989). We examined the effects of season, year, length of post-fledging dependence period, estimated hatch date, productivity of the nesting territory, and brood size on survival by comparing a series of models. We based our inference on the model or models that best fit the date as determined by comparisons of AIC_c values (Burnham and Anderson 1998). The AIC_c indicated the most parsimonious models by balancing the goodness-of-fit of each model (using maximum likelihood) with the number of parameters to be estimated. The aim of using the AIC_c is to select the model that represents the data adequately with the minimal number of parameters and to find a balance between potential bias resulting from too few parameters and poor precision of parameter estimates resulting from too many parameters. Using this approach, the model with the lowest AIC_c indicates the parameters that are supported by the data, which we interpreted as factors related to variation in survival. Use of AIC_c to direct model selection and inference deviates from traditional analyses based on significance testing, but is supported by a growing body of literature summarizing the pitfalls of statistical hypothesis testing (Johnson 1999), particularly for observational data (Esler et al. 2000).

We present first-year survival estimates as proportions with 95% confidence intervals. We used S-Plus Version 6 software (Insightful 2001) for all statistical analyses.

Results

Survival

The Kaplan-Meier estimate of cumulative first year survival was 0.24 (95% C.I. = 0.09-0.39; Figure 6.1). Estimated survival decreased from 1.00 at two weeks after independence to 0.47 (95% CI = 0.32-0.63) at 16 weeks after independence (Figure 6.1). We contrasted seven different models with one variables and one model with two variables (Table 6.1). In the best-fitting model (Model 1), brood size had an effect on survival. Radio-marked eagles from single fledgling broods had an estimated survival of 0.41 (SE = 0.17, 95% CI = 0.15-0.74); radio-marked eagles from two fledgling broods had an estimated survival of 0.13 (SE =0.07, 95% CI = 0.04-0.33).

Timing and Causes of Mortality

Mortality was more likely to occur during autumn migration and winter than in other seasons (Table 6.2); 84% of all mortalities occurred during autumn migration and winter. Most mortality (22.6%) occurred in winter in Alberta, Canada (Table 6.2).

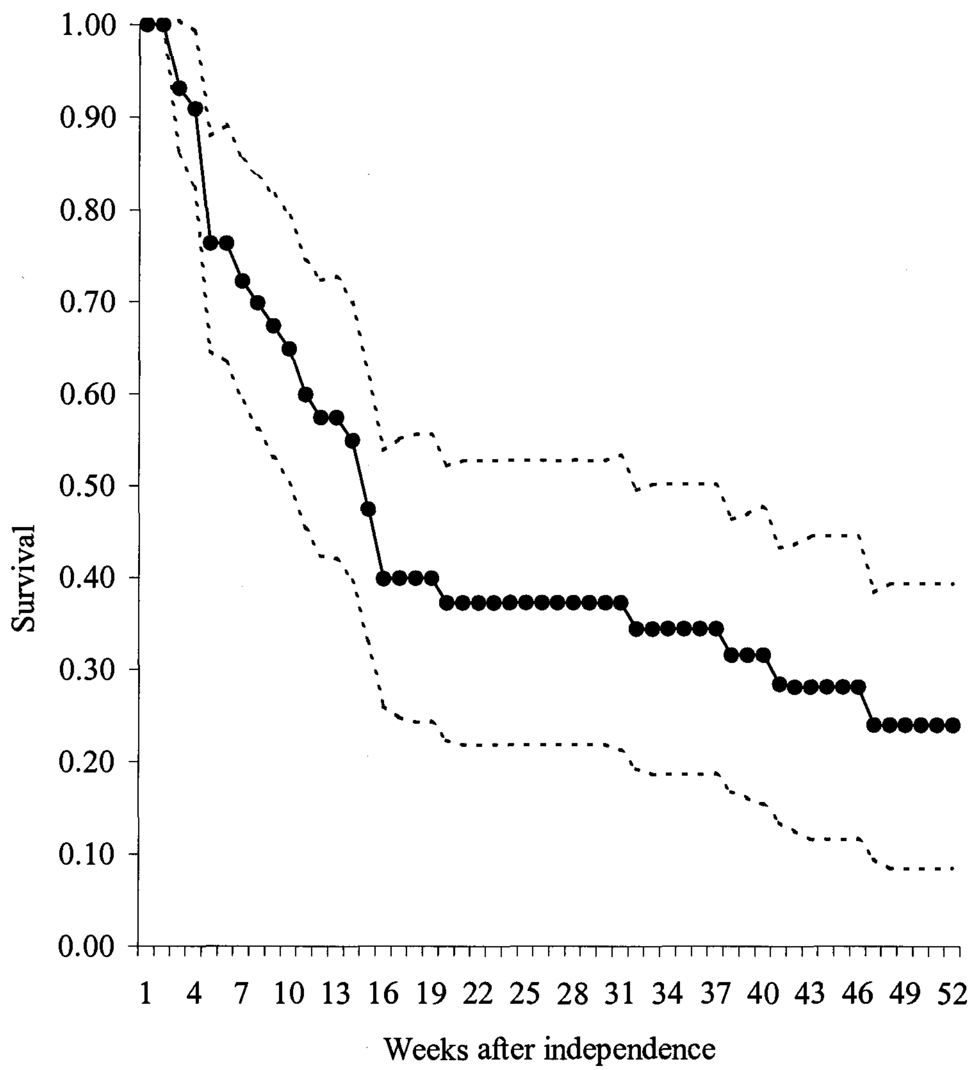

Figure 6.1. Estimated first-year survival rates of radio-marked Golden Eagles (n = 44) from Denali National Park and Preserve, Alaska, 1997-1999, across the first year of independence. Dotted lines represent 95% confidence limits.

Table 6.1. Models used to estimate first year survival rates of radio-marked Golden Eagles from Denali National Park and Preserve, Alaska. The best model is that with the lowest Akaike information criterion, adjusted for small sample size (AIC_c, Burnham and Anderson 1998). Support for each model is indicated by differences in AIC_c values, not their absolute magnitude; therefore, we present AIC_c values as differences from the best model (Δ AIC_c).

Models	Model description	Number of parameters in model	AIC_c weight	Δ AIC_c
1	Brood size effect	2	0.15763	0.00
2	No constraints on survival	1	0.09733	0.96
3	Season effect	4	0.08947	1.13
4	Year and brood size	3	0.08005	1.36
5	Year effect	2	0.03768	2.86
6	Hatch date effect	2	0.03658	2.92
7	Post-fledging dependence period effect	2	0.03392	3.07
8	Productivity history effect	3	0.01542	4.65

Table 6.2. Geographic and seasonal attributes of mortalities of radio-marked migratory juvenile Golden Eagles from Denali National Park and Preserve, Alaska, 1997-1999.

	Season				
Geographic area	Autumn migration	Winter	Spring migration	Summer	Total
Alaska, USA	3	1	0	4	8
Yukon, Canada	2	1	0	0	3
British Columbia, Canada	4	1	0	0	5
Alberta, Canada	3	6	0	0	9
Saskatchewan, Canada	1	1	0	0	2
Idaho, USA	0	2	0	0	2
Montana, USA	0	0	1	0	1
Total	13	12	1	4	30

Four radio-marked Golden Eagles died from 5 Jan through 16 Jan 1998, in western Alberta. Their deaths coincided with a period of extreme winter weather when daily temperatures rarely rose above -25°C and dropped as low as -40°C (Environmental Canada Daily Climate Report, Alberta).

We recovered 16 of the radio-marked Golden Eagles that died during their first year of independence and one PTT without the Golden Eagle. We conducted post-mortem examinations on 13 Golden Eagles (n = 10 females, 3 males) recovered as whole carcasses. We could not conduct post-mortem examinations on three Golden Eagles that we recovered as partial or scavenged carcasses. Causes of mortality included starvation (n = 9), electrocution (n = 1) and unknown (n = 3). Golden Eagles that died from starvation were emaciated, dehydrated, and usually had moderately to severely atrophied pectoral muscles. One emaciated Golden Eagle had a substantial infection of tapeworms. Another radio-marked Golden Eagle was observed attacking domesticated pigs and cats, and feeding on the carcass of a domesticated sheep several days before its death. In contrast, the Golden Eagle that died from electrocution had high levels of subcutaneous and abdominal fat. Three Golden Eagles had elevated levels of lead, but the level was not considered significant or related to their death. We could not determine the cause of death for heavily scavenged Golden Eagle carcasses. We found evidence of terrestrial mammals including lynx (*Lynx canadensis*), marten (*Martes americanus*), and coyote (*Canis latrans*) at several of the scavenged carcasses and the canine tooth of a coyote had punctured the skull of one Golden Eagle carcass. However, there was no evidence of the initial cause of death at any of the scavenged carcasses. We found one PTT in a garbage dumpster. The PTT had been cut off the Golden Eagle and, based on information provided by the biologist who found the PTT, we assumed that Golden Eagle was poached (G. Court, personal communication). We recovered three Golden Eagle carcasses and one PTT ≤ 1 km of human activities and 13 Golden Eagle carcasses >10 km from human activities.

Discussion

Our results indicated an effect of brood size on first year survival of Golden Eagles; fledglings from single fledgling broods had a higher survival rate than fledglings from two-fledgling broods. Mean brood size of Golden Eagles in North America ranges from one to three, with three fledgling broods being rare (Kochert et al. 2002). In North America, productivity of Golden Eagles varies in response to food supplies and in years of abundant prey, productivity increases (Kochert et al. 2002). Natural selection is expected to favor parents that optimize their reproductive value at each breeding episode (Winkler 1987). Our results, however, suggest that basing estimates of reproductive success of Golden Eagles using only measures of productivity may be misleading if productivity is not a predictor of recruitment. Further, our results suggest that low production nesting territories, where single-fledgling broods are common, are important for producing potential recruits to the breeding population.

Nesting success may provide a misleading measure of the chances of survival of an individual due to the effect of factors such as brood size (Spear and Nur 1994). The relationship between brood size and survival has not been studied in most raptors. Survival of Sparrowhawks (*Accipiter nisus*) was not related to brood size (Newton and

Moss 1986). However, in studies of Great Tits (*Parus major*), Pied Flycatchers (*Ficedula hypoleuca*) and Herring Gulls (*Larus argentatus*), individual survival declined in larger broods (Perrins 1965, Lack 1966, Nisbet and Drury 1972, Perrins and Moss 1975).

Golden Eagles do not provide different amounts of food to different size broods (Collopy 1984), make no attempt to distribute food equally among nestlings, and ignore aggressive interactions between siblings (Edwards and Collopy 1983). Collopy (1984) suggested that several aspects of Golden Eagle reproductive behavior supports the interpretation that this species exhibits a conservative parental investment strategy. Our findings raise several questions regarding the effect of brood size on survival. Sibling aggression is commonly observed in two-fledgling broods (Watson 1997, Kochert et al. 2002). Fledglings from single fledgling broods are free from aggressive encounters with siblings, but do they receive more food and greater parental care throughout the nestling and post-fledging dependence period than fledglings from two-fledgling broods? Unfortunately, our data set is too small to address this question. Although our findings are limited to first year survival, they suggest that more research is needed to determine if productivity is a good predictor of recruitment in Golden Eagles. Further, until this hypothesis is tested, we suggest not using the term "good quality" for breeders that raise the most young. Rather, we suggest using the term "good quality" breeders to describe those individuals that produce the most recruits.

This study provides the first estimates of first year survival for migratory Golden Eagles; thus, comparisons with other estimates of survival for migratory

Golden Eagles are not possible. Our study, however, provides new insight on potential differences of survival rates of non-migratory and migratory Golden Eagles and sources of mortality. Our results also illustrate potential differences in the life history characteristics of migratory and non-migratory Golden Eagles in North America. Radio-marked migratory Golden Eagles from Denali exhibited low survivorship during their first year of independence. The estimates of first-year survival of migratory Golden Eagles from Denali (95% C.I. = 0.09-0.39) are much lower than those reported in for non-migratory Golden Eagles in western California (95% CI = 0.85-0.99; Hunt et al. 1996). We suggest that the fundamental differences in the life history characteristics of migratory Golden Eagles from Denali and non-migratory Golden Eagles from western California could result in significantly different survival rates and population dynamics between these populations.

Much more work needs to be done to quantify survival rates of Golden Eagles and examine variation in survival and population dynamics among populations. Estimated survival rate of juvenile, subadult, and floater (subadult and adult non-breeders) Golden Eagles in western California was 0.78 (SE = 0.03); the survival rate of territorial breeding Golden Eagles was 0.89 (SE = 0.04) (Hunt et al. 1998). Conversely, Harmata (2002) found that 50% of Golden Eagles banded in the Rocky Mountain region were dead by age 2 yr, 7 mo; 75% by age 5 yr, 1 mo; and 95% by 11 yr, 1 mo. Watson (1997) suggests that the pre-adult survival rate for Golden Eagles may be 15%, but that survival probably varies considerably between populations and temporally within populations. We agree that the survival rate of Golden Eagle may vary across their range, but suggest that more research is needed to provide estimates of survival.

Bald Eagles are the only other large-bodied, long-lived raptor occurring commonly in North America. Estimates of first year survival for non-migratory Bald Eagles are high; 87% in the Greater Yellowstone Ecosystem (Harmata et al. 1999), 76.9% in northern California (Jenkins et al. 1999), 71% in Prince William Sound, Alaska (Bowman et al. 1995), and 100% in the Chesapeake Bay area (Buehler et al. 1991). In contrast, estimated first year survival rates for migratory Bald Eagles are somewhat lower than those reported for non-migratory populations; 63% in Florida (Wood 1992), 54% in Maine (McCollough 1986) and 37% in Saskatchewan (Gerrard et al. 1978). These findings, in conjunction with our results, suggest first-year survival for migratory Golden Eagles and migratory Bald Eagles is lower than first year survival of non-migratory populations of these species in North America.

In many bird species, juveniles exhibit higher mortality rates than adults (Lack 1954, Newton 1979). Further, high mortality is usually related to an increased risk when young birds become independent and disperse (Rohner and Hunter 1996). Our results indicate that the risk of mortality for juvenile Golden Eagles is greatest within 16 weeks of leaving their natal nesting territories during autumn migration and early winter. Higher risks of mortality coincides with the period immediately after gaining independence when fledglings are traveling thousands of kilometers over unfamiliar terrain during autumn migration and establishing winter ranges. Most mortalities during this time were caused by starvation and dehydration, suggesting that juveniles are more susceptible to mortality due to inferior hunting or foraging skills.

Prey and weather can interact to limit Golden Eagle productivity (Steenhof et al. 1997). We hypothesize that prey and weather (Mitchell et al. 2000, Laugtimm and Beck 2003) can interact to affect survival of migratory juvenile Golden Eagles as well. We have limited anecdotal evidence that weather may influence survival. Four of the radio-marked Golden Eagles died within an 11-day period in western Alberta, Canada, during a period of extreme winter conditions when daily temperatures rarely rose above -25°C and dropped to -40°C. We recovered the carcasses of two of the four radio-marked Golden Eagles that died during this period and both died from starvation. Additionally, another radio-marked juvenile Golden Eagle and three other Golden Eagles (one juvenile and two adults) starved to death during a period of extremely cold weather during Dec 1999 in the southern Yukon Territory, Canada. Therefore, we hypothesize that juvenile migratory Golden Eagles who fail to accumulate sufficient body fat reserves may be at a higher risk of mortality during extended periods of extremely cold temperatures during winter.

The latitudinal range of the recovery area for Golden Eagle mortalities spanned 21° of latitude (69° N latitude to 48° N) and 43° of longitude (153° W to 106° W). Our sample of radio-marked Golden Eagles migrated over some of the most remote lands in western North America and we could not recover all mortalities due to their inaccessibility. Our ability to recover a mortality depended on its' geographic location, our success at locating assistance to retrieve the PTT, and physically finding the PTT. Most mortalities occurred in very remote areas, and often necessitated traveling via airplane or helicopter, and then by foot to the recovery site. The probability of finding many of the mortalities would have been very low without the use of conventional radio telemetry because most mortality occurred in remote locations where we had to use aerial tracking to find the PTT.

The largest number of mortalities occurred in winter in Alberta, Canada. Based on their field observations, several biologists from Alberta suggested that some of these radio-marked Golden Eagles may have interrupted their autumn migration to feed on gut piles of ungulates left behind by hunters in northern and central Alberta (G. Court, personal communication).

Many Golden Eagle deaths in North America are attributed directly to human-related activities (Kochert et al. 2002). However, our results indicate that many of the radio-marked Golden Eagles starved to death. It is difficult to find evidence of starvation in wild birds because corpses disappear quickly and most deaths are undoubtedly overlooked (Watson 1997). Further, documenting starvation requires recovery and post-mortem examination of carcasses (Kenward et al. 1999). We hypothesize that starvation probably resulted due to inexperienced Golden Eagles traveling long distances over unfamiliar territory, presumably at a time when they are food stressed. Low incidences of direct human-induced mortality in this study may have resulted because the Golden Eagles migrated over remote areas with relatively few human activities.

One assumption in using radio telemetry to estimate survival is that the radio-transmitters and the harness attaching them to the eagles do not effect survival (White and Garrott 1990). We have no evidence to suggest that radio-marked Golden Eagles were negatively affected by their radio package. There is some evidence that radio-marked Golden Eagles exhibit reduced productivity (Marzluff et al. 1997). However, there are no reports of radio-marked Golden Eagles exhibiting reduced survival and there is no evidence that radio marking influences survival of juvenile Bald Eagles (see Buehler et al. 1991, Wood 1992, Bowman et al. 1995).

Conclusions

Understanding how basic demographic parameters, including survival and reproduction, vary with age and among populations is essential to understanding the population dynamics of long-lived vertebrates (Charlesworth 1980), such as Golden Eagles. Further, survival and lifespan often account for most of the variance in the lifetime reproductive success of long-lived, slow reproducing birds with delayed breeding (Clutton-Brock 1988, Newton 1989). Very slight differences in yearly survival rates may have significant effects on population dynamics (Van der Jeung and Larsson 1998); therefore, we suggest that future studies of Golden Eagle population trends include estimates of survival, as well as productivity and reproductive success. While estimating demographic parameters of Golden Eagles and other long-lived raptors is difficult, we agree with Kenward et al. (1999) that it may be more important to use our limited resources to better understand population demography than focus all our efforts on obtaining on estimates of productivity.

Modeling population dynamics of Golden Eagles requires reliable estimates of survival; however, estimating survival rates of long distance migrants or long-lived birds is difficult using traditional banding and color-marking studies. Banding, color-marking and wing-marking studies often require large sample sizes because the recovery of bands and resighting of visual markers accumulate slowly, and estimating survival ultimately depends on encounter rates of banded or marked birds (Kenward et al. 1999). Further, band recovery data may produce erroneous results (McFadzen and Marzluff 1996). Conventional radio-telemetry studies can provide precise estimates of survival (Buehler et al. 1991, Bowman et al. 1995); however, it is difficult to track a large number of migratory Golden Eagles over large remote areas. Satellite telemetry and global positioning system (GPS) telemetry allow users to track radio-marked animals anywhere on Earth with nearly 100% probability of re-sighting the radio-marked animal. Satellite and GPS telemetry are well suited for studying movements and survival of birds that travel thousands of kilometers over large remote areas each year.

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CHAPTER 7

SUMMARY

The five chapters of this dissertation examined Golden Eagle productivity and survival in relation to landscape characteristics of nesting territories. I described landscape characteristics using remote sensing data (color-infrared photographs), and the length of the post-fledging dependence period and the survival of fledglings using satellite radio telemetry. The results of this dissertation provide new information on the landscape characteristics of the area surrounding Golden Eagle nest sites, the relationship between landscape characteristics and productivity, the post-fledging dependence period, and first-year survival of Golden Eagles raised in the northern latitudes of North America.

My results suggest that broad-scale land cover descriptions are useful for assessing the potential reproductive output of Golden Eagle nesting territories in Denali. Using a coarse-resolution land cover map, I determined that Upland land cover (primarily shrub cover) dominates low production Golden Eagle nesting territories in Denali. Changes in climate may result in an increase in shrub cover within Golden Eagle nesting territories in Denali. Increased shrub cover may negatively influence the availability of prey and foraging habitat for Golden Eagles in Denali. Therefore, I recommend that the long-term ecological study of Golden Eagle ecology in Denali continue to monitor land cover characteristics of nesting territories.

Using data collected by satellite telemetry, I estimated the length of the post-fledging dependence period, survival of fledglings during the post-fledging dependence period, and first-year survival of Golden Eagles. My results suggest that there is no difference in the length of the post-fledging dependence period, post-fledging survival, and first-year survival of Golden Eagles from low and high production nesting territories. However, I did find evidence to suggest that fledglings from single fledgling broods have a higher survival rate than fledglings from two fledgling broods. These findings suggest using caution when using reproductive success as an indicator of potential survival and recruitment of migratory Golden Eagles.

My results suggest that survival during the post-fledging dependence period is high and, on average, counts of the number of young fledged per nest made before fledging are good estimates of reproductive success. However, because we conducted this study over a short time period (3 years), we recommend additional measurements of post-fledging survival be made over a longer period and include an entire snowshoe hare population cycle (8 to 11 years).

The period between fledging and entering a breeding population is the least studied portion of a Golden Eagle's life. My results suggest that the length of the post-fledging dependence period of Golden Eagles is shorter in Denali than in temperate study areas. This shorter post-fledging dependence period may result in a lower survival rate of first-year Golden Eagles. My results also suggest that first-year survival of migratory Golden Eagles from Denali is lower than first-year survival of resident Golden Eagles in California. Lower survival rates may reflect the differences in the life history characteristics of a migratory versus a resident population.

Many facets of Golden Eagle ecology remain unexplored. Future research and monitoring efforts should include: (1) estimating the demographic parameters of populations including survival and recruitment rates because they provide a measure of population status and provide insight into the mechanisms underlying population change; and (2) identifying and monitoring the factors that influence the demographic parameters of Golden Eagles including habitat, climate and prey abundance.

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