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GOLDEN EAGLE DIET BREADTH AND REPRODUCTION IN RELATION TO FLUCTUATIONS IN PRIMARY PREY ABUNDANCE IN WYOMING'S BIGHORN BASIN

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ABSTRACT.—Golden Eagles (*Aquila chrysaetos*) are facing rapid environmental changes that may reduce the abundance and distribution of their prey in the western United States. Mitigation of negative effects depends in part on understanding Golden Eagle diet and the relationship between prey abundance and eagle reproduction. We documented reproduction and diet for Golden Eagles nesting in Wyoming's Bighorn Basin 2009–2015 and examined relationships between primary prey abundance and Golden Eagle diet breadth and reproductive rate. Annual Golden Eagle reproductive rate averaged 0.73 (range = 0.38–1.32) fledglings per occupied nesting territory. Cottontails (*Sylvilagus* spp.) dominated the diet in each year of the study, although cottontail abundance fluctuated markedly from year to year. The annual occurrence of cottontails in prey remains collected from nests ranged from 60.1% to 90.9% (frequency) and from 46% to 96% (biomass). Annual Golden Eagle diet breadth (Levins index) averaged 1.91 (frequency) and 1.98 (biomass). Both measures of annual diet breadth were negatively related to cottontail abundance. Annual eagle reproductive rate increased significantly as cottontail abundance increased ($r^2 = 0.78$, $F_{1,5} = 17.35$, $P = 0.009$). Our results suggest that the abundance of cottontails was the critical factor influencing Golden Eagle reproduction in a given year during our study. To mitigate negative effects of environmental changes on the Golden Eagle population in the Bighorn Basin, we suggest maintaining or improving habitat conditions that support robust cottontail populations and improving conditions for potential alternative prey species where ecologically feasible and socially acceptable.

KEY WORDS: *Golden Eagle*; Aquila chrysaetos; *cottontails*; Sylvilagus; *Bighorn Basin*; *diet breadth*; *primary prey*; *reproduction*.

AMPLITUD DE DIETA Y REPRODUCCIÓN EN *AQUILA CHRYSAETOS* EN RELACIÓN CON LAS FLUCTUACIONES EN LA ABUNDANCIA DE LA PRESA PRINCIPAL EN LA CUENCA DE BIGHORN, WYOMING

RESUMEN.—*Aquila chrysaetos* se está enfrentando cambios ambientales rápidos que pueden reducir la abundancia y la distribución de sus presas en el oeste de los Estados Unidos. La mitigación de los efectos negativos depende en parte de nuestro conocimiento de la dieta de esta especie y de la relación entre la abundancia de presas y la reproducción del águila. Documentamos la reproducción y la dieta de individuos de *A. chrysaetos* nidificando en la Cuenca de Bighorn, Wyoming, entre 2009 y 2015 y examinamos las relaciones entre la abundancia de la presa principal y la amplitud del espectro trófico y la tasa reproductiva. La tasa reproductiva anual promedio de *A. chrysaetos* fue de 0.73 (rango = 0.38–1.32) volantones por territorio reproductor ocupado. *Sylvilagus* spp. dominó la dieta en cada año del estudio, aunque la abundancia de esta especie fluctuó marcadamente entre años. La aparición anual de *Sylvilagus* spp. en los restos de presa recolectados en los nidos osciló desde el 60.1% al 90.9% (en frecuencia) y desde el 46% al 96% (en biomasa). La amplitud anual de la dieta de *A. chrysaetos* (Índice de Levins) promedió 1.91 (en

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frecuencia) y 1.98 (en biomasa). Ambas mediciones de la amplitud anual de la dieta estuvieron negativamente relacionadas con la abundancia de *Sylvilagus* spp. La tasa reproductiva anual de *A. chrysaetos* aumentó significativamente a medida que la abundancia de *Sylvilagus* spp. incrementó ($r^2 = 0.78$, $F_{1,5} = 17.35$, $P = 0.009$). Nuestros resultados sugieren que la abundancia de *Sylvilagus* spp. fue un factor crítico que influyó la reproducción de *A. chrysaetos* en cualquier año durante nuestro estudio. Para mitigar los efectos negativos de los cambios ambientales sobre la población de *A. chrysaetos* en la Cuenca de Bighorn, sugerimos el mantenimiento o la mejora de las condiciones del hábitat que mantengan poblaciones importantes de *Sylvilagus* spp. y la mejora de las condiciones para especies presa potenciales alternativas, donde sea ecológicamente posible y socialmente aceptable.

[Traducción del equipo editorial]

The Golden Eagle (*Aquila chrysaetos*) is an apex predator, a federally protected species under the Migratory Bird Treaty Act and the Bald and Golden Eagle Protection Act, and an iconic and charismatic species in the American West. Some recent studies and syntheses have indicated that Golden Eagles may be declining at least in some regions of North America (Kochert and Steenhof 2002, Hoffman and Smith 2003, Smith et al. 2008), although recent reviews (Millsap et al. 2013, Nielson et al. 2014) have indicated that Golden Eagle populations are generally stable in the western U.S. Nielson et al. (2016) suggested that this stability may be short-lived due in part to human-caused decline in habitats used by Golden Eagles. Anthropogenic landscape use and changes related to spread of invasive species (Kochert et al. 1999), exurban expansion (Boeker 1974, Scott 1985), agricultural development (Beecham and Kochert 1975, Craig et al. 1986), recreation (Scott 1985, Watson 2010, Kochert et al. 2002, Steenhof et al. 2014), and energy development (Madders and Walker 2002, Rowland et al. 2011, Pagel et al. 2013) can negatively affect Golden Eagle reproduction and/or survival. Grasslands, sagebrush steppe, desert shrub, and other open landscapes provide important Golden Eagle habitat in the western United States and are undergoing especially rapid changes from human land use, altered fire regimes, and invasive species (Davies et al. 2011). One approach to mitigating any negative effects of these changes on Golden Eagle reproduction and survival is to increase prey abundance and availability on a local or regional scale where possible (e.g., U.S.F.W.S. 2013). Effectively increasing prey abundance and availability for Golden Eagles requires a thorough understanding of generalized and local eagle diet, prey characteristics, and eagle-prey dynamics; however, current knowledge of Golden Eagle ecology is insufficient to support prey-based mitigation.

Golden Eagles capture a wide variety of species across their range (Kochert et al. 2002, Watson 2010, Bedrosian et al. 2017). However, Golden Eagles in the western U.S. prey principally on mammals, especially on locally available leporids (Family Leporidae) and sciurids (Family Sciuridae) weighing 0.5–4.0 kg (Kochert et al. 2002, Watson 2010). Several studies have suggested that changes in primary prey abundance profoundly affect Golden Eagle diet breadth (e.g., Steenhof and Kochert 1988, Steenhof et al. 1997, McIntyre and Adams 1999) and reproduction (e.g., Murphy 1975, Tjernberg 1983, Watson et al. 1992, Steenhof et al. 1997, Oakleaf et al. 2014).

We initiated a study in Wyoming's Bighorn Basin in 2009 to document the status, distribution, and ecology of nesting Golden Eagles in advance of anticipated landscape changes sweeping the region. Here, we report on Golden Eagle reproduction and breeding-season diet breadth in relation to fluctuations of primary prey during 2009–2015. We predicted that Golden Eagle diet breadth would increase and reproductive rate would decrease with any significant declines in primary prey abundance.

METHODS

Study Area. We delineated the study area in consultation with officials from Bureau of Land Management, Wyoming Game and Fish Department, and The Nature Conservancy. It encompasses substantial cliff-nesting opportunities for Golden Eagles and holds significant potential for increased exurban sprawl, energy development, and human recreation in the near future. Land ownership is divided between approximately 25% private and 75% public land, with most of the public land administered by the Bureau of Land Management. The study area lies in the northwestern region of Wyoming's Bighorn Basin, in the northern Wyoming Basin, along the northeastern margin of the Greater Yellowstone Ecosystem (Fig. 1). It is a multiple-use

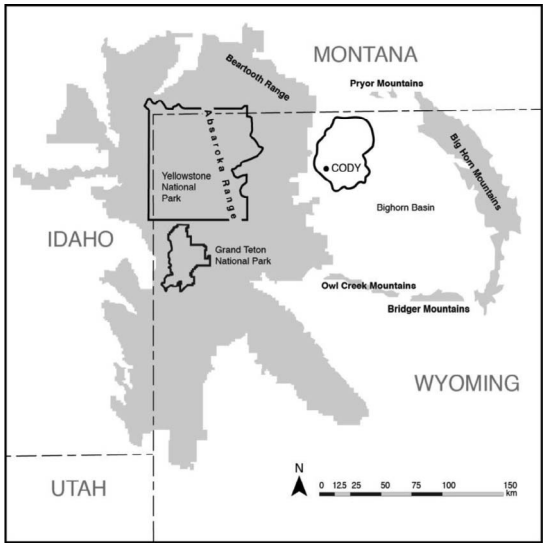


Figure 1. Approximate Golden Eagle study area where 34 Golden Eagles nesting territories were monitored, 2009–2015. Study extent surrounds Cody, Wyoming.

landscape of approximately 250,000 ha that contains approximately 50% native sagebrush steppe, 15% native salt desert shrub, and 10% juniper shrubland (Chapman et al. 2004, Knight et al. 2014), interspersed with 10% irrigated croplands. Most of the remaining 15% of the study area includes a mosaic of exurban residential development and development associated with oil and gas fields and livestock ranching. Flat and rolling terrain is broken sharply by sandstone outcroppings, cliffs, and ravines. There are few large trees outside of residential areas and narrow riparian corridors along the Shoshone and Greybull river drainages. Elevation in the study area varies between 1300–1700 masl, precipitation averages 12–23 cm (U.S.F.S. 2013), and there are typically 90–120 frost-free days per year (Young et al. 1999). Depending on local soil characteristics and topography, native vegetation is dominated by a complex of shrubs, including big sagebrush (*Artemisia tridentata*), greasewood (*Sarcobatus vermiculatus*), saltbush (*Atriplex* spp.), rabbitbrush (*Ericameria* spp.), and Rocky Mountain juniper (*Juniperus scopulorum*). Native grasses include bluebunch wheatgrass (*Pseudoroegneria spicata*), prairie junegrass (*Koeleria macrantha*) and needle-and-thread (*Hesperostipa comata*). Invasive cheatgrass (*Bromus tectorum*) is present and increasing in small patches near roads and other disturbed sites through much of the study area, but has not yet replaced large tracts of native vegetation. There are approximately 25,000–30,000 human residents in and around the adjacent towns of Cody, Powell, Greybull, and Meeteetse.

Golden Eagle Reproduction. A nesting territory is defined here as the area having one or more alternate nests used or formerly used by a single pair of eagles in a year (Steenhof and Newton 2007). A nesting territory was determined to be occupied in a given year if two adult eagles were observed within the area during the nesting season, if there was evidence that one or more nests had been recently refurbished or used (i.e., fresh greenery or egg present), or if we confirmed the presence of egg(s), and/or nestling(s). Nesting success was defined as the percent of occupied territories that produced at least one nestling reaching 51 d of age, or 80% of the average age at first flight (Steenhof and Newton 2007). During 2007 and 2008, we conducted ground and aerial searches (e.g., Lehman et al. 1998, McIntyre 2002, McIntyre et al. 2006), to locate and map historical nesting territories recorded during previous, unpublished Bureau of Land Management surveys and to record any additional occupied nesting territories encountered. Beginning in 2009, we conducted fixed-wing and helicopter aerial surveys and intensive ground surveys of these territories between late February and early April to determine occupancy each year through 2015. We repeated the aerial surveys as necessary and/or followed with ground observations with 60× spotting scopes at distances between 300 and 800 m as needed to confirm territory status. A cadre of up to 15 trained, volunteer citizen scientists assisted with systematic ground observations each year. We did not classify a nesting territory as unoccupied until aerial surveys and at least 8 hr of ground observations were conducted without evidence of occupancy. When nest sites were not clearly visible during aerial surveys and no activity was observed during ground observations, we used an unmanned aerial vehicle fitted with camera to examine nests for greenery, eggs, or other signs of occupation. We conducted follow-up ground and aerial surveys of occupied nesting territories in late June to early July each year to determine nesting success and number of fledglings produced.

Diet. To assess diet during the nesting period, we collected all prey remains we could find from a sample of 3–13 successful nesting territories each year after young fledged. We collected remains from within and immediately surrounding the nest and in

an area extending up to approximately 5 m in all directions below the nest. We selected these territories according to permitted access and to best represent habitat distribution within the study area. The number of nests sampled increased during the study as our resources increased and we gained permission to access more nesting territories. We placed prey remains in sealed, polyethylene bags labeled with nest ID and date, transported them to the Draper Natural History Museum laboratory, and stored them in a freezer for at least 2 wk until they were sorted and identified. We used skin and skeletal specimens housed in the Draper Natural History Museum collections as reference material to help identify remains to the lowest taxonomic level possible. Our results reflect minimum number of individuals (MNI) identified in each taxon, (e.g., if we identified three hind feet as white-tailed jackrabbit (*Lepus townsendii*), the minimum number of white-tailed jackrabbits in this sample was two). In some cases, a bird species was represented by a single feather, (i.e., one individual in a sample). But even if several feathers of a species were present, we counted this as one individual unless we found evidence of multiple individuals (e.g., two skulls, three wings). We calculated biomass from mean body mass data provided in Byers (1998), Dunning (2007), and Buskirk (2016), from snakes and mammals captured live in the study area and museum specimen records accessed through ARCTOS collaborative collections management database.

Leporid Abundance. To obtain an index to annual cottontail (*Sylvilagus* spp.) abundance, we acquired hunter survey data from the Wyoming Game and Fish Department (WGFD) for the management zone encompassing our study area. Each year, the WGFD conducts seasonal hunter harvest surveys via questionnaires mailed to a random sample of hunters who purchased small game licenses. Hunters provide information about how many days they hunted and how many cottontails they harvested during those days. The survey does not distinguish between desert (*S. audubonii*) and mountain (*S. nuttallii*) cottontails, both of which occur in our study area (Buskirk 2016). Each seasonal survey included hunter harvests from September through February. For example, we recorded cottontails harvested from September 2008 through February 2009 under 2009 hunter harvest to compare with 2009 eagle reproductive rate. The index we calculated in this report is the number of cottontails per hunter-day in a given year. To corroborate the hunter harvest survey and gain information on white-tailed jackrabbit abundance, we conducted roadside surveys (Smith and Nydegger 1985) 2010–2015 in our study area. We did not attempt to distinguish between the two cottontail species occurring in our area due to difficulty identifying the species in the field. We divided our study area into five roughly equal zones and divided dirt/gravel roads in each zone into numbered 8-km segments. We then used a random numbers generator to select one segment in each zone as a survey route. We surveyed each of these routes during or as near as possible to full-moon nights, depending on weather and road conditions, in each of three stages of the eagle breeding season (i.e., incubation, nestling, and fledgling). We repeated the surveys along the same routes each year 2010–2015 and calculated the average number of cottontails and jackrabbits recorded per survey route in each year. We initiated surveys between 2100–2200 H Mountain Daylight Time during nights without precipitation and low-to-moderate wind conditions. Two trained observers conducted each survey, using vehicle headlights and a handheld spotlight to illuminate leporids, and recording each rabbit and hare observed within approximately 50 m of the road.

Diet Breadth. We calculated diet breadth using the Levins (1968) index:

$$B = 1/\sum_{i=1}^{n} p_i^2,$$

where p_i is the relative occurrence/biomass of prey taxon i in the diet (Steenhof and Kochert 1985). Values of this index range from 1 to n. Most prey families were represented in our remains by very few individuals in only one or two genera. To calculate diet breadth, we grouped reptiles by order; leporids by genus; and other birds and mammals by family. Bird and mammal remains that could not be identified to family were omitted from calculations. To examine the relationship of breeding performance and diet breadth among years, we standardized Levins' index to range from 0–1 using:

$$B_s = B - 1/(n - 1),$$

where 0 is a uniform diet and 1 is a highly diverse diet (Hurlbert 1978).

Statistical Analyses. We performed Pearson product-moment correlation analysis to assess the strength of the relationship between hunter harvest

Table 1. Annual reproduction at 34 Golden Eagle nesting territories monitored in Bighorn Basin, Wyoming 2009–2015.

YEAR	NUMBER OF OCCUPIED NESTING TERRITORIES	NESTING SUCCESS[a]	REPRODUCTIVE RATE[b]
2009	31	71	1.13
2010	31	48	0.87
2011	30	33	0.50
2012	32	28	0.38
2013	28	39	0.39
2014	27	48	0.55
2015	31	77	1.32
Mean (SD)	30 (1.8)	49 (18.6)	0.73 (0.4)

[a] Percent of occupied nesting territories producing at least one young to fledging age.
[b] Number of young reaching fledging age/number occupied nesting territories.

surveys and roadside surveys of cottontails, and used simple linear regression analyses in the General Linear Models procedures in STATISTICA, Version 13.2 (2016) to examine relationships between annual hunter harvest surveys, diet breadth, and Golden Eagle reproductive rate (i.e., the number of birds reaching fledgling age/occupied nesting territory). Because we were missing roadside survey data for 2009, we chose to use hunter harvest data to examine the relationships between annual diet breadth and cottontail abundance and between Golden Eagle reproductive rate and cottontail abundance. We assigned statistical significance level to $\alpha = 0.05$. We examined the casewise plots of residuals and Mahalanobis distances to identify any extreme outliers that might seriously bias results and examined normality plots of residuals to identify any substantial departures from normality.

RESULTS

Reproduction. During preliminary surveys, we identified 34 nesting territories that we subsequently monitored through failure or fledging each year 2009–2015. All but two nests that we discovered in our study area were located on cliff faces; the other two were in plains cottonwood (*Populus deltoides*) trees. Territory occupation, nesting success, and reproductive rate varied annually (Table 1). The annual occupancy rates remained fairly constant, but nest success and reproductive rate fluctuated markedly. Annual nesting success and reproductive rate generally followed the same pattern, with both high in 2009, declining 2010–2012, and increasing again 2013–2015. Reproduction was especially high in 2015, when we recorded three nests that produced three fledglings each.

Diet. We identified 960 prey individuals collected from a total of 27 nesting territories (range 16–84 prey items/nest, SD = 21.3). Cottontails were the primary prey, dominating the sampled diet of nesting Golden Eagles in each year of our study. Cottontail frequencies ranged from 60.1% to more than 90%, with an annual mean of 73.2% (Table 2). The percent of cottontails in the diet declined each year between 2010 and 2012, increased slightly in 2013, and rose again markedly in 2014 and 2015. We found a similar pattern when we examined percent prey by biomass (Table 3). The biomass of cottontails in the diet ranged from 46% to 96%, with a mean of 68.7%. Even in years with lowest cottontail abundance, no other species rose to primary

Table 2. Frequency of prey in the diet of Golden Eagles in Bighorn Basin, Wyoming 2009–2015.

YEAR	NUMBER OF PREY	(NO. NESTS)	COTTONTAILS (%)	JACKRABBITS (%)	PRONGHORN (%)	OTHER MAMMALS (%)	BIRDS (%)	REPTILES (%)	DIET BREADTH[a]
2009	44	(3 nests)	90.9	0	0	2.2	4.4	2.2	1.20
2010	88	(4 nests)	77.2	3.3	4.3	4.2	11.0	0	1.68
2011	114	(4 nests)	76.3	1.7	7.0	6.1	8.7	0	1.69
2012	118	(5 nests)	60.1	15.2	11.0	2.5	11.0	0	2.50
2013	147	(6 nests)	61.9	10.2	3.4	9.5	13.6	1.3	2.54
2014	214	(13 nests)	69.1	9.3	4.2	5.1	11.6	<1	2.04
2015	235	(13 nests)	77.0	8.5	2.9	2.5	8.0	<1	1.66
Mean (SD)			73.2 (10.6)	6.9 (5.4)	4.7 (3.5)	4.6 (2.6)	9.7 (3.0)	0.6 (0.8)	1.91 (0.5)

[a] $(B = 1/\sum_{i=1}^{n} p_i^2)$.

Table 3. Estimated biomass of prey in the diet of Golden Eagles in Bighorn Basin, Wyoming 2009–2015.

YEAR	NUMBER OF PREY	(NO. NESTS)	COTTONTAILS (%)	JACKRABBITS (%)	PRONGHORN (%)	OTHER MAMMALS (%)	BIRDS (%)	REPTILES (%)	DIET BREADTH[a]
2009	44	(3 nests)	96.0	0	0	<1	3.0	<1	1.07
2010	88	(4 nests)	75.3	5.3	10.0	3.7	6.0	0	1.73
2011	114	(4 nests)	71.4	4.0	19.0	<1	5.2	0	1.83
2012	118	(5 nests)	46.0	28.0	24.6	<1	1.7	0	2.86
2013	147	(6 nests)	62.0	24.1	9.9	<1	3.8	<1	2.16
2014	214	(13 nests)	62.0	20.0	11.0	<1	6.2	<1	2.25
2015	235	(13 nests)	68.0	18.0	7.6	1.3	5.9	<1	1.94
Mean (SD)			68.7 (16.5)	14.2 (11.0)	11.7 (8.0)	0.60 (1.3)	4.54 (1.7)	0.33 (0.4)	1.98 (0.55)

[a] $(B = 1/\sum_{i=1}^{n} p_i^2)$.

importance in frequency or biomass. White-tailed jackrabbits and pronghorn (*Antilocapra americana*) fawns, mostly newborn or only a few days old, were the most frequent secondary prey species recorded in the diet. Neither of these species alone composed more than 15.2% of the diet by frequency or 28% by biomass in any year. Together, however, they made up 26.2% of number of prey items and a 52.6% majority of prey biomass in 2012. The frequency of other mammals in the diet included 1.7% sciurids, mostly white-tailed prairie dogs (*Cynomys leucurus*) and least chipmunks (*Tamias minimus*) and 1.1% cricetids (Family Cricetidae), mostly bushy-tailed woodrats (*Neotoma cinerea*) and deer mice (*Peromyscus maniculatus*), and <1% each Ord's kangaroo rats (*Dipodomys ordii*), northern pocket gophers (*Thomomys talpoides*), and carnivores, mostly feral cats (*Felis catus*), red foxes (*Vulpes vulpes*), coyote pups (*Canis latrans*), and an American badger (*Taxidea taxus*). Taken together, the frequency of these other mammals never reached 10% of prey numbers or more than 3.7% of prey biomass in any year.

We identified a wide variety of bird species from nest remains, but no one family contributed more than 2.5% by frequency to the overall diet. Corvids (Family Corvidae; 2.5%) and phasianids (Family Phasianidae; 2.3%) were the avian families occurring most frequently in the diet. The most commonly occurring species included Common Raven (*Corvus corax*), Black-billed Magpie (*Pica hudsonia*), Ring-necked Pheasant (*Phasianus colchicus*), and Greater Sage-Grouse (*Centrocercus urophasianus*). Among other raptors, we found 16 Great Horned Owl (*Bubo virginianus*) and five American Kestrel (*Falco sparverius*) remains in nests. Although Rock Pigeons (*Columba livia*) and Eurasian Collared-Doves (*Streptopelia decaocto*) were common in some sections of our study area, we recorded only three pigeons and no doves in the prey remains. Together, birds contributed no more than 13.6% of prey numbers or 6.2% of prey biomass in any one year. Reptiles accounted for <1% of the diet overall. Bullsnakes (*Pituophis catenifer*) and prairie rattlesnakes (*Crotalus viridis*) were the most frequently occurring reptiles in prey remains.

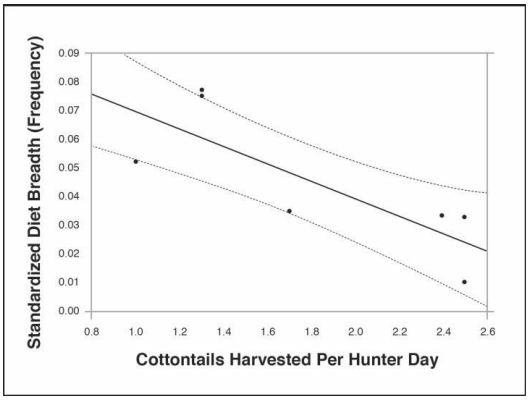
Leporid Abundance. Our roadside surveys showed a trough in cottontail numbers during 2011–2014, before a dramatic rebound in 2015 (Table 4). During this same period, our white-tailed jackrabbit counts remained relatively constant between an average of 1.8 and 2.2 individuals recorded per survey route in a given year. Regional cottontail hunter-harvest surveys provided by the WGFD showed a pattern similar to our roadside cottontail counts. The two indices were strongly correlated ($r = 0.940$, $P = 0.003$).

Table 4. Annual cottontail indices to relative abundance in the Bighorn Basin, Wyoming.

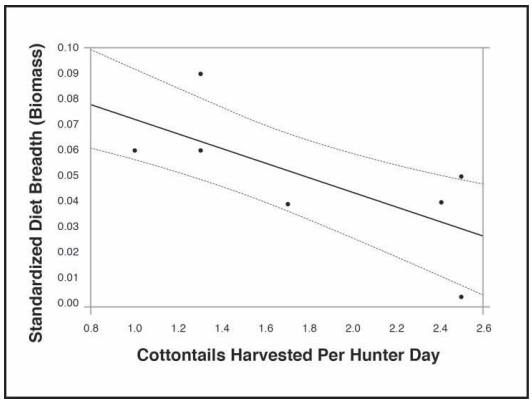
YEAR	ROADSIDE SURVEYS[a]	HUNTER HARVEST[b]
2009	No survey conducted	2.5
2010	11.7	2.4
2011	3.8	1.7
2012	3.9	1.3
2013	3.1	1.3
2014	3.5	1.0
2015	12.9	2.5

[a] Average number of cottontails recorded per survey route in each year.

[b] Cody/Bighorn Basin regional cottontails/hunter day during September–February season, (i.e., 2009 index reflects September 2008–February 2009).



A



B

Figure 2. Relationships (with 95% confidence intervals) between (A) standardized Golden Eagle diet breadth by frequency and annual cottontails harvested per hunter day ($r^2 = 0.64$; $F_{1,5} = 8.8$; $P = 0.031$), and (B) standardized Golden Eagle diet breadth by biomass and annual cottontails harvested per hunter day ($r^2 = 0.58$; $F_{1,5} = 7.0$; $P = 0.08$).

Cottontail Abundance and Diet Breadth. Golden Eagle diet breadth was negatively related to cottontail abundance (Fig. 2A, B). Only the relationship between diet breadth by frequency and cottontails harvested per hunter day, however, was statistically significant ($r^2 = 0.64$; $F_{1,5} = 8.8$; $P = 0.031$). Our examination of residuals and Mahalanobis distances revealed no significant outliers or substantial departures of residuals from normality.

Cottontail Abundance and Golden Eagle Reproductive Rate. Eagle reproductive rate increased significantly with our cottontail abundance index of rabbits harvested per hunter day ($r^2 = 0.78$; $F_{1,5} = 17.35$; $P = 0.009$; Fig. 3). We detected no significant outliers or departures from normality from an examination of residuals and Mahalanobis distances.

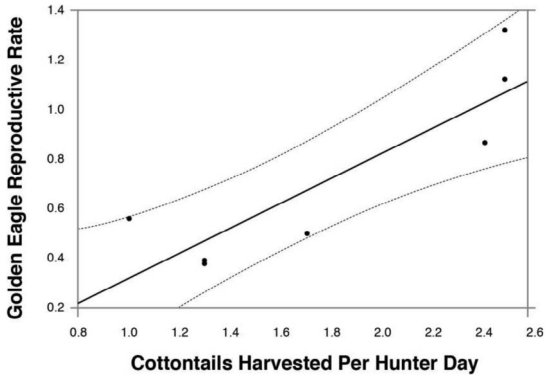


Figure 3. Relationship (with 95% confidence intervals) between Golden Eagle reproductive rates and annual cottontails harvested per hunter day ($r^2 = 0.78$; $F_{1,5} = 17.35$; $P = 0.009$).

DISCUSSION

Diet. We found that cottontails were the primary prey of nesting Golden Eagles, and that cottontail abundance fluctuated markedly during our study. Statewide cottontail populations in Wyoming exhibit 7- to 8-yr fluctuations (Fedy and Doherty 2011), and our results suggest a similar pattern in our study area. Our assessment of diet may be biased in some ways because the annual sample sizes were unequal, and we collected prey remains only once at the end of each nesting season. Although end-of-season collecting is least invasive to nesting eagles and is economical and energy-efficient, it is potentially fraught with well-known biases. It reflects only a sample of prey items brought to the nest for young, not necessarily representative of adult diet, and larger, heavier bones may be overrepresented because they persist longer in the nest (e.g., Marti et al. 2007). In contrast, larger prey may also be underrepresented. For example, Lockhart (1976) found that cottontail bones were underrepresented in prey remains compared to prey deliveries documented with time-lapse photography, and Tjernberg (1981) suggested that Golden Eagles may selectively remove remains of large prey items from the nest throughout the season. Collopy (1983) compared direct observations of prey deliveries with prey remains, and found that total prey biomass was underestimated by prey remains. He found no

significant difference in the two methods with respect to calculating the frequency of prey occurrence. However, Collopy collected prey remains systematically throughout the nesting season, rather than once at the end of the season, as in our study. Although we are confident in identifying cottontails as the primary prey species brought to nests by Golden Eagles during our study, our overall diet assessment and calculations of diet breadth should be interpreted with caution.

Leporids are frequently identified as primary prey of Golden Eagles in the western United States (Kochert et al. 2002). In a review of breeding season studies conducted at locations across the western U.S., Bedrosian et al. (2017) found that leporids made up more than half of the Golden Eagle prey remains identified. Black-tailed jackrabbits (*Lepus californicus*) were typically the most frequently occurring leporid species in the diets summarized by Bedrosian et al. (2017). In our study, cottontails remained the primary prey for nesting Golden Eagles, even during substantial declines in cottontail numbers. The Bighorn Basin supports relatively few alternative prey species for Golden Eagles. Jackrabbits and sciurids, especially prairie dogs, are important prey in the southern Wyoming Basin (Arnold 1954, Schmalzried 1976, MacLaren et al. 1988), but many of these species are missing or uncommon in the Bighorn Basin (Grenier and Filipi 2009, Olson et al. 2015, Buskirk 2016). Black-tailed jackrabbits do not occur in our study area (Buskirk 2016), and white-tailed jackrabbits were relatively scarce and sparsely distributed during our study. Because of its legal designation as a "predatory animal" by the State of Wyoming (Wyoming Legislature 2016) and its presumed commonness, white-tailed jackrabbits have received little management attention or research in Wyoming (Buskirk 2016). White-tailed jackrabbit populations are considered much reduced in some areas of northwestern Wyoming, particularly in Yellowstone and Grand Teton National Parks, but there is no clear explanation for the decline (Buskirk 2016).

Prairie dogs and other sciurids were also scarce and sparsely distributed during our study. Uinta ground squirrels (*Urocitellus armatus*) occur in foothills environments at the margins of our study area, but are absent from most of the area. Harrell and Marks (2009) reported a 71% decline in area occupied by prairie dogs in the northern Bighorn Basin between the mid-1980s and the early 2000s. Expanding residential and agricultural development, direct persecution (shooting and poisoning), and especially sylvatic plague (*Yersinia pestis*) are among the causes of the decline, but no quantitative data are available on the relative contribution of these or other factors.

We expected that Greater Sage-Grouse would occur with greater frequency in the nesting diet of Golden Eagles, especially during declines in cottontail abundance (see Hagen 2011). Sage-grouse weigh approximately 1.3–3.2 kg, and are fairly abundant within our study area (Harrell 2008). Sage-grouse are not widely reported from nesting Golden Eagle diet (Kochert et al. 2002, Bedrosian et al. 2017), but Arnold (1954) reported that Greater Sage-Grouse were the third most frequently occurring prey species (after cottontails and black-tailed jackrabbits) at 18% of prey remains he examined in southern Wyoming. Sample size was small in this study, however, including 120 prey samples from only four nests. Fedy and Doherty (2011) reported that Greater Sage-Grouse and cottontail fluctuations are highly correlated in Wyoming, and it is possible that this relationship reduces the likelihood that Golden Eagles switch to sage-grouse during cottontail declines. Our data do not address Golden Eagle use of Greater Sage-Grouse outside the period when eagles are feeding nestlings.

Diet Breadth. As predicted, we found that Golden Eagle diet breadth generally increased with declines in primary prey (i.e., cottontail) abundance. Additional years of data with varying cottontail abundance are needed to more thoroughly evaluate this relationship. Steenhof and Kochert (1988) argued that Golden Eagles face selective pressure for both generalization and specialization. Golden Eagle foraging behavior would thus be expected to conform to Schluter's (1981) optimal diet predictions that: (1) when prey are abundant, predators should specialize on only the most valuable prey; (2) inclusion of other prey types in the diet should depend not on their own abundance but on the abundance of more profitable prey; and (3) as prey abundance declines, diet breadth should increase. In our study, jackrabbits, pronghorn fawns, and a variety of bird species occurred more frequently in the nesting eagles' diet when cottontails were less abundant, but we did not detect a dramatic switch to any single alternative prey species when cottontails declined. When cottontails were least abundant in 2012, jackrabbit and pronghorn fawn biomass together only slightly surpassed cottontail biomass. Following Schluter (1981), if cottontails are more

profitable prey than the current alternatives available in the Bighorn Basin, then Golden Eagles would be expected to rely more heavily on alternative prey only when cottontail populations drop below some threshold level or alternative prey become significantly more profitable.

The average diet breadth of nesting eagles in our study was among the lowest recorded in the western U.S., and consistent with other diet studies in shrub-steppe and desert shrub environments (Bedrosian et al. 2017). Our measure of diet breadth could be misleading, however, because some species were less detectable in prey remains collected at the end of the season (e.g., Collopy 1983). The greatest Golden Eagle diet breadth reported in the contiguous western U.S. was 12.27 from prey remains collected in the Columbia Plateau 2007–2013, where high landscape heterogeneity supported high diversity and availability of appropriately sized prey (Watson and Davies 2015). Comparisons of diet breadth among different studies should be interpreted cautiously due to differences in methods of obtaining diet information and in prey groupings used in diet breadth calculations.

Reproductive Rate. Our results also upheld our second prediction that Golden Eagle reproductive rate would decline with declines in primary prey abundance. Despite increased diet breadth, particularly the inclusion of more jackrabbits and pronghorn fawns in the diet during years with low cottontail abundance, Golden Eagle reproductive rate was lowest in these years. Several other studies have shown that Golden Eagle reproductive rates were lower when and where primary prey, e.g., mountain hares (*Lepus timidus*) and Willow Ptarmigan (*Lagopus lagopus*; Tjernberg 1983, Watson et al. 1992), and black-tailed jackrabbits (Murphy 1975, Steenhof et al. 1997) were less abundant. Our results underscore how important cottontail abundance was to Golden Eagle reproduction during our study. Prey abundance, however, is not always enough to explain raptor reproductive rates. For example, habitat features, such as vegetation, can interact with prey abundance to influence the availability of prey to raptors (e.g., Preston 1990); and other factors, particularly weather, also interact with prey abundance to affect raptor reproduction (e.g., Steenhof et al. 1997). Additional years of study under varying conditions are needed to refine our understanding of cottontail abundance and Golden Eagle reproduction. The relationship could change with dramatic increases in alternative prey and/or more pronounced or prolonged declines in cottontails.

Conservation Implications and Recommendations. To effectively predict Golden Eagle conservation challenges and manage landscapes to mitigate challenges in the changing landscapes of the western U.S., managers must understand factors important to eagles on local, as well as regional, scales. Not surprisingly, our results suggest that primary prey abundance, and ultimately availability, is a critical factor. At the local scale of northwestern Bighorn Basin, cottontails were the most critical prey resource during our study, and Golden Eagle reproductive rates were associated with cottontail abundance in a given year. Therefore, it would be helpful to understand habitat conditions important to cottontail abundance and availability to Golden Eagles, and to maintain or improve those conditions as possible under continuing landscape changes. Little information is available regarding specific habitat requirements of cottontails in the Bighorn Basin, but cottontails generally prefer habitats with plentiful grasses and forbs and access to shrubs and other sources of cover, including human-made structures (Bock et al. 2006). Cottontails tend to avoid landscapes dominated by significant livestock grazing, tilled agriculture, and suburban development (MacCracken and Hansen 1982, Mankin and Warner 1999, Litvaitis et al. 2003). Therefore, maintaining and enhancing mosaic landscapes that provide a mixture of cover and food, interspersed with some open areas providing Golden Eagle hunting opportunities, would help support both cottontail abundance and availability to eagles. Nonetheless, cottontail populations should be expected to exhibit population fluctuations, stimulating eagles to adjust diet and/or experience periodic declines in reproduction.

Therefore, land managers may be able to improve Golden Eagle reproduction by diversifying prey alternatives in the Bighorn Basin, particularly by enhancing conditions for white-tailed prairie dogs and white-tailed jackrabbits where ecologically feasible and socially acceptable. A relatively new, virally vectored, oral vaccine developed to prevent plague in wild prairie dogs (Abbott et al. 2012) holds promise as a tool to support prairie dog recovery in the Bighorn Basin. The status and population dynamics of white-tailed jackrabbits in northwestern Wyoming are poorly understood. Jackrabbits, like cottontails, may benefit from management directed at creating and maintaining

a heterogeneous mixture of native shrub and grassland habitats where possible (e.g., Marzluff et al. 1997). Shrub cover is particularly important for both jackrabbits and cottontails, and these species would likely be negatively affected by any large-scale disturbances that remove or reduce shrub cover and encourage cheatgrass expansion. Additionally, the legal status of the white-tailed jackrabbit as a predatory animal in Wyoming may warrant further review. Social acceptance is an important factor in reducing prairie dog and jackrabbit persecution and minimizing human disturbance near Golden Eagle nesting sites. We encourage the establishment of a collaborative partnership among managers, private landowners, scientists, policy-makers, and public education institutions and organizations to create a well-informed community that will support management efforts to conserve Golden Eagles and other wildlife in the Bighorn Basin.

Suggestions for Future Monitoring and Research. Long-term, intensive monitoring of Golden Eagle diet, reproduction, and prey abundance in the Bighorn Basin and other areas in the Western U.S. is needed to detect any negative population trends related to continued environmental change. Annual monitoring in perpetuity may not be feasible in each area, but we recommend that a future monitoring schedule be coordinated with a common protocol among areas and agencies and at least include several successive years per monitoring effort to account for normal fluctuations in Golden Eagle breeding performance related to prey fluctuations. We found that our study area in the Bighorn Basin supports a robust Golden Eagle breeding population, but cliff nests are especially difficult to locate in our study area amidst the shifting shadows, labyrinthine topography, and often challenging ground access. Nearly constant winds also complicate aerial surveys. Golden Eagle nesting territories in the Bighorn Basin are locally clustered around rugged topography, with vast areas devoid of nesting pairs. Olson et al. (2015) reported finding only one occupied Golden Eagle nest in seven sampled townships of the Bighorn Basin during statewide aerial surveys in April and May 2010–2011. However, these surveys covered less than 5% of our study area. Because Ferruginous Hawks (*Buteo regalis*) were the initial primary focus of their study, Olson et al. (2015) limited their surveys to townships likely to support these birds.

Our study provides strong evidence for a link between cottontail abundance and Golden Eagle reproduction in the northern Bighorn Basin region of the Greater Yellowstone Ecosystem. It also provides some insights into the dietary response of Golden Eagles in our area to declines in primary prey abundance and a valuable database of nesting territory locations and histories for future research. Additional studies are needed to better understand habitat features most important to cottontail abundance. Research is also needed to identify the cause(s) of leporid fluctuations in arid and semiarid environments, so that these fluctuations can be accurately predicted. We have helped lay the groundwork for expanded, design-based studies of Golden Eagle diet and population dynamics in relation to landscape composition and prey availability in the Bighorn Basin and beyond. For example, a comparison of Golden Eagle diet and nesting ecology between our Bighorn Basin study area and other areas of the Wyoming Basin ecoregion and with ongoing studies in nearby study areas spanning varied elevations and habitats in the Greater Yellowstone Ecosystem, would help provide a broader perspective on Golden Eagle reproduction and population dynamics among varying landscapes and prey regimens in this important region of the western U.S. Future studies should be designed as long-term programs, carefully coordinated with one another, to facilitate valid comparisons. Researchers should focus on identifying opportunities to prevent or mitigate negative effects of Golden Eagle habitat alteration and loss within and among diverse landscapes and involving different primary prey species and dynamics. It is important to understand dynamics of prey populations and how they respond to landscape changes. Additional information is especially needed on how increased recreation, habitat fragmentation, energy development, and changing climate affect Golden Eagles directly and indirectly by influencing vegetation and prey abundance and availability across varied landscapes.

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