SPATIAL AND TEMPORAL PATTERNS IN GOLDEN EAGLE DIETS IN THE WESTERN UNITED STATES, WITH IMPLICATIONS FOR CONSERVATION PLANNING

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ABSTRACT.—Detailed information on diets and predatory ecology of Golden Eagles (Aquila chrysaetos) is essential to prioritize prey species management and to develop landscape-specific conservation strategies, including mitigation of the effects of energy development across the western United States. We compiled published and unpublished data on Golden Eagle diets to (1) summarize available information on Golden Eagle diets in the western U.S., (2) compare diets among biogeographic provinces, and (3) discuss implications for conservation planning and future research. We analyzed 35 studies conducted during the breeding season at 45 locations from 1940–2015. Golden Eagle diet differed among western ecosystems. Lower dietary breadth was associated with desert and shrub-steppe ecosystems and higher breadth with mountain ranges and the Columbia Plateau. Correlations suggest that percentage of leporids in the diet is the factor driving overall diversity of prey and percentage of other prey groups in the diet of Golden Eagles. Leporids were the primary prey of breeding Golden Eagles in 78% of study areas, with sciurids reported as primary prey in 18% of study areas. During the nonbreeding season, Golden Eagles were most frequently recorded feeding on leporids and carrion. Golden Eagles can be described as both generalist and opportunistic predators; they can feed on a wide range of prey species but most frequently feed on abundant medium-sized prey species in a given habitat. Spatial variations in Golden Eagle diet likely reflect regional differences in prey community, whereas temporal trends likely reflect responses to long-term change in prey

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Golden Eagles (*Aquila chrysaetos*) are federally protected under both the Bald and Golden Eagle Protection Act and the Migratory Bird Treaty Act. These large raptors inhabit a wide range of environments year-round across the western United States (Kochert et al. 2002). The U.S. Fish and Wildlife Service (U.S.F.W.S.) released “Eagle Conservation Plan Guidance” for proposed wind energy developments because of the risk of injury and mortality of eagles from collisions with wind turbines (Pagel et al. 2013). One of the recommendations in this document is for compensatory mitigation actions that increase prey availability (U.S.F.W.S. 2013). Despite this recommendation, there is insufficient information on prey selection by Golden Eagles, the dynamics of prey populations, and the effects of changes in prey communities on Golden Eagle populations across the western U.S. to achieve such mitigation.

A thorough understanding of diets and predatory ecology of Golden Eagles is essential to prioritize prey species for management and develop conservation strategies, including mitigation measures. Across their range, Golden Eagles feed on a variety of vertebrate prey species. Local populations typically feed on medium-sized mammals ranging from 0.5–4.0 kg, as well as birds and, occasionally, reptiles (Olendorff 1976, Hunt et al. 1995, Kochert et al. 2002), and expand their diet when preferred prey species are scarce (Watson 2010). Steenhof and Kochert (1988) found that Golden Eagle diets were consistent with Schluter’s (1981) optimal diet theory, which predicts that (1) when prey are abundant, predators should eat 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 the more profitable prey; and (3) as prey abundance declines, diet diversity should increase.

Here, we review published literature, contemporary diet studies, and previously unpublished data, and we analyze factors that may drive Golden Eagle prey selection. Specifically, we: (1) summarize available information on Golden Eagle breeding- and nonbreeding-season diets in the western U.S.; (2) organize studies by biogeographic province to provide overviews, facilitate comparisons of regional diets by prey frequency and dietary breadth, and describe temporal patterns in diet for long-term study areas; and (3) discuss implications for conservation planning and opportunities for future research.

Methods

We limited our dietary review to the North American Golden Eagle (subspecies canadensis) within the conterminous western U.S. Sources were identified from previous diet reviews (Olendorff 1976, Kochert et al. 2002), searching for “Golden Eagle” and “diet” within raptor journal databases, and personal communication with contemporary researchers. We included quantified diet studies from peer-reviewed, government, academic, and unpublished sources. We classified diet studies as occurring during the breeding season when prey observations were collected throughout or at the end of the period when adults were feeding young at nests. We considered the rest of the year to be the nonbreeding season. We used geographic provinces defined by the Commission for Environmental Cooperation (CEC) to classify study areas by CEC Level II and III Ecoregions (CEC 2016).

Habitat change and declines in prey populations have raised concerns over status and temporal trends of Golden Eagle populations in the western U.S. (Kochert and Steenhof 2002, U.S.F.W.S. 2016). Because long-term diet information for Golden Eagles was not available for most areas of the West, we report here on temporal patterns in areas where modern diet studies were available for comparison to historical data.

Diet Study Methods. Methods for researching Golden Eagle diets included identification of prey based on uneaten remains at nests, regurgitated pellet analysis, photographic and digital image recording, direct observation, stomach content analysis, or some combination of these (Appendix 1). Analysis of prey remains and regurgitated pellets collected from nests during the breeding season was the most widely used technique, but this approach is likely biased toward prey items that eagles brought to nests to feed young. Analysis of prey remains may be biased toward larger prey whose heavier bones may persist longer in nests (Marti et al. 2007), but including pellets in the analysis should reduce this bias and also represent some prey items not brought to the nest due to size or other factors. Eagles rarely brought large prey items to the nest whole and more commonly delivered remains as either joined legs or the pelvic girdle with legs and lower back (Lockhart 1976). Remains of large ungulates at nests were classified as carrion, but the biomass consumed from carrion was unknown (Marr and Knight 1983). Analysis of prey remains and regurgitated pellets collected at nests underestimated total prey biomass compared to direct observation, but the two methods did not differ significantly with regard to percent biomass (Collopy 1983a) or percent frequency (Watson and Davies 2015). More prey species were detected by camera observations than by identification of prey remains (Longshore et al. 2017).

We used the percentage of identified prey individuals to draw comparisons among different studies and ecoregions because it was the most commonly reported statistic for Golden Eagle diet studies. We did not use prey biomass data, although this approach has been used to assess dietary energetics and the relative importance of larger prey species (Connolly et al. 1976, Lockhart 1976, Knight and Erickson 1978, Smith and Murphy 1979, U.S.D.I. 1979, Bloom and Hawks 1982, Collopy 1983a, MacLaren et al. 1988, Phillips et al. 1990, Hunt et al. 1995, Collins and Latta 2009, Losee et al. 2014, Watson and Davies 2015, Preston et al. 2017).

Statistical Analyses. We calculated dietary breadth (B) using Levins’ (1968) formula:

\[ B = 1 / \left( \sum_{i=1}^{n} p_i \right) \]

where \( p_i \) is the frequency of occurrence of prey species \( i \) at each study area. We used Spearman’s rank-order correlation (\( r_s \)) to assess relationships among reported values from breeding-season diet studies with a sample of prey individuals >35, with \( P \) values adjusted to \( q \) values to control the false discovery rate (Benjamini and Hochberg 1995). We described diet reported by Collins and Latta (2009), but excluded it from our analyses due to the
unique ecology of the Channel Islands. We performed analyses in software environment R (ver. 3.2.3, R Core Team 2013).

RESULTS

Diet During the Breeding Season. We assessed 35 studies conducted at 45 study areas (Fig. 1) from 1940–2015 that quantified diet of Golden Eagles during the breeding season. Jackrabbits (Lepus spp.) and cottontails (Sylvilagus spp.; Family Leporidae, hereafter leporids) made up more than half of all prey items identified for all breeding-season data sets across the western U.S. Ground squirrels (Otospermophilus spp., Urocitellus spp.), marmots (Marmota spp.) and prairie dogs (Cynomys spp.; Family Sciuridae, hereafter sciurids) were frequently identified prey, along with a diversity of bird species (Fig. 2). The percentage of prey groups in the diet overlapped

Figure 1. Locations of studies on Golden Eagle diet during the breeding season. Map labels (capital letters) correspond to the sources listed in Appendices 1 and 2. Map numbers correspond to CEC Level II Ecoregions (CEC 2016). Study locations were adjusted to be distinguishable at this scale.

Figure 2. Variation in the diet of Golden Eagles during the breeding season from 37 study areas in the western United States. Bold lines within boxes represent the median, edges are the first and third quartiles, whiskers contain 1.5 times the interquartile range, and circles are outliers.
greatly among CEC Level II Ecoregions. Generally there were higher numbers of leporids in desert ecoregions and higher numbers of ground squirrels in Mediterranean California (Fig. 3). Black-tailed jackrabbits (Lepus californicus) were reported as the most prevalent prey of Golden Eagles in the southwestern U.S., and white-tailed jackrabbits (Lepus townsendii) were more commonly found in Wyoming and Montana (Fig. 4). Dietary breadth varied from 1.36 to 12.27, with lower breadth associated with desert and shrub-steppe ecosystems and higher breadth in mountain ranges and the Columbia Plateau (Appendix 1).

Leporids were the most prevalent prey of Golden Eagles in 78% of study areas, with sciurids reported as the most prevalent prey in 18% of study areas (Appendix 2). Dietary breadth had a significant negative association with the proportion of leporids, and significant positive associations with sciurids, other mammals, and birds (Table 1). Leporids had significant negative associations with sciurids, other mammals, and birds. Collection year and study duration were not correlated with any prey groups, and the number of prey identified was significantly associated with study duration.

In the sections below, we present Golden Eagle breeding-season diets by prey group for CEC Level II Ecoregions (Table 2) and discuss frequently identified prey species, where “primary prey” refers to the most frequently identified prey in a study area. We also present temporal patterns in relation to habitat change and fluctuations in prey population densities for study areas with multiple sampling periods.

**Western Cordillera.** The Western Cordillera ecoregion includes the high elevation mountains and plateaus of the Rocky Mountains from northern New Mexico to Montana, and across the intermountain west to California, Oregon, and Washington. Diets of Golden Eagles in the Western Cordillera were more diverse than eagle diets in the adjacent Cold Deserts ecoregion (Table 2). In the Wasatch and Uinta Mountains of northern Utah, sciurids (primarily rock squirrels [Otospermophilus variegatus]) were the most frequently identified prey group from a large sample of prey remains in nests (n = 3859; Keller 2015), but in a smaller sample (n = 34) leporids were the primary prey (Arnell 1971). In the Southern

![Figure 3. Diet of Golden Eagles during the breeding season from 34 study areas in the western United States. The number of study areas included in each ecoregion are given in the legend. Bold lines within boxes represent the median, edges are the first and third quartiles, whiskers contain 1.5 times the interquartile range, and circles are outliers.](https://bioone.org/journals/Journal-of-Raptor-Research)
Primary Prey

- Black-tailed Jackrabbits
- White-tailed Jackrabbits
- Cottontails
- Leporids (unidentified spp.)
- Sciurids
- Other

CEC Level II Ecoregions

- 6.2 Western Cordillera
- 9.3 West Central Semi-Arid Prairies
- 9.4 South Central Semi-Arid Prairies
- 10.1 Cold Deserts
- 10.2 Warm Deserts
- 11.1 Mediterranean California
- 13.1 Upper Gila Mountains

Figure 4. Primary prey of Golden Eagles during the breeding season. Map labels correspond to the prey group identified most for each study area listed in Appendix 2. Map numbers correspond to CEC Level II Ecoregions (CEC 2016). Study locations were adjusted to be distinguishable at this scale.

Table 1. Spearman’s rank-order correlation (rₛ) values from breeding-season Golden Eagle diet studies (n = 37) in the western United States with a sample of prey remains >35. Dietary breadth (B) was calculated using Levins’ formula

\[ B = 1 / \sum_{i=1}^{n} p_i^2 \]

using the frequency (p_i) of prey species i’s occurrence among nest remains. The last year of a study was used for collection year, and study duration was number of years in which data were collected. Significant relationships are indicated by asterisks (***, p < 0.001; **, p < 0.01; *, p < 0.05).

<table>
<thead>
<tr>
<th>VARIABLE</th>
<th>LEPORIDS</th>
<th>SCIURIDS</th>
<th>OTHER MAMMALS</th>
<th>BIRDS</th>
<th>REPTILES</th>
<th>COLLECTION YEAR</th>
<th>STUDY DURATION</th>
<th>NO. OF PREY</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dietary breadth</td>
<td>***-0.702</td>
<td>*0.491</td>
<td>*0.465</td>
<td>**0.592</td>
<td>0.086</td>
<td>0.003</td>
<td>0.215</td>
<td>-0.008</td>
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<tr>
<td>Leporids</td>
<td>-</td>
<td>***-0.796</td>
<td>**-0.577</td>
<td>***-0.658</td>
<td>-0.212</td>
<td>-0.094</td>
<td>-0.08</td>
<td>0.113</td>
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<tr>
<td>Sciurids</td>
<td>-</td>
<td>-</td>
<td>0.333</td>
<td>0.217</td>
<td>-0.088</td>
<td>0.018</td>
<td>0.037</td>
<td>-0.052</td>
</tr>
<tr>
<td>Other mammals</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>0.279</td>
<td>-0.057</td>
<td>0.067</td>
<td>-0.191</td>
<td>-0.216</td>
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<tr>
<td>Birds</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>0.403</td>
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<td>0.106</td>
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<tr>
<td>Reptiles</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>0.335</td>
<td>0.318</td>
<td>0.176</td>
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<tr>
<td>Collection year</td>
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<td>-</td>
<td>-</td>
<td>-</td>
<td>***0.771</td>
</tr>
</tbody>
</table>
Rockies, leporids were identified most frequently among prey remains collected from three nests, and dietary breadth was greater than in the adjacent Wyoming Basin (Schmalzried 1976). Eagles nesting in the forested mountains likely used adjacent shrubland habitat for foraging on leporids. In the North Cascades, mountain beaver (Aplodontia rufa) remains were found at Golden Eagle nests (Servheen 1978, Bruce et al. 1982), and made up 23 of 38 observed prey deliveries during the 2015 breeding season (L. Hansen pers. comm.).

West Central Semi-Arid Prairies. The West Central Semi-Arid Prairies ecoregion includes the western Great Plains from northeastern Wyoming to south-eastern Montana. In the Northwestern Great Plains of Montana, the contents of 51 stomachs from Golden Eagles killed during a bounty in March 1948 included white-tailed jackrabbits and pronghorn (Antilocapra americana) as the most frequently eaten species (Woodgerd 1952). The researchers believed it was likely that at least some pronghorn and domestic sheep (Ovis aries) were eaten as carrion. In the Northwestern Great Plains near Livingston, Montana, studies from the 1960s found Golden Eagles most frequently fed on white-tailed jackrabbits and cottontails (McGahan 1968, Reynolds 1969). A contemporary study in this same area identified pronghorn as the primary prey (R. Grandall and C. Preston unpubl. data). In the Northwestern Great Plains of North Dakota, black-tailed prairie dogs (Cynomys ludovicianus) and cottontails were the most commonly identified prey items of nesting Golden Eagles (Coyle 2008) and constituted the highest prey biomass along the Montana–Wyoming border (Phillips et al. 1990). Prairie dogs were not uniformly distributed, and the localized nature of their colonies likely precluded some nesting eagles from using them as prey. However, cottontails were widely distributed throughout the study area and overall prey abundance correlated with increased eagle numbers in the study area between 1983–1985.

South Central Semi-Arid Prairies. The South Central Semi-Arid Prairies ecoregion includes the western Great Plains from northern Texas to southeastern Wyoming. In the High Plains of northern Colorado, Golden Eagles fed primarily on leporids, despite low cottontail abundance and high abundance of prairie dogs (Arnold 1954). On the Front Range of the Rocky Mountains in New Mexico, Colorado, and Wyoming, more than 75% of prey remains in nests were leporids, and the second most abundant were prairie dogs (Boeker and Ray 1971). In the Southwestern Tablelands of New Mexico, Golden Eagle diet was mostly leporids, particularly black-tailed jackrabbits (Mollhagen et al. 1972). In the Moreno Valley, New Mexico, the number of observed Golden Eagles declined during a sylvatic plague (Yersinia pestis) event among Gunnison’s prairie dogs (Cynomys gunnisoni), suggesting that the absence of prairie dogs may have resulted in insufficient food resources for nesting eagles in this area (Cully 1991).
Cold Deserts. The Cold Deserts ecoregion includes the sagebrush steppe ecosystems of high elevation intermountain basins and plateaus from northern New Mexico to eastern Washington. In the Columbia Plateau of Washington, yellow-bellied marmots (Marmota flaviventris) were the primary prey of nesting Golden Eagles, both by frequency in the diet and biomass (Knight and Erickson 1978, Marr and Knight 1983, Watson and Davies 2015). The number of land-cover types within a 2-km radius of Golden Eagle nest sites was not associated with the number of prey species or prey items, suggesting greater habitat diversity at this scale did not increase dietary breadth (Marr and Knight 1983).

In the Northern Basin and Range of Oregon, black-tailed jackrabbits were the primary prey species of Golden Eagles, and the relative importance of Nuttall’s cottontails (Sylvilagus nuttallii) and ducks (Anas spp.) differed between studies (Hickman 1968, Groves 1940 [reported in Thompson et al. 1982]). We included the Butte Valley of northern California south of Klamath Falls, Oregon, in the Northern Basin and Range for our diet analysis due to its ecological similarity, although it is designated as Eastern Cascades Slopes and Foothills by the CEC (2016). Golden Eagle feeding habits in the Butte Valley were unusual due to the proximity of the nesting territories to a high density of Belding’s ground squirrels (Urocitellus beldingi) associated with alfalfa fields. Belding’s ground squirrels were the primary prey from 1986–1995 (B. Woodbridge unpubl. data), and observations through 2015 indicate that they remain an important prey species of Golden Eagles in this area (B. Woodbridge pers. comm.).

In the Wyoming Basin, leporids were identified as the primary prey group, with primary prey species being either cottontails (Arnold 1954, Millsap 1978, Preston et al. 2017) or white-tailed jackrabbits (Schmalzried 1976). In southeastern Wyoming, sciruids were the most frequent prey, but leporids comprised the highest biomass and there was a high between-year difference in dietary breadth (MacLaren et al. 1988). In the Bighorn Basin of northwestern Wyoming, Golden Eagles overwhelmingly preyed on cottontails in periods of both low and high cottontail abundance (Preston et al. 2017). Scuruids and jackrabbits were scarce in the Bighorn Basin during this study, in contrast to some other areas of Wyoming and other intermountain basin study areas.

In the Central Great Basin of Utah, black-tailed jackrabbits were the primary prey of Golden Eagles (Arnell 1971, Smith and Murphy 1979, AMEC 2015, Keller 2015). The largest single dietary dataset in the U.S. was initiated in central Utah in 1970 and comprised 150 prey species identified from 27,523 individual prey at 1621 nests over 45 yr (Keller 2015). Overall, diet was composed of mostly leporids, plus a high diversity of bird species. Dietary breadth was lower in desert territories than mountain territories due to the predominance of black-tailed jackrabbits in and around the desert territories.

Multiple studies on diets of Golden Eagles have taken place in the Snake River Plain in southwestern Idaho, largely due to support for research in the Morley Nelson Snake River Birds of Prey National Conservation Area (NCA). In the NCA, the most common prey items used by Golden Eagles were black-tailed jackrabbits (Hickman 1968, Beecham 1970, Kochert 1972, K. Steenhof and M. Kochert unpubl. data [includes data from U.S.D.I. 1979, Collopy 1983a, 1983b, and Steenhof and Kochert 1988]).

In the Colorado Plateau, Golden Eagle prey remains at nests comprised mainly black-tailed jackrabbits (in the Navajo Nation), and cottontails (in the Jicarilla Nation; Stahlecker et al. 2009). In the Arizona/New Mexico Plateau, black-tailed jackrabbits were the primary prey and Gunnison’s prairie dogs (Cynomys gunnisoni) were also prevalent (Mollhagen et al. 1972). In northern Arizona, black-tailed jackrabbits were the primary prey found in Golden Eagle nests (Losee et al. 2014), with fewer prairie dogs compared to nests in a nearby study area (Stahlecker et al. 2009).

Warm Deserts. The Warm Deserts ecoregion includes the arid region from southeastern California to the Trans-Pecos region of Texas. In the Mojave Basin and Range of southern Nevada and California, leporids were the primary prey of Golden Eagles (Longshore et al. 2017). Reptiles composed a higher percentage of Golden Eagle diet in the Mojave Desert than in any other ecoregion (Appendix 1), and included primarily chuckwalla (Sceloporus ater), gopher snake (Pituophis catenifer), and desert tortoise (Gopherus agassizii).

In an area of central Arizona overlapping the Arizona/New Mexico Mountains, Arizona/New Mexico Plateau, and Sonoran Desert, leporids were the primary prey group of Golden Eagles (Millsap 1981, Eakle and Grubb 1986). One study reported the
highest proportion of leporid remains in nests of all analyzed studies (Millsap 1981, Appendix 1).

In the Chihuahuan Desert, black-tailed jackrabbits were the primary prey of Golden Eagles (Mollhagen et al. 1972, Lockhart 1976). However, a comparison of prey remains at Golden Eagle nests with prey recorded using time-lapse photography in the Trans-Pecos region of Texas showed that cottontails were underrepresented among prey remains compared to photography (Lockhart 1976).

Mediterranean California. The Mediterranean California ecoregion includes the mixed chaparral, grassland, and oak woodlands of California bordered by the Sierra Nevada and deserts to the east and the Pacific Ocean to the west. Diets of Golden Eagles in the California Coastal Sage, Chaparral, and Oak Woodlands differed greatly from those in other regions (Fig. 3). In the inner coastal ranges of California, California ground squirrels (Otospermophilus beecheyi) were the primary prey when nests were in rugged and wooded terrain, and jackrabbits were primary prey in more open and rolling terrain (Carnie 1954). In the Altamont Pass Wind Resource Area of California, nesting Golden Eagles primarily fed on California ground squirrels by percentage and biomass (Hunt et al. 1995). In San Diego County, Golden Eagle nests contained squirrels (ground and tree), leporids, water birds, and a variety of other mammals (Dixon 1937). In one nest near Hopland, California, prey items included high numbers of gray squirrels (Sciurus griseus) and stillborn or newborn deer (Odocoileus sp.; Connolly et al. 1976).

On the Channel Islands, Golden Eagles exhibited distinctive feeding habits and unique prey species compared to other areas (Collins and Latta 2009, Appendix 2). The Channel Islands lacked leporid and sciurid species, and nesting Golden Eagles preyed on a diverse range of bird and mammal species. Golden Eagles were translocated off the islands starting in 1999 to mitigate effects of predation on island foxes (Urocyon littoralis; Latta et al. 2003).

Upper Gila Mountains. The Upper Gila Mountains ecoregion includes the forested hills, scrublands, and grassland valleys of Arizona and New Mexico. In the Arizona/New Mexico Mountains, nesting locations of Golden Eagles were surveyed in response to residents’ claims of eagle predation on lambs. Evidence of sheep and goat (Capra spp.) remains were found at nests in one study area, but the most frequent prey items were jackrabbits and cottontails (Mollhagen et al. 1972).

Temporal Patterns in Breeding-season Diet. In the Northwestern Great Plains near Livingston, Montana (West Central Semi-Arid Prairie ecoregion), the percentages of white-tailed jackrabbits and cottontails in diets of Golden Eagles were higher in 1962–1964 (McGahan 1968) than in 1965–1967 (Reynolds 1969), and dietary breadth increased between those time periods. This change corresponded with widespread decreases in leporids as evident in field observations and a 70% decrease in commercial jackrabbit harvests between study periods (Reynolds 1969). A smaller sample (n = 68) of prey remains in 2014 demonstrated this ongoing trend, with a lower percentage of white-tailed jackrabbits, higher dietary breadth, and a range-wide high percentage of pronghorn (25.4%; R. Crandall and C. Preston unpubl. data).

In the Columbia Plateau of eastern Oregon (Cold Deserts ecoregion), Watson and Davies (2015) compared Golden Eagle diets determined between 2007 and 2013 to those reported for a study conducted 30 yr earlier in the same area (Marr and Knight 1983). Watson and Davies (2015) found evidence for a dietary shift away from sciurids and phasianids (family Phasianidae) and toward coyote pups (Canis latrans) and deer fawns (Odocoileus sp.). This dietary shift coincided with decreased populations of Townsend’s ground squirrel (Urocitellus townsendii townsendii), Washington ground squirrel (Urocitellus washingtoni), and both species of jackrabbit, which was consistent with conversion of shrub-steppe habitat to agriculture. Our analysis of data from Watson and Davies (2015) found Golden Eagles in this area had the highest dietary breadth compared to all other studies (Appendix 1), which resulted from a high diversity of avian prey in the diets of these eagles.

In the Snake River Plain of southwestern Idaho (also Cold Deserts ecoregion), frequency of predation on jackrabbits was directly proportional to their abundance, but the rates at which alternative prey species were taken were unrelated to their abundances (Steenhof and Kochert 1988). Instead, Golden Eagle use of alternative prey among years varied inversely with the abundance of their primary prey, jackrabbits. Thus, dietary breadth was inversely correlated with jackrabbit density, not with squirrel or total prey density (Steenhof and Kochert 1988). Selectivity calculations indicated that Golden Eagles had a strong preference for black-tailed jackrabbits over Plute ground squirrels (Urocitellus mollis; formerly Townsend’s ground squirrels Spermophilus
towsendii; \( S = 0.92 \)), and preferred Piute ground squirrels over all other prey combined (\( S = 0.85 \); Steenhof and Kochert 1988). The high number of Piute ground squirrels and low number of black-tailed jackrabbits observed among 18 kills by radioed eagles (Marzluff et al. 1997) may be related to decreases in abundance of jackrabbits in the NCA (Steenhof et al. 1997) following extensive wildfires (Kochert et al. 1999). Breadth of Golden Eagle diet increased after wildfires, and prey included more birds and fewer black-tailed jackrabbits and cottontails compared to pre-burn years (Heath and Kochert 2016). Similar results were obtained from a study in the Central Basin and Range of Utah based on identified prey remains at Golden Eagle nests from 1970–2015. Keller (2015) found that the percentage of rock squirrels in the diet was higher in years when the percentage of jackrabbits was lower.

**Diet During the Nonbreeding Season.** Information on the diet of Golden Eagles during the nonbreeding season is far more limited than that available for the breeding season. This is largely due to the difficulty in recording feeding events dispersed across a larger landscape. Field observations of feeding may be biased toward feeding that occurs near accessible roads or other places humans frequent. Prey use varied greatly among territorial pairs of Golden Eagles in northeastern Wyoming (Hayden 1984) and southwestern Idaho (Marzluff et al. 1997). Available research indicates that leporids are an important food source and that feeding on carrion may be substantial in some areas (Table 3). The amount that Golden Eagles feed on carrion might be influenced by the severity of winter weather and local availability of other food (Woodgerd 1952, Hayden 1984). Craig and Craig (1984) hypothesized that peak numbers of roosting Golden Eagles were attracted to an abundance of black-tailed jackrabbits in 1982 on the upper Snake River Plain.

Observations in the Wyoming Basin confirmed that Golden Eagles can kill young (Arnold 1954, Goodwin 1977) and adult pronghorn (Deblinger and Alldredge 1996). Although predation on young pronghorn can be common in some areas (C. Preston and R. Crandall unpubl. data, Preston et al. 2017), predation on adults is likely rare. Golden Eagles in the Central California Valley and Klamath Basin attacked Cackling Geese (Branta hutchinsii) more than Ross’ Geese (Chen rossii), most likely because Cackling Geese often grazed in pastures. Golden Eagles also likely fed on hunter-killed geese as carrion (McWilliams et al. 1994).

**Discussion**

**Predatory Ecology of Golden Eagles.** Golden Eagles can be described as both generalist and opportunistic predators; they can feed on a wide range of prey species, but most frequently feed on abundant medium-sized prey species in a given habitat. Reports of primary prey other than jackrabbits in the diet may indicate depressed or absent populations of jackrabbits in those ecoregions. Correlation analyses support the inference that the percentage of leporids in the diet is the driving factor for overall diversity of prey and percentage of other prey groups in the diet of Golden Eagles (Table 1). Spatial variations in Golden Eagle diet likely reflect among-region differences in prey community, whereas temporal trends likely reflect responses to long-term change in prey populations.

Golden Eagles exhibited the capacity for dietary shifts in response to changing abundance in primary prey species (MacLaren et al. 1988, Steenhof and Kochert 1988, Keller 2015, Watson and Davies 2015, Preston et al. 2017). This inference could be better supported using information on prey availability. Many researchers assumed Golden Eagles used prey that was locally abundant and available, but did not assess prey availability (e.g., Knight and Erickson 1978, Bloom and Hawks 1982, Marr and Knight 1983, Phillips et al. 1990, McWilliams et al. 1994, Marzluff et al. 1997, Stahlecker et al. 2009). Prey availability depends on both prey density and environmental features that influence prey accessibility, such as vegetative cover (Preston 1990).

The occurrence of leporids and large-bodied sciurids in the breeding-season diet of Golden Eagles (Appendix 2) was consistent with Watson’s (2010) generalization that Golden Eagles prefer medium-sized prey (0.5–4.0 kg). The abundance and availability of prey in the preferred size range may influence Golden Eagle distribution at continent-wide scales (Schweiger et al. 2015). The exception was the high percentage of smaller-bodied ground squirrels in the Northern Basin and Range (B. Woodbridge unpubl. data) and Snake River Plain (Heath and Kochert 2016).

**Influence of Prey Quality on Golden Eagle Reproduction.** Prey abundance and dietary shifts of Golden Eagles affect reproduction and therefore may have significant population effects when projected on a regional scale. Jackrabbit density in the
Table 3. Golden Eagle nonbreeding-season diet in the western United States. No. of prey are the minimum number of individuals identified, and prey groups are given as the percentage in which they occurred among identified prey items. Collection methods included identification of prey remains from pellets (PE) and stomach contents (SC), or direct observation including the use of radio transmitters (DO).

<table>
<thead>
<tr>
<th>Ecoregion Level II</th>
<th>Ecoregion Level III</th>
<th>Sampling Period</th>
<th>No. of Prey</th>
<th>Carrion (%)</th>
<th>Leporids (%)</th>
<th>Sciurids (%)</th>
<th>Other Mammals (%)</th>
<th>Birds (%)</th>
<th>Method</th>
<th>Source</th>
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<tr>
<td>Western Cordillera and Cold Deserts</td>
<td>North Cascades and Columbia Plateau</td>
<td>September–March 1974–1981</td>
<td>40</td>
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<td>5.0</td>
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</tr>
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<td>Northwestern Great Plains</td>
<td>March 1948</td>
<td>65</td>
<td>51.0</td>
<td>4.6</td>
<td>36.4</td>
<td>6.0</td>
<td>SC</td>
<td>Woodgerd (1952)</td>
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<td>Cold Deserts</td>
<td>Central Great Basin</td>
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<td>382</td>
<td>1.0</td>
<td>96.6</td>
<td>0.0</td>
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<td>1.0</td>
<td>PE²</td>
<td>Edwards (1969)</td>
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<td>Cold Deserts</td>
<td>Snake River Plain</td>
<td>Varied 1992–1994</td>
<td>29</td>
<td>44.8</td>
<td>24.1</td>
<td>6.9</td>
<td>17.0</td>
<td>DO</td>
<td>Marzluff et al. (1997)</td>
<td></td>
</tr>
<tr>
<td>Multiple (western U.S. and Alaska)</td>
<td>Multiple</td>
<td>November–March early–mid–1990s</td>
<td>74</td>
<td>23.0</td>
<td>50.0</td>
<td>4.1</td>
<td>92.0</td>
<td>8.0</td>
<td>SC</td>
<td>Arnold (1954)</td>
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</table>

* Sample size is the number of identified prey remains from pellets. Each occurrence of prey remains in a pellet was counted as a single individual.

* Pellets were collected from roosting areas used by both Golden Eagles and Bald Eagles (Haliaeetus leucocephalus) and were not distinguished by species.
Sage-Grouse (Centrocercus urophasianus) during years in which primary prey populations decrease. Golden Eagles fed on Greater Sage-Grouse during the breeding season, but at relatively low frequencies compared to other prey species (Appendix 2). It is therefore possible that conservation of sagebrush-steppe habitats could be mutually beneficial to both Golden Eagles and Greater Sage-Grouse.

**Suggestions for Future Research.** Future studies on Golden Eagle diet would benefit from using design-based sampling, as opposed to convenience sampling, along with larger sample sizes that capture variations in frequency of prey over a multiyear time period. Diet studies should use the nest as the sampling unit, not the pellet or prey item, to reduce pseudoreplication and allow for more robust statistical inference. Before-after-control-impact (BACI) design could be used to assess the potential effects of prey enhancement protocols, such as prairie dog relocation and plague mitigation, on Golden Eagle prey selection and productivity. Incorporating prey management into conservation planning and considering actions that support a diverse prey community could buffer against periodic fluctuations in leporid population density (Simes et al. 2015).

**Implications for Conservation.** Knowledge of Golden Eagle diets is important for informing landscape conservation across the West. Marzluff et al. (1997) recommended managing for shrub habitat interspersed with grassland to support jackrabbits in areas where foraging eagles focus their efforts. This approach could be applied to many sagebrush-steppe habitats where habitat change threatens Golden Eagle prey populations. For example, efforts to recover sagebrush following cheatgrass (Bromus tectorum) invasion are likely to benefit the recovery of jackrabbit populations (Knick and Dyer 1997).

Hagen (2011) raised concern over the potential for increased predation by Golden Eagles on Greater Sage-Grouse (Centrocercus urophasianus) during years in which primary prey populations decrease. Golden Eagles fed on Greater Sage-Grouse during the breeding season, but at relatively low frequencies compared to other prey species (Appendix 2). It is therefore possible that conservation of sagebrush-steppe habitats could be mutually beneficial to both Golden Eagles and Greater Sage-Grouse.

**Solutions to Future Research.** Studies on breeding-season diets of Golden Eagles are lacking or outdated in large areas of the West. Examples include the Central Great Basin throughout most of Nevada, and areas of central and southern Wyoming where wind resource development coincides with breeding and winter habitat for Golden Eagles (Tack and Fedy 2015). Far less information is available on diets of nonbreeding Golden Eagles, yet this information may be critical to understanding overwinter survival of adults and subadults. Carrion is likely an important food source for Golden Eagles during winter, and this hypothesis could be tested using a radiotelemetry protocol to observe eagle feeding behavior.

**Acknowledgments**

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**Literature Cited**


Benjamin, Y. and Y. Hochberg. 1995. Controlling the false discovery rate: a practical and powerful approach to


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Appendix 1. Summary of Golden Eagle breeding-season diets in the western United States. Sample sizes are the minimum number of individuals identified. Prey groups are presented as the frequency in which they occurred among identified food items. Dietary breadth (B) was calculated using Levins’ formula $B = 1/\sum b_i^2$, using the frequency ($p_i$) of prey species $i$’s occurrence among nest remains. Data collection methods were categorized as identification of prey remains in nests and pellets (PR), or direct observation including photography (DO).

<table>
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<th>MAP LABEL</th>
<th>ECOREGION LEVEL II</th>
<th>STUDY YEARS</th>
<th>NO. OF NEST VISITS (NO. OF NESTS)</th>
<th>NO. OF PREY</th>
<th>LEPORIDS (%)</th>
<th>SCIURIDS (%)</th>
<th>OTHER MAMMALS (%)</th>
<th>BIRDS (%)</th>
<th>REPTILES (%)</th>
<th>FISH (%)</th>
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<th>METHOD</th>
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*a Total for both study areas (Arnell 1971).

*b Reported as percent biomass.

*c From Collins and Latta (2006).

*d From MacLaren et al. (1988).


*f No. of prey was calculated as a sum. Proportion of prey groups and dietary breadth were calculated as means.
Appendix 2  Top primary, secondary, and tertiary prey species of Golden Eagles during the breeding season in the Western United States.

<table>
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<th>Ecoregion Level II</th>
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<th>Prey 2 (Species)</th>
<th>Prey 3 (%)</th>
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<td>Cottontail (<em>Sylvilagus spp.</em>)</td>
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<td>Rock squirrel (<em>Otocospilus variegatus</em>)</td>
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<td>Yellow-bellied marmot (<em>Marmota flaviventris</em>)</td>
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<td>White-tailed jackrabbit (<em>Lepus townsendii</em>)</td>
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<td>Mediterranean California</td>
<td>68.7</td>
<td>California ground squirrel</td>
<td>4.4</td>
<td>Unidentified Snakes</td>
<td>2.9</td>
<td>Black-tailed jackrabbit</td>
<td>Hunt et al. (1995)</td>
</tr>
<tr>
<td>SS</td>
<td>Upper Gila Mountains</td>
<td>52.4</td>
<td>Black-tailed jackrabbit</td>
<td>23.2</td>
<td>Cottontail</td>
<td>8.3</td>
<td>Sheep and goat</td>
<td>Mollhagen et al. (1972)</td>
</tr>
</tbody>
</table>