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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 We compiled published and unpublished data on Golden Eagle diets to (1) summarize available information on Golden Eagle diets in the western U.S., (2) compare diets among biogeographic provinces,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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populations. Evidence suggests dietary shifts from traditional (leporid) prey can have adverse effects on Golden Eagle reproductive rates. Land management practices that support or restore shrub-steppe ecosystem diversity should benefit Golden Eagles. More information is needed on nonbreeding-season diet to determine what food resources, such as carrion, are important for overwinter survival.

KEY WORDS: *Golden Eagle*; Aquila chrysaetos; *diet*; *prey remains*.

PATRONES ESPACIALES Y TEMPORALES EN LA DIETA DE *AQUILA CHRYSAETOS* EN EL OESTE DE LOS ESTADOS UNIDOS, CON IMPLICACIONES PARA LA PLANIFICACIÓN DE LA CONSERVACIÓN

RESUMEN.—La información detallada sobre la dieta y la ecología trófica de *Aquila chrysaetos* es esencial para priorizar el manejo de las especies presa y para desarrollar estrategias específicas de conservación del paisaje, incluyendo la mitigación de los efectos de las iniciativas de desarrollo energético a través del oeste de los Estados Unidos. Recopilamos los datos publicados e inéditos sobre la dieta de *A. chrysaetos* para (1) compendiar la información disponible sobre la dieta de la especie en el oeste de los Estados Unidos, (2) comparar las dietas entre provincias biogeográficas y (3) discutir las implicaciones para la planificación de la conservación y para investigaciones futuras. Analizamos 35 estudios realizados durante la época reproductiva en 45 sitios entre 1940 y 2015. La dieta de *A. chrysaetos* difirió entre los ecosistemas del oeste. Una menor amplitud de la dieta se asoció con los ecosistemas del desierto y de la estepa arbustiva y una amplitud mayor con las cadenas montañosas y la Planicie de Columbia. Las correlaciones sugieren que el porcentaje de lepóridos en la dieta es el factor que impulsa la diversidad total de presas y el porcentaje de otros grupos de presas en la dieta de *A. chrysaetos*. Los lepóridos fueron la presa principal de los individuos reproductores de *A. chrysaetos* en el 78% de las áreas de estudio, y los esciúridos fueron la presa principal en el 18% de las áreas de estudio. Durante la época no reproductora, *A. chrysaetos* fue registrada alimentándose con mayor frecuencia de lepóridos y carroña. *A. chrysaetos* puede ser descrita como un depredador generalista y oportunista; puede alimentarse de un amplio rango de especies presa pero se alimenta con mayor frecuencia de las especies presa de tamaño mediano que son abundantes en un hábitat dado. Las variaciones espaciales en la dieta de *A. chrysaetos* probablemente reflejan las respuestas a los cambios a largo plazo en las poblaciones de sus presas. Las pruebas sugieren que los cambios en la dieta de presas tradicionales (lepóridos) pueden tener efectos adversos en las tasas reproductivas de *A. chrysaetos*. Las prácticas de manejo del suelo que apoyen o restauren la diversidad del ecosistema de estepa arbustiva deberían beneficiar a *A. chrysaetos*. Se necesita mayor información sobre la dieta en la época no reproductora para determinar qué fuentes de alimento, tales como la carroña, son importantes para la supervivencia invernal.

[Traducción del equipo editorial]

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:

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

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

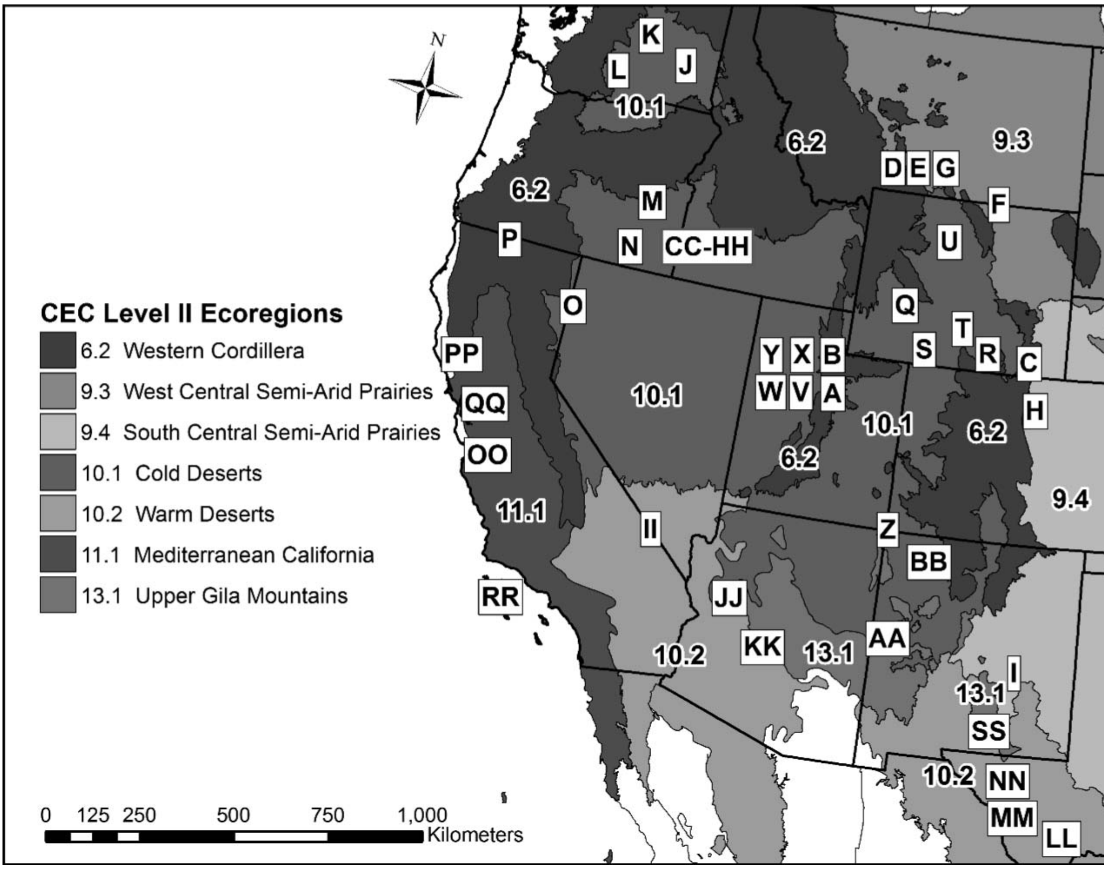

Figure 1. Locations of studies on Golden Eagle diet during the breeding season. Map labels (capital letters) correspond to the sources listed in Appendices 1 and 2. Map numbers correspond to CEC Level II Ecoregions (CEC 2016). Study locations were adjusted to be distinguishable at this scale.

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

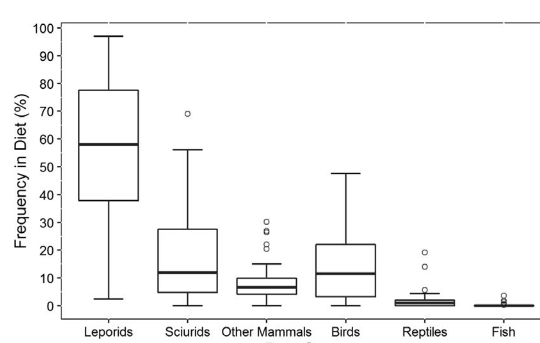

Figure 2. Variation in the diet of Golden Eagles during the breeding season from 37 study areas in the western United States. Bold lines within boxes represent the median, edges are the first and third quartiles, whiskers contain 1.5 times the interquartile range, and circles are outliers.

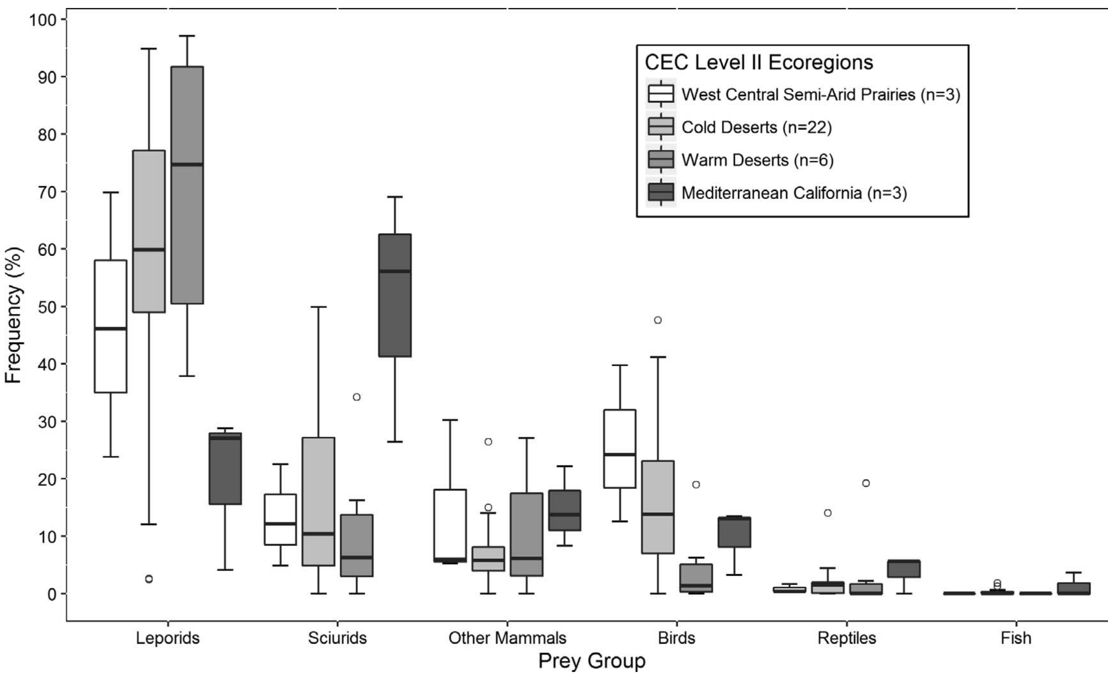

Figure 3. Diet of Golden Eagles during the breeding season from 34 study areas in the western United States. The number of study areas included in each ecoregion are given in the legend. Bold lines within boxes represent the median, edges are the first and third quartiles, whiskers contain 1.5 times the interquartile range, and circles are outliers.

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

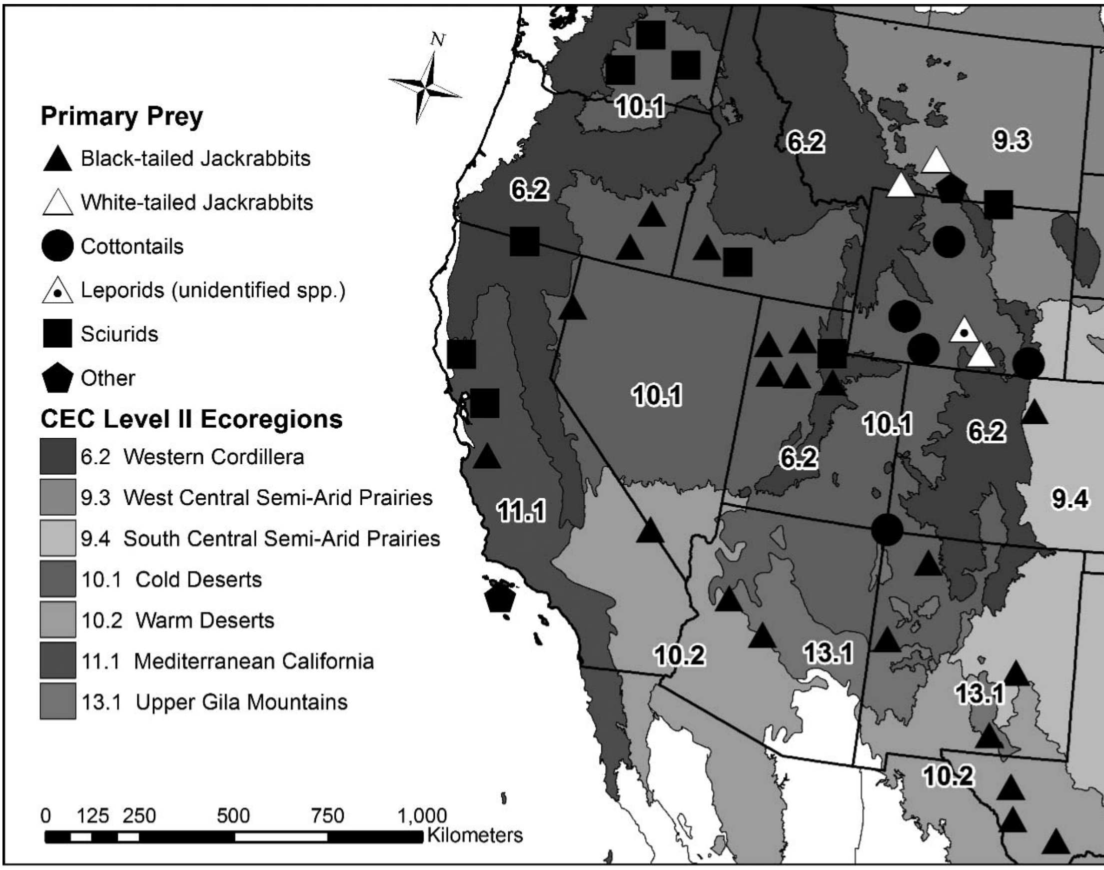

Figure 4. Primary prey of Golden Eagles during the breeding season. Map labels correspond to the prey group identified most for each study area listed in Appendix 2. Map numbers correspond to CEC Level II Ecoregions (CEC 2016). Study locations were adjusted to be distinguishable at this scale.

Table 1. Spearman's rank-order correlation (r_s) 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 (*** $q < 0.001$; ** $q < 0.01$; * $q < 0.05$).

Variable	Leporids	Sciurids	Other Mammals	Birds	Reptiles	Collection Year	Study Duration	No. of Prey
Dietary breadth	***−0.702	*0.491	*0.465	**0.592	0.086	0.003	0.215	−0.008
Leporids	–	***−0.796	**−0.577	***−0.658	−0.212	−0.094	−0.08	0.113
Sciurids	–	–	0.333	0.217	−0.088	0.018	0.037	−0.052
Other mammals	–	–	–	0.279	−0.057	0.067	−0.191	−0.216
Birds	–	–	–	–	0.403	0.121	0.333	0.106
Reptiles	–	–	–	–	–	0.335	0.318	0.176
Collection year	–	–	–	–	–	–	0.304	0.144
Study duration	–	–	–	–	–	–	–	***0.771

Table 2. Golden Eagle breeding-season diet in the western United States summarized by CEC Level II Ecoregions. Number of prey is the minimum number of individuals identified. Prey groups are given as the average percentage in which they occurred among identified prey items. 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.

Ecoregion Level II	No. of Study Areas	No. of Prey[a]	Leporids (%)	Sciurids (%)	Other Mammals (%)	Birds (%)	Reptiles (%)	Fish (%)	Dietary Breadth
Western Cordillera	1	3859	24.2	43.3	9.6	22.0	0.80	0.0	8.37
West Central Semi-Arid Prairies[b]	3	2052	46.6	13.1	13.8	25.5	0.8	0	5.80
South Central Semi-Arid Prairies	1	200	82.5	10.0	7.5	0	0	0	2.44
Cold Deserts	22	36,641	57.4	18.0	6.9	16.3	1.9	0.2	3.90
Warm Deserts	6	1790	70.7	10.9	10.4	4.6	3.6	0	2.94
Mediterranean California[c]	3	904	20.0	50.5	14.7	9.9	3.7	1.2	3.51
Upper Gila Mountains	1	336	75.6	11.9	12.5	0	0	0	2.92

[a] No. of prey was calculated as a sum. Proportion of prey groups and dietary breadth were calculated as means.
[b] Phillips et al. (1990) was excluded because frequency was reported as biomass.
[c] Collins and Latta (2009) was excluded because the Channel Islands are a unique ecosystem that is not representative of those found on the California mainland.

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 southeastern 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. Crandall 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, sciurids 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). Sciurids 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 (*Sauromalus 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 depredation 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 Piute ground squirrels (*Urocitellus mollis*; formerly Townsend's ground squirrels *Spermophilus* *townsendii*; 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. 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).

Ecoregion Level II	Ecoregion Level III	Sampling Period	No. of Prey	Carrion (%)	Leporids (%)	Sciurids (%)	Other Mammals (%)	Birds (%)	Method	Source
Western Cordillera and Cold Deserts	North Cascades and Columbia Plateau	September–March 1974–1981	40	90.0	5.0	0.0	87.5	7.5	DO	Marr and Knight (1983)
West Central Semi-Arid Prairies	Northwestern Great Plains	March 1948	65		51.0	4.6	36.4	6.0	SC	Woodgerd (1952)
West Central Semi-Arid Prairies	Northwestern Great Plains	November–April 1979–1981	191[a]		46.1	19.9	27.7	6.3	PE	Hayden (1984)
Cold Deserts	Central Great Basin	January–April 1966–1969	382[b]	1.0	96.6	0	1.6	1.0	PE[b]	Edwards (1969)
Cold Deserts	Snake River Plain	Varied 1992–1994	29		44.8	24.1	6.9	17.0	DO	Marzluff et al. (1997)
Multiple (western U.S. and Alaska)	Multiple	November–March early–mid–1900s	74	23.0	50.0	4.1	92.0	8.0	SC	Arnold (1954)

[a] 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.
[b] Pellets were collected from roosting areas used by both Golden Eagles and Bald Eagles (*Haliaeetus leucocephalus*) and were not distinguished by species.

Snake River Plain was strongly related to reproductive parameters of Golden Eagles, including hatch date, percent of nesting pairs laying eggs, percent of laying pairs successful, brood size at fledging, and number fledged per pair (Steenhof et al. 1997). Similarly, leporids positively affected Golden Eagle reproductive rates in Oregon (Thompson et al. 1982), Montana (Reynolds 1969), and Wyoming (Millsap 1978, Oakleaf et al. 2014, Preston et al. 2017).

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.

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).

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.

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LITERATURE CITED

AMEC ENVIRONMENT AND INFRASTRUCTURE. 2015. Final summary report for Golden Eagle activity on Air Force ranges in the western United States. Prepared for Air Force Civil Engineer Center. Under contract to U.S. Army Corps of Engineers. San Diego, CA U.S.A.

ARNELL, W.B. 1971. Prey utilization by nesting Golden Eagles (*Aquila chrysaetos*) in central Utah. M.S. thesis. Brigham Young Univ., Provo, UT U.S.A.

ARNOLD, L.W. 1954. The Golden Eagle and its economic status. U.S. Fish and Wildlife Circular 27. Pages 1–35 *in* E.R. Kalmbach, R.H. Imler, and L.W. Arnold [EDS.], The American eagles and their economic status. U.S.D.I. Fish and Wildlife Service and Bureau of Sport Fisheries and Wildlife, Washington, DC U.S.A.

BEECHAM, J.J. 1970. Nesting ecology of the Golden Eagle in southwestern Idaho. M.S. thesis. Univ. Idaho, Moscow, ID U.S.A.

BENJAMINI, Y. AND Y. HOCHBERG. 1995. Controlling the false discovery rate: a practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society Series B* 57:289–300.

Bloom, P.H. and S.J. Hawks. 1982. Food habits of nesting Golden Eagles in northeast California and northwest Nevada. *Journal of Raptor Research* 16:110–115.

Boeker, E.L. and T.D. Ray. 1971. Golden Eagle population studies in the southwest. *Condor* 73:463–467.

Bruce, A.M., R.J, Anderson, and G.T. Allen. 1982. Observations of Golden Eagles nesting in western Washington. *Journal of Raptor Research* 16:132–134.

Carnie, S.K. 1954. Food habits of nesting Golden Eagles in the coast ranges of California. *Condor* 56:3–12.

Collins, P.W. and B.C. Latta. 2006. Nesting season diet of Golden Eagles on Santa Cruz and Santa Rosa islands, Santa Barbara County, California. Santa Barbara Museum of Natural History Technical Reports No. 3, CA U.S.A.

————. 2009. Food habits of nesting Golden Eagles (*Aquila chrysaetos*) on Santa Cruz and Santa Rosa islands, California. Pages 255–268 *in* C.C. Damiani and D.K. Garcelon [Eds.], Proceedings of the 7th California Islands Symposium. Institute for Wildlife Studies, Arcata, CA U.S.A.

Collopy, M.W. 1983a. A comparison of direct observation and collections of prey remains in determining the diet of Golden Eagles. *Journal of Wildlife Management* 47:360–368.

————. 1983b. Foraging behavior and success of Golden Eagles. *Auk* 100:747–749.

Commission for Environmental Cooperation (CEC). 2016. Terrestrial ecoregions: level II. Montréal, QC Canada. http://www.cec.org/tools-and-resources/north-american-environmental-atlas/map-files (last accessed 29 August 2016).

Connolly, G.E., M.E. Fry, and J. Fammatre. 1976. Prey remains at a Golden Eagle, *Aquila chrysaetos*, nest near Hopland, California. *California Fish and Game* 62:85–86.

Coyle, A.M. 2008. An investigation of the ecology of nesting Golden Eagles in North Dakota. Ph.D. dissertation. Univ. of North Dakota, Grand Forks, ND U.S.A.

Craig, T.H. and E.H. Craig. 1984. A large concentration of roosting Golden Eagles in southeastern Idaho. *Auk* 101:610–613.

Cully, J.F., Jr. 1991. Response of raptors to reduction of Gunnison's prairie dog population change by plague. *American Midland Naturalist* 125:140–149.

Deblinger, R.D. and A.W. Alldredge. 1996. Golden Eagle predation on pronghorns in Wyoming's Great Divide Basin. *Journal of Raptor Research* 30:157–159.

Dixon, J.B. 1937. The Golden Eagle in San Diego county, California. *Condor* 39:49–56.

Eakle, W.L. and T.G. Grubb. 1986. Prey remains from Golden Eagle nests in central Arizona. *Western Birds* 17:87–89.

Edwards, C.C. 1969. Winter behavior and population dynamics of American eagles in western Utah. Ph.D. thesis. Brigham Young Univ., Provo, UT U.S.A.

Goodwin, G.A. 1977. Golden Eagle predation on pronghorn antelope. *Auk* 94:789–790.

Hagen, C.A. 2011. Predation on Greater Sage-Grouse: facts, process, and effects. Pages 95–100 *in* S.T. Knick and J.W. Connelly [Eds.], Greater Sage-Grouse: ecology and conservation of a landscape species and its habitats. Studies in Avian Biology Vol. 38. Univ. of California Press, Berkeley, CA U.S.A.

Hayden, S.L. 1984. Winter food habits and ecology of Golden and Bald eagles in northeastern Wyoming. M.S. thesis. Univ. of Wyoming, Lander, WY U.S.A.

Heath, J.A. and M.N. Kochert. 2016. Golden Eagle dietary shifts in response to habitat alteration and consequences for eagle productivity in the Morley Nelson Snake River Birds of Prey National Conservation Area. Cooperator Final Report to the U.S. Fish and Wildlife Service. Boise State Univ., Boise, ID U.S.A.

Hickman, G.L. 1968. The ecology and breeding biology of the Golden Eagle in southwestern Idaho and southeastern Oregon. U.S.D.I. Bureau of Sport Fisheries and Wildlife, Division of Wildlife Services. Unpubl. report.

Hunt, W.G., R.E. Jackman, T.L. Brown, J.G. Gilardi, D.E. Driscoll, and L. Culp. 1995. A pilot Golden Eagle population study in the Altamont Pass Wind Resource Area, California. Predatory Bird Research Group, Univ. of California, Santa Cruz, CA U.S.A.

Keller, K.R. 2015. Golden Eagle nesting survey report for the central Utah study area, March–July 2015. Report submitted to the Utah Division of Wildlife Resources and Natural Resources Department, U.S. Army. Dugway Proving Ground, UT U.S.A.

Knick, S.T. and D.L. Dyer. 1997. Distribution of black-tailed jackrabbit habitat determined by GIS in southwestern Idaho. *Journal of Wildlife Management* 61:75–85.

Knight, R.L. and A.W. Erickson. 1978. Marmots as a food source of Golden Eagles along the Columbia River. *Murrelet* 59:28–30.

Kochert, M.N. 1972. Population status and chemical contamination in Golden Eagles in southwestern Idaho. M.S. thesis, Univ. of Idaho, Moscow, ID U.S.A.

———— and K. Steenhof. 2002. Golden Eagles in the US and Canada: status, trends, and conservation challenges. *Journal of Raptor Research* 36:32–40.

————, ————, L.B. Carpenter, J.M. Marzluff. 1999. Effects of fire on Golden Eagle occupancy and reproductive success. *Journal of Wildlife Management*. 63:773–780.

————, ————, C.L. McIntyre, and E.H. Craig. 2002. Golden Eagle (*Aquila chrysaetos*). *In* P.G. Rodewald [Ed.], The birds of North America. Cornell Lab of Ornithology, Ithaca, NY U.S.A. https://birdsna.org/Species-Account/bna/species/goleag (last accessed 28 March 2017).

Latta, B.C., D.E. Driscoll, J.L. Linthicum, R.E. Jackman, and G. Doney. 2003. Capture and translocation of Golden Eagles from the California Channel Islands to mitigate depredation of endemic island foxes. Pages

314–350 *in* D.K. Garcelon and C.A. Schwemm [EDS.], Proceedings of the Sixth California Islands Symposium. Institute for Wildlife Studies, Ventura, CA U.S.A.

LEVINS, R. 1968. Evolution in changing environments. Princeton Univ. Press, Princeton, NJ U.S.A.

LOCKHART, J.M. 1976. The food habits, status and ecology of nesting Golden Eagles in the Trans-Pecos region of Texas. M.S. thesis. Sul Ross State Univ., Alpine, TX U.S.A.

LONGSHORE, K.M., T.C. ESQUE, K.E. NUSSEAR, D.R. JOHNSON, AND S.M. SIMES. 2017. An assessment of food habits, prey availability, and nesting success of Golden Eagles within the Desert Renewable Energy Conservation Plan Area. California Energy Commission. Publication Number 500-1216-003.

LOSEE, M.J., K. JACOBSON, K. LICENSE, AND K. MCCARTY. 2014. The diet of Arizona's Golden Eagle: preliminary findings. Proceedings of Arizona Field Ornithologists Meeting. Sierra Vista, AZ U.S.A.

MACLAREN, P.A., H.A. STANLEY, AND D.E. RUNDE. 1988. Food habits and nest characteristics of breeding raptors in southwestern Wyoming. *Great Basin Naturalist* 48:548–553.

MARR, N.V. AND R.L. KNIGHT. 1983. Food habits of Golden Eagles in eastern Washington. *Murrelet* 64:73–77.

MARTI, C.D., BECHARD, M., AND F.M. JAKSIC. 2007. Food habits. Pages 129–151 *in* D.M. Bird and K.L. Bildstein [EDS.], Raptor research and management techniques. Raptor Research Foundation and Hancock House, Blaine, WA U.S.A.

MARZLUFF, J.M., S.T. KNICK, M.S. VEKASY, L.S. SCHUECK, AND T.J. ZARRIELLO. 1997. Spatial use and habitat selection of Golden Eagles in southwestern Idaho. *Auk* 114:673–687.

MCGAHAN, J. 1968. Ecology of the Golden Eagle. *Auk* 85:1–12.

MCWILLIAMS, S.R., J.P. DUNN, AND D.G. RAVELING. 1994. Predator-prey interactions between eagles and Cackling Canada and Ross' geese during winter in California. *Wilson Bulletin* 106:272–288.

MILLSAP, B.A. 1978. Raptor nesting and production in southern Wyoming during 1978. U.S.D.I. Bureau of Land Management, Denver, CO U.S.A.

————. 1981. Distributional status of falconiformes in westcentral Arizona – notes on ecology, reproductive success, and management. U.S.D.I. Bureau of Land Management, Phoenix, AZ U.S.A.

MOLLHAGEN, T.R., R.W. WILEY, AND R.L. PACKARD. 1972. Prey remains in Golden Eagle nests: Texas and New Mexico. *Journal of Wildlife Management* 36:784–792.

OAKLEAF, R.J., L.E. OLSON, J.R. SQUIRES, AND Z.P. WALLACE. 2014. The status of Golden Eagles in Wyoming: a preliminary review. Pages 357–396 *in* A.C. Orabona and N. Cudworth [EDS.], Threatened, endangered, and nongame bird and mammal investigations: annual completion report. Wyoming Game and Fish Department, Cheyenne, WY U.S.A.

OLENDORFF, R.R. 1976. The food habits of North American Golden Eagles. *American Midland Naturalist* 95:231–236.

PAGEL, J.E., K.J. KRITZ, B.A. MILLSAP, AND R.K. MURPHY. 2013. Bald Eagle and Golden Eagle mortalities at wind energy facilities in the contiguous United States. *Journal of Raptor Research* 47:311–315.

PHILLIPS, R.L., A.H. WHEELER, N.C. FORRESTER, J.M. LOCKHART AND T.P. MCENEANEY. 1990. Nesting ecology of Golden Eagles and other raptors in southeastern Montana and northern Wyoming. U.S.D.I. Fish and Wildlife Service Tech. Rep. 26. Denver Wildlife Research Center, CO U.S.A.

PRESTON, C.R. 1990. Distribution of raptor foraging in relation to prey biomass and habitat structure. *Condor* 92:107–112.

————, R.E. JONES, AND N.S. HORTON. 2017. Golden Eagle diet breadth and reproduction in relation to fluctuations in primary prey abundance in Wyoming's Bighorn Basin. *Journal of Raptor Research* 51:334–346.

R CORE TEAM. 2013. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org (last accessed 4 January 2016).

REYNOLDS, H.V., III. 1969. Population status of the Golden Eagle in south-central Montana. M.S. thesis. Univ. of Montana, Missoula, MT U.S.A.

SCHLUTER, D. 1981. Does the theory of optimal diets apply in complex environments? *American Naturalist* 118:139–147.

SCHMALZRIED, J.T. 1976. Nesting and food habits of the Golden Eagle on the Laramie plains. M.S. thesis. Univ. of Wyoming, Laramie, WY U.S.A.

SCHWEIGER, A., H. FUNFSTUCK, AND C. BEIERKUHNLEIN. 2015. Availability of optimal-sized prey affects global distribution patterns of the Golden Eagle *Aquila chrysaetos*. *Journal of Avian Biology* 46:81–88.

SERVHEEN, C. 1978. Mountain beaver as a prey species of the Golden Eagle. *Murrelet* 59:77.

SIMES, M.T., K.M. LONGSHORE, K.E. NUSSEAR, G.L. BEATTY, D.E. BROWN, AND T.C. ESQUE. 2015. Black-tailed and white-tailed jackrabbits in the American west: history, ecology, ecological significance, and survey methods. *Western North American Naturalist* 75:491–519.

SMITH, D.G. AND J.R. MURPHY. 1979. Breeding response of raptors to jackrabbit density in the eastern Great Basin Desert of Utah. *Journal of Raptor Research* 13:1–14.

STAHLECKER, D.W., D.G. MIKESIC, J.N. WHITE, S. SHAFFER, J.P. DELONG, M.R. BLAKEMORE, AND C.E. BLAKEMORE. 2009. Prey remains in nests of Four Corners Golden Eagles, 1998–2008. *Western Birds* 40:301–306.

STEENHOF, K. AND M.N. KOCHERT. 1988. Dietary responses of three raptor species to changing prey densities in a natural environment. *Journal of Animal Ecology.* 57:37–48.

————, ————, AND T.L. MCDONALD. 1997. Interactive effects of prey and weather on Golden Eagle reproduction. *Journal of Animal Ecology.* 66:350–362.

TACK, J.D. AND B.C. FEDY. 2015. Landscapes for energy and wildlife: conservation prioritization for Golden Eagles across large spatial scales. *PLoS ONE* 10(8): e0134781. doi:10.1371/journal.pone.0134781 (last accessed 11 August 2015).

THOMPSON, S.P., R.S. JOHNSTONE, AND C.D. LITTLEFIELD. 1982. Nesting history of Golden Eagles in Malheur-Harney Lakes Basin, southeastern Oregon. *Raptor Research* 16:116–122.

U.S. DEPARTMENT OF THE INTERIOR (U.S.D.I.). 1979. Snake River Birds of Prey special research report to the Secretary of the Interior. U.S.D.I. Bureau of Land Management, Boise District, Boise, ID U.S.A.

U.S. FISH AND WILDLIFE SERVICE (U.S.F.W.S.). 2013. Eagle Conservation Plan guidance: Module 1 – land-based wind energy, Version 2. U.S.D.I. Fish and Wildlife Service, Division of Migratory Bird Management. Washington, DC U.S.A.

————. 2016. Final programmatic environmental impact statement for the Eagle Rule revision. U.S.D.I. Fish and Wildlife Service, Washington, DC U.S.A.

WATSON, J. 2010. The Golden Eagle. T. and A.D. Poyser, London, U.K.

WATSON, J.W. AND R.W. DAVIES. 2015. Comparative diets of nesting Golden Eagles in the Columbia Basin between 2007–2013 and the late 1970s. *Northwestern Naturalist* 96:81–86.

WOODGERD, W. 1952. Food habits of the Golden Eagle. *Journal of Wildlife Management* 16:457–459.

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

Map Label	Ecoregion Level II	Study Years	No. of Nest Visits (No. of Nests)	No. of Prey	Leporids (%)	Sciurids (%)	Other Mammals (%)	Birds (%)	Reptiles (%)	Fish (%)	Dietary Breadth	Method	Source
A	Western Cordillera	1969–1970	59[a] (19)	34	52.9	20.6	5.9	20.6	0.0	0.0	5.16	PR	Arnell (1971)
B	Western Cordillera	1970–2015	447 (323)	3859	24.2	43.3	9.6	22.0	0.8	0.0	8.37	PR	Keller (2015)
C	Western Cordillera	1974–1975	(3)	31	41.9	16.1	22.6	19.4	0.0	0.0	7.94	PR	Schmalzried (1976)
D	West Central Semi-Arid Prairies	1962–1964	95 (38)	980	69.8	12.1	5.2	12.5	0.4	0.0	1.97	PR	McGahan (1968)
E	West Central Semi-Arid Prairies	1965–1967	(39)	1009	46.1	22.5	5.9	24.2	0.4	0.0	6.99	PR	Reynolds (1969)
F	West Central Semi-Arid Prairies	1977	4		14.4	65.7						PR[b]	Phillips et al. (1990)
G	West Central Semi-Arid Prairies	2012	(8)	63	23.8	4.8	30.2	39.7	1.6	0.0	8.57	PR	R. Crandall and C. Preston (unpubl. data)
H	South Central Semi-Arid Prairies	1943	3	11	91.0	0.0	0.0	9.0	0.0	0.0	1.75	PR	Arnold (1954)
I	South Central Semi-Arid Prairies	1968	(7)	200	82.5	10.0	7.5	0.0	0.0	0.0	2.44	PR	Mollhagen et al. (1972)
J	Cold Deserts	1975	(2)	50	12.0	38.0	14.0	22.0	14.0	0.0	4.35	PR	Knight and Erickson (1978)
K	Cold Deserts	1974–1981	80	315	2.6	41.2	7.3	47.6	1.0	0.3	4.92	PR	Marr and Knight (1983)
L	Cold Deserts	2007–2013	(24)	244	2.4	27.6	26.4	41.2	2.0	0.4	12.27	DO, PR	Watson and Davies (2015)
M	Cold Deserts	1940			73.0	5.0	0.0	22.0	0.0	0.0	1.92	PR	Thompson et al. (1982)

Appendix 1. Continued.

Map Label	Ecoregion Level II	Study Years	No. of Nest Visits (No. of Nests)	No. of Prey	Leporids (%)	Sciurids (%)	Other Mammals (%)	Birds (%)	Reptiles (%)	Fish (%)	Dietary Breadth	Method	Source
N	Cold Deserts	1966–1967		209	61.7	4.8	4.3	27.8	1.4	0.0	3.73	PR	Hickman (1968)
O	Cold Deserts	1976–1981	119	1156	85.5	4.6	1.9	6.4	1.6	0.0	1.36[c]	PR	Bloom and Hawks (1982)
P	Cold Deserts	1986–1995	300 (10)	627	18.7	49.9	9.1	20.8	1.6	0.0	5.45	PR	B. Woodbridge (unpubl. data)
Q	Cold Deserts	1943	8 (4)	120	57.5	9.2	15.0	18.3	0.0	0.0	4.33	PR	Arnold (1954)
R	Cold Deserts	1974–1975	(8)	159	46.9	25.8	3.9	23.4	0.0	0.0	4.10	PR	Schmalzried (1976)
S	Cold Deserts	1978		58	70.7	22.4	0.0	5.1	1.7	0.0	3.31	PR	Millsap (1978)
T	Cold Deserts	1981–1982	43	560	39.5	45.5	6.1	8.6	0.0	0.6	4.63[d]	PR	MacLaren et al. (1988)
U	Cold Deserts	2009–2015	48 (27)	960	79.4	1.8	8.3	9.8	0.6	0.1	1.91	PR	Preston et al. (2017)
V	Cold Deserts	1969–1970	59[a] (19)	484	94.8	1.9	0.4	2.7	0.2	0.0	5.16	PR	Arnell (1971)
W	Cold Deserts	1967–1970		542	88.4		9.9	1.7	0.0	0.0		PR	Smith and Murphy (1979)
X	Cold Deserts	1970–2015	2050 (1298)	23,664	77.6	6.7	2.7	11.5	1.5	0.0	2.09	PR	Keller (2015)
Y	Cold Deserts	2013	6	45	77.8	0.0	6.7	11.1	4.4	0.0	1.84	PR	AMEC (2015)
Z	Cold Deserts	1998–2008	191 (182)	660	75.6	9.7	1.7	9.5	3.3	0.2	3.35	PR	Stahlecker et al. (2009)
AA	Cold Deserts	1968	(3)	169	58.0	37.9	4.1	0.0	0.0	0.0	2.93	PR	Mollhagen et al. (1972)
BB	Cold Deserts	2013	6 (6)	68	73.5	16.2	4.4	5.9	0.0	0.0	2.07	PR	Losee et al. (2014)
CC	Cold Deserts	1966–1967		386	54.9	11.1	6.3	25.6	1.8	0.3	4.09	PR	Hickman (1968)
DD	Cold Deserts	1968–1969	61	483	56.7	6.0	7.5	26.5	2.1	1.2		PR	Beecham (1970)
EE	Cold Deserts	1970–1971	28	1302	72.3	4.8	5.5	16.1	1.1	0.2	1.83[c]	PR	Kochert (1972)
FF	Cold Deserts	1972–1981, 1987		4380[e]	56.9	13.3	5.5	18.0	4.3	1.8	4.90	PR	K. Steenhof and M. Kochert (unpubl. data)
GG	Cold Deserts	1992–1993	9	18	17.0	56.0	16.0	11.0	0.0	0.0	2.66	DO	Marzluff et al. (1997)
HH	Cold Deserts	2012	1 (1)	13	46.1	0.0	38.5	15.4	0.0	0.0	8.05	PR	AMEC (2015)
II	Warm Deserts	2014–2015	(18)	852	65.6	6.1	2.9	6.2	19.2	0.0	3.04	DO, PR	Longshore et al. (2017)
JJ	Warm Deserts	1979–1981		89	97.0	0.0	0.0	1.1	2.2	0.0	2.05	PR	Millsap (1981)

Appendix 1. Continued.

MAP LABEL	ECOREGION LEVEL II	STUDY YEARS	NO. OF NEST VISITS (NO. OF NESTS)	NO. OF PREY	LEPORIDS (%)	SCIURIDS (%)	OTHER MAMMALS (%)	BIRDS (%)	REPTILES (%)	FISH (%)	DIETARY BREADTH	METHOD	SOURCE
KK	Warm Deserts	1985	15 (9)	37	37.8	16.2	27.0	18.9	0.0	0.0	5.17	PR	Eakle and Grubb (1986)
LL	Warm Deserts	1968	(10)	187	45.4	34.2	20.4	0.0	0.0	0.0	3.52	PR	Mollhagen et al. (1972)
MM	Warm Deserts	1968	(2)	54	94.4	1.9	3.7	0.0	0.0	0.0	1.52	PR	Mollhagen et al. (1972)
NN	Warm Deserts	1974–1975	21 (8)	571	83.7	6.3	8.4	1.6	0.0	0.0	2.36	DO, PR	Lockhart (1976)
OO	Mediterranean California	1947–1952	(17)	503	22.8	26.4	22.1	13.5	5.6	3.6	5.30[c]	PR	Carnie (1954)
PP	Mediterranean California	1974	1 (1)	62	27.0	56.1	13.7	3.2	0.0	0.0	3.14	PR	Connolly et al. (1976)
QQ	Mediterranean California	1994	(20)	339	4.1	69.0	8.3	13.0	5.6	0.0	2.09	PR	Hunt et al. (1995)
RR	Mediterranean California	2000–2007	11	425	0.0	0.0	45.9	52.2	1.9	0.0	3.95	PR	Collins and Latta (2009)
SS	Upper Gila Mountains	1968	(19)	336	75.6	11.9	12.5	0.0	0.0	0.0	2.92	PR	Mollhagen et al. (1972)
	Western United States			46,314[f]	53.5	19.6	10.4	15.1	1.8	0.2	4.04		

[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).
[e] K. Steenhof and M. Kochert (unpubl. data) includes data published in U.S.D.I. (I979), Collopy (1983a, 1983b), and Steenhof and Kochert (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.

Map Label	Ecoregion Level II	Prey 1 (%)	Prey 1 (Species)	Prey 2 (%)	Prey 2 (Species)	Prey 3 (%)	Prey 3 Species)	Source
A	Western Cordillera	35.2	Black-tailed jackrabbit (*Lepus californicus*)	17.6	Cottontail (*Sylvilagus* spp.)	14.7	Rock squirrel (*Otospermophilus variegatus*)	Arnell (1971)
B	Western Cordillera	25.5	Rock squirrel	14.4	Yellow-bellied marmot (*Marmota flaviventris*)	10.9	Black-tailed jackrabbit	Keller (2015)
C	Western Cordillera	22.6	Cottontail	19.4	White-tailed jackrabbit (*Lepus townsendii*)	9.7	Mule deer (*Odocoileus hemionus*)	Schmalzried (1976)
D	West Central Semi-Arid Prairies	37.2	White-tailed jackrabbit	32.6	Cottontail	7.1	Yellow-bellied marmot	McGahan (1968)
E	West Central Semi-Arid Prairies	26.2	White-tailed jackrabbit	19.9	Cottontail	11.5	Yellow-bellied marmot	Reynolds (1969)
F	West Central Semi-Arid Prairies	65.7	Prairie dog (*Cynomys* spp.)	14.4	Cottontail	19.9	Other species	Phillips et al. (1990)
G	West Central Semi-Arid Prairies	25.4	Pronghorn (*Antilocapra americana*)	15.9	White-tailed jackrabbit	7.9	Cottontail	R. Crandall and C. Preston (unpubl. data)
H	South Central Semi-Arid Prairies	73.0	Cottontail	18.0	Jackrabbit (*Lepus* spp.)	9.0	Duck (*Anas* spp.)	Arnold (1954)
I	South Central Semi-Arid Prairies	59.0	Black-tailed jackrabbit	23.5	Cottontail	5.5	Rock squirrel	Mollhagen et al. (1972)
J	Cold Deserts	38.0	Yellow-bellied marmot	10	Cottontail	10.0	Black-billed Magpie (*Pica hudsonia*)	Knight and Erickson (1978)
K	Cold Deserts	40.3	Yellow-bellied marmot	13.0	Dusky Grouse (*Dendragapus obscurus*)	11.8	Chukar (*Alectoris chukar*)	Marr and Knight (1983)
L	Cold Deserts	21.2	Yellow-bellied marmot	12.8	Deer fawn (*Odocoileus* spp.)	6.8	Coyote pups (*Canus latrans*)	Watson and Davies (2015)
M	Cold Deserts	69.0	Black-tailed jackrabbit	20.0	Duck	5.0	Yellow-bellied marmot	Thompson et al. (1982)
N	Cold Deserts	49.3	Black-tailed jackrabbit	12.4	Cottontail	4.3	Ring-necked Pheasant (*Phasianus colchicus*)	Hickman (1968)
O	Cold Deserts	76.0	Black-tailed jackrabbit	9.0	Cottontail	6.4	Birds	Bloom and Hawks (1982)

Appendix 2. Continued.

Map Label	Ecoregion Level II	Prey 1 (%)	Prey 1 (Species)	Prey 2 (%)	Prey 2 (Species)	Prey 3 (%)	Prey 3 Species)	Source
P	Cold Deserts	37.3	Belding's ground squirrel (*Urocitellus beldingi*)	11.1	Black-billed Magpie	10.4	Black-tailed jackrabbit	B. Woodbridge (unpubl. data)
Q	Cold Deserts	34.0	Cottontail	20.0	Black-tailed jackrabbit	18.0	Greater Sage-Grouse (*Centrocercus urophasianus*)	Arnold (1954)
R	Cold Deserts	42.2	White-tailed jackrabbit	20.3	Wyoming ground squirrel (*Urocitellus elegans*)	18.8	Duck	Schmalzried (1976)
S	Cold Deserts	46.6	Cottontail	24.1	White-tailed jackrabbit	12.1	Wyoming ground squirrel	Millsap (1978)
T	Cold Deserts	39.5	Leporids (Leporidae)	27.3	White-tailed prairie dog (*Cynomys ludovicianus*)	18.0	Wyoming ground squirrel	MacLaren et al. (1988)
U	Cold Deserts	71.4	Cottontail	8.0	White-tailed jackrabbit	4.7	Pronghorn	Preston et al. (2017)
V	Cold Deserts	80.8	Black-tailed jackrabbit	14	Cottontail	1.2	White-tailed Antelope Squirrel (*Ammospermophilus leucurus*)	Arnell (1971)
W	Cold Deserts	69.6	Black-tailed jackrabbit	18.8	Cottontail	9.9	Other mammals	Smith and Murphy (1979)
X	Cold Deserts	68.3	Black-tailed jackrabbit	9.2	Cottontail	3.4	Rock squirrel	Keller (2015)
Y	Cold Deserts	77.8	Jackrabbit	4.4	Unidentified snakes	2.2	Various species	AMEC (2015)
Z	Cold Deserts	42.4	Cottontail	33.2	Black-tailed jackrabbit	6.1	Gunnison's prairie dog (*Cynomys gunnisoni*)	Stahlecker et al. (2009)
AA	Cold Deserts	47.3	Black-tailed jackrabbit	32.0	Gunnison's prairie dog	10.7	Cottontail	Mollhagen et al. (1972)
BB	Cold Deserts	67.6	Black-tailed jackrabbit	14.7	Rock squirrel	5.9	Cottontail	Losee et al. (2014)
CC	Cold Deserts	46.6	Black-tailed jackrabbit	9.8	Yellow-bellied marmot	8.3	Cottontail	Hickman (1968)
DD	Cold Deserts	35.2	Jackrabbit	21.5	Cottontail	16.5	Ring-necked Pheasant	Beecham (1970)
EE	Cold Deserts	54.7	Jackrabbit	17.6	Cottontail	7.7	Ring-necked Pheasant	Kochert (1972)

Appendix 2. Continued.

Map Label	Ecoregion Level II	Prey 1 (%)	Prey 1 (Species)	Prey 2 (%)	Prey 2 (Species)	Prey 3 (%)	Prey 3 Species)	Source
FF	Cold Deserts	38.3	Black-tailed jackrabbit	18.6	Mountain cottontail (*Sylvilagus nuttellii*)	10.6	Piute ground squirrel (*Urocitellus mollis*)	Steenhof and Kochert (unpubl. data)
GG	Cold Deserts	55.6	Piute ground squirrel	16.7	Black-tailed jackrabbit	11.1	Rock Dove (*Columba livia*)	Marzluff et al. (1997)
HH	Cold Deserts	23.1	Jackrabbit	15.4	Cottontail	7.7	Various species	AMEC (2015)
II	Warm Deserts	54.9	Black-tailed jackrabbit	10.1	Desert cottontail (*Sylvilagus audubonii*)	9.9	Chuckwalla (*Sauromalus ater*)	Longshore et al. (2017)
JJ	Warm Deserts	58.4	Black-tailed jackrabbit	38.2	Cottontail	2.2	Gopher snake (*Pituophis catenifer*)	Millsap (1981)
KK	Warm Deserts	37.8	Black-tailed jackrabbit	16.2	Rock squirrel	8.1	Striped skunk (*Mephitis mephitis*)	Eakle and Grubb (1986)
LL	Warm Deserts	37.4	Black-tailed jackrabbit	34.2	Rock squirrel	13.9	Sheep and goat (*Ovis* spp. and *Capra* spp.)	Mollhagen et al. (1972)
MM	Warm Deserts	79.6	Black-tailed jackrabbit	14.8	Cottontail	1.9	Black-tailed prairie dog (*Cynomys ludovicianus*)	Mollhagen et al. (1972)
NN	Warm Deserts	60.6	Black-tailed jackrabbit	22.6	Cottontail	6.3	Rock squirrel	Lockhart (1976)
OO	Mediterranean California	28.6	Black-tailed jackrabbit	26.4	California ground squirrel (*Otospermophilus beecheyi*)	12.7	Deer	Carnie (1954)
PP	Mediterranean California	48	Grey squirrel (*Sciurus californicus*)	26	Jackrabbit	9.7	Deer	Connolly et al. (1976)
QQ	Mediterranean California	68.7	California ground squirrel	4.4	Unidentified Snakes	2.9	Black-tailed jackrabbit	Hunt et al. (1995)
RR	Mediterranean California	21.2	Common Raven (*Corvus corax*)	18.4	Feral pig (*Sus scrofa*)	11.1	Gulls (*Larus* spp.)	Collins and Latta (2009)
SS	Upper Gila Mountains	52.4	Black-tailed jackrabbit	23.2	Cottontail	8.3	Sheep and goat	Mollhagen et al. (1972)