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## Golden Eagle Dietary Shifts Following Wildfire and Shrub Loss Have Negative Consequences for Nestling Survivorship

Julie A. Heath  
*Boise State University*

Michael N. Kochert  
*U.S. Geological Survey*

Karen Steenhof  
*Owyhee Desert Studies*



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## RESEARCH ARTICLE

**Golden Eagle dietary shifts following wildfire and shrub loss have negative consequences for nestling survivorship**Julie A. Heath,<sup>1,\*</sup> Michael N. Kochert,<sup>2</sup> and Karen Steenhof<sup>3</sup><sup>1</sup> Department of Biological Sciences and Raptor Research Center, Boise State University, Boise, Idaho, USA<sup>2</sup> U.S. Geological Survey, Forest and Rangeland Ecosystem Science Center, Boise, Idaho, USA<sup>3</sup> Owyhee Desert Studies, Murphy, Idaho, USA\*Corresponding author: [julieheath@boisestate.edu](mailto:julieheath@boisestate.edu)

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**ABSTRACT**

Wildfires and invasive species have caused widespread changes in western North America's shrub-steppe landscapes. The bottom-up consequences of degraded shrublands on predator ecology and demography remain poorly understood. We used a before–after paired design to study whether Golden Eagle (*Aquila chrysaetos*) diet and nestling survivorship changed following wildfires in southwestern Idaho, USA. We assessed burn extents from 1981 to 2013 and vegetation changes between 1979 (pre-burn) and 2014 (post-burn) within 3 km of Golden Eagle nesting centroids. We measured the frequency and biomass of individual prey, calculated diet diversity indexes, and monitored nestling survivorship at 15 territories in 1971–1981 and 2014–2015. On average, 0.70 of the area within 3 km of nesting centroids burned between 1981 and 2013, and the mean proportion of unburned shrubland decreased from 0.73 in 1979 to 0.22 in 2014. Diets in post-burn years were more diverse and had a lower proportion of some shrub-associated species, such as black-tailed jackrabbits (*Lepus californicus*) and mountain cottontails (*Sylvilagus nuttallii*), and a higher proportion of American Coots (*Fulica americana*), Mallards (*Anas platyrhynchos*), Piute ground squirrels (*Urocitellus mollis*), and Rock Pigeons (*Columba livia*) compared with pre-burn years. A high proportion of waterfowl represented a novel change in Golden Eagle diets, which are typically dominated by mammalian prey. Nestling survivorship was positively associated with the proportion of black-tailed jackrabbits and negatively associated with the proportion of Rock Pigeons in eagle diets. Rock Pigeons are a vector for *Trichomonas gallinae*, a disease-causing protozoan lethal to young eagles. Nesting attempts were more likely to fail (all young die) in the post-burn period compared with the pre-burn period. Dietary shifts are a common mechanism for predators to cope with landscape change, but shifts away from preferred prey to disease vectors affect nestling survivorship and could lead to population-level effects on productivity.

**Keywords:** *Aquila chrysaetos*, black-tailed jackrabbit, climate change, prey, Rock Pigeon, shrub, trichomonosis

**LAY SUMMARY**

- Wildfires have led to the conversion of native shrub-steppe vegetation into non-native grasslands in the Great Basin, USA.
- We studied how diet and nestling survivorship of Golden Eagles, a top avian predator in this ecosystem, responded to landscape change that affected preferred prey populations.
- The shrubland area around eagle nesting territories decreased after fires and, consequently, the number of cottontails and jackrabbits in eagle diets decreased as the number of birds, such as waterfowl and Rock Pigeons, increased.
- Nestling survivorship was positively related to the proportion of black-tailed Jackrabbits in the diet and negatively associated with the number of Rock Pigeons. Survivorship tended to be lower in the post-burn period compared with the pre-burn period.
- Eagles seem resilient to changes in preferred prey populations, except for increased exposure to disease when they foraged on Rock Pigeons.

**Los cambios en la dieta de *Aquila chrysaetos* después de los incendios silvestres y la pérdida de arbustos tienen consecuencias negativas para la supervivencia de los polluelos****RESUMEN**

Los incendios de ambientes silvestres y las especies invasoras han provocado cambios generalizados en los paisajes de estepas arbustivas del oeste de América del Norte. Las consecuencias de abajo hacia arriba de los matorrales

degradados sobre la ecología y la demografía de los depredadores siguen siendo poco conocidas. Utilizamos un diseño pareado de antes y después para estudiar si la dieta y la supervivencia de los polluelos del águila *Aquila chrysaetos* cambiaron después de los incendios silvestres en el suroeste de Idaho, EEUU. Evaluamos la extensión de las quemaduras desde 1981 hasta 2013 y los cambios en la vegetación entre 1979 (antes de la quema) y 2014 (después de la quema) dentro de los 3 km de los centroides de anidación de *A. chrysaetos*. Medimos la frecuencia y la biomasa de presas individuales, calculamos índices de diversidad de la dieta y monitoreamos la supervivencia de los polluelos en 15 territorios en 1971–1981 y 2014–2015. En promedio, 0,70 del área dentro de los 3 km de los centroides de anidación se quemó entre 1981 y 2013, y la proporción media de matorrales no quemados disminuyó de 0,73 en 1979 a 0,22 en 2014. Las dietas en los años posteriores a la quema fueron más diversas y tuvieron una proporción menor de algunas especies asociadas a arbustos, como las liebres *Lepus californicus* y *Sylvilagus nuttallii*, y una mayor proporción de *Fulica americana*, *Anas platyrhynchos*, la ardilla *Urocyon mollis* y *Columba livia*, en comparación con los años anteriores a la quema. Una alta proporción de aves acuáticas representó un cambio novedoso en la dieta de *A. chrysaetos*, que suele estar dominada por presas de mamíferos. La supervivencia de los polluelos se asoció positivamente con la proporción de *L. californicus* y negativamente con la proporción de *C. livia* en la dieta de las águilas. *C. livia* es un vector de *Trichomonas gallinae*, un protozoo causante de enfermedades letales para las águilas jóvenes. Los intentos de anidación tuvieron más probabilidades de fallar (todas las crías mueren) en el período posterior a la quema en comparación con el período anterior a la quema. Los cambios en la dieta son un mecanismo común que usan los depredadores para enfrentar a los cambios del paisaje, pero los cambios de presas preferidas a aquellas que son vectores de enfermedades afectan la supervivencia de los polluelos y podrían provocar efectos a nivel poblacional sobre la productividad.

**Palabras clave:** *Aquila chrysaetos*, arbusto, cambio climático, *Columba livia*, depredador, dieta, *Lepus californicus*, presa, tricomoniasis

## INTRODUCTION

Population dynamics of predatory birds are strongly linked to population cycles of herbivore prey. For example, lemmings (*Dicrostonyx* spp.) and common voles (*Microtus epiroticus*) are the preferred prey of Snowy Owls (*Bubo scandiacus*; Schmidt et al. 2012) and Long-eared Owls (*Asio otus*; Korpimäki 1992), respectively. In years of high prey abundance, these predatory birds have higher productivity and recruitment compared with years with lower prey abundance (Korpimäki 1992, Sundell et al. 2004). Changes in climate and landscapes are decreasing the amplitude of herbivore population cycles in many areas (Ims et al. 2008, Kausrud et al. 2008, Cornulier et al. 2013). Given the strong link between herbivore dynamics and predator populations, it is important to understand how predators may respond to chronically depressed prey populations. Here, we studied how diet and nestling survivorship of Golden Eagles (*Aquila chrysaetos*), an apex predator in shrub-steppe habitat, were affected by wildfires that decreased the habitat of their preferred prey, black-tailed jackrabbits (*Lepus californicus*; Steenhof and Kochert 1988).

Predatory birds may increase diet breadth and diversity, shift to alternative prey (Angelstam et al. 1984), or both (Palma et al. 2006, Salafsky et al. 2007) in response to decreased abundance of preferred prey. However, dietary shifts can have reproductive consequences if alternative prey does not have the same nutritional or energetic benefits as the preferred prey (but see Murgatroyd et al. 2016). For example, diet diversification in response to reduced numbers of preferred prey led to lower breeding success in

Montagu's Harriers (*Circus pygargus*; Arroyo and Garcia 2006). Small shifts in the proportion of marine to terrestrial prey led to decreased egg size and changes in shape and pigmentation of eggs in Herring Gulls (*Larus argentatus*; O'Hanlon et al. 2020). Dietary shifts that incur costs such as increased exposure to toxins or pathogens may be particularly harmful. As the preferred prey of Bonelli's Eagles (*Aquila fasciata*) declined, these eagles consumed more Rock Pigeons (*Columba livia*) and had increased incidence of disease associated with nestling death (Real et al. 2000). Increased exposure to disease or toxins resulting from dietary shifts may act as a threat multiplier with landscape and climate change, leading to population-level effects.

The Morley Nelson Snake River Birds of Prey National Conservation Area (NCA) is part of the sagebrush steppe ecosystem of the Great Basin of North America and is known for its high density of raptors, including Golden Eagles, nesting along the cliffs on the Snake River (Marti 1992, Kochert and Collopy 1998). Wildfires, livestock grazing, and drought have interacted to cause extensive vegetation changes in the NCA since the early 1980s (U.S. Department of the Interior 1996, Paprocki et al. 2015). The incidence of fires in the NCA was relatively low between 1950 and 1980 (Kochert et al. 1999). Intensive fires in the NCA began in September 1981 (Boise District Bureau of Land Management fire records), likely related to an increase in cheatgrass (*Bromus tectorum*), a non-native annual grass (Whisenant 1990). Many fires occurred between 1981 and 1985, but the incidence of fires in the NCA was again relatively low between 1990 and 1994 (Kochert et al. 1999). Though, by 1994, 48% of the native shrub communities had been converted to extensive stands of cheatgrass

and other annual, non-native plants (U.S. Department of the Interior 1996).

Conversion of shrublands to grasslands reduces the density of shrub-reliant herbivores (Wiens 1985). The lower peak in the jackrabbit cycle observed in the NCA in the early 1990s (Figure 1 in Steenhof et al. 1997) suggests that conversion of shrublands to grasslands contributed to dampening population cycles of black-tailed jackrabbits over the last several decades. Previous research in the NCA has shown that Golden Eagle reproduction is closely tied to black-tailed jackrabbit abundance (Steenhof et al. 1997) and that eagle nesting success declined 1–3 years following major fires within eagle territories (Kochert et al. 1999). However, eagle nesting success increased 4–5 years after fires, despite continued shrub degradation and loss, suggesting that shifts in eagle behavior (e.g., taking alternative prey; Marzluff et al. 1997) may have mitigated some negative effects of landscape change (Kochert et al. 1999).

Our objectives were to study whether Golden Eagle diets have changed in response to large-scale habitat alteration (i.e. effects of fires) and to identify the consequences of any dietary shifts between pre- and post-burn periods on eagle nestling survivorship. We used a before–after paired approach to assess whether Golden Eagle diet diversity and composition differed between pre-burn and post-burn years at 15 focal nesting territories that were sampled in both periods. We quantified the burn extents between 1981 and 2013 and the amount of change in shrub vegetation between 1979 (pre-burn) and 2014 (post-burn) within 3 km of eagle nesting centroids. Then, we evaluated changes in diet diversity and composition between 1971–1981 (pre-burn) and 2014–2015 (post-burn). Finally, we examined relationships between diet composition and nestling survivorship. Specifically, we evaluated whether (1) the proportion of black-tailed jackrabbits correlated with nestling survivorship because Golden Eagle reproductive rates have been associated with jackrabbit abundance in the NCA (Steenhof et al. 1997) and elsewhere (Murphy 1975, Thompson et al. 1982) and (2) the proportion of Rock Pigeons correlated with nestling survivorship because pigeons are a vector of trichomonosis, a deadly disease for eagle nestlings (Dudek et al. 2018). We included a variable for weather in nestling survivorship models because extreme heat during brood-rearing can influence brood survival (Kochert et al. 2019) and brood size at fledging (Steenhof et al. 1997).

## METHODS

### Fire and Vegetation

The Morley Nelson Snake River Birds of Prey NCA is in southwestern Idaho, USA (43.13°N, –116.07°W; Figure 1). Native vegetation is characteristic of shrub-steppe and salt-desert shrub communities, and the principal

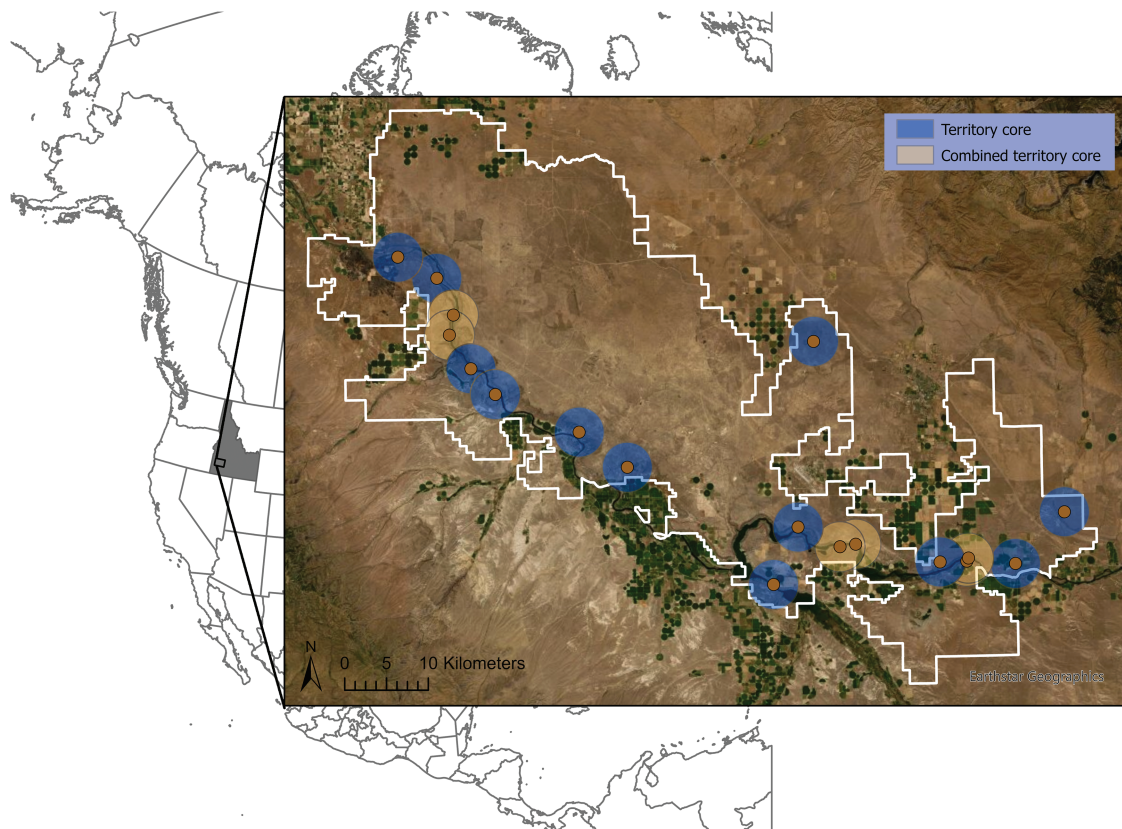
physiographic feature of the NCA is the Snake River Canyon where Golden Eagles nest on steep canyon walls (U.S. Department of the Interior 1996).

We created a circular polygon with a 3-km radius around the nesting centroids of each Golden Eagle pair (hereafter “territory core”; McIntyre et al. 2006) following procedures described in Kochert et al. (1999) to estimate burn extents and vegetation types. A circular, 3-km radius polygon was approximately the average size of 95% core use areas of radio-marked Golden Eagles (Marzluff et al. 1997) and represents likely high-use foraging areas. The nesting centroid was the weighted mean of the Universal Transverse Mercator (UTM) coordinates for all nests in which Golden Eagles from a particular territory laid eggs from 1971 to 2013. We calculated the proportion of burned area in each territory core by adding the areas that burned at least once between 1981 and 1994 (Kochert et al. 1999) to the area that burned at least once between 1995 and 2013 (Bureau of Land Management, Boise Fire records) and dividing by the total area within each core. Proportions >1 represent areas within some territory cores that burned at least once in 1981–1994 and again between 1995 and 2013. We assessed the area of shrub cover in pre-burn years from a vegetation map developed via visual interpretation of low-level aerial photographs and field verification of vegetation stands during 1977 and 1978 (U.S. Department of the Interior 1979). We assessed the area of unburned shrubs remaining in 2014 from a vegetation map developed by Pacific Northwest National Laboratory via classification of 2002 Landsat satellite imagery and field verification (Tagestad and Downs 2007). We overlaid the boundaries of fires that occurred from 2002 to 2013 (Bureau of Land Management, personal communication) and subtracted the area of shrub burned from total shrub to calculate the area of unburned shrub within each territory core. The 3-km radius polygons for the focal territories were overlaid on vegetation and burn layers using ARC/INFO (ESRI, Redlands CA) for the 1979 vegetation analysis and ArcGIS 10.2.1 (ESRI, Redlands CA) for the 2014 analysis.

### Diet

We studied diet composition and diet diversity through the analysis of prey remains and pellets collected from Golden Eagle nests at 15 nesting territories sampled in both pre-burn years (1971–1981; U.S. Department of the Interior 1979, Steenhof and Kochert 1988) and post-burn years (2014 and 2015). We defined a nesting territory (also called territory) as “an area that contains, or historically contained, one or more nests within the home range of a mated pair: a confined locality where nests are found, usually in successive years, and where no more than one pair is known to have bred at one time” (Steenhof et al. 2017). We selected territories for sampling based on the presence





**FIGURE 1.** Location of Golden Eagle nesting territories sampled in the Morley Nelson Snake River Birds of Prey NCA (white outline) in southwestern Idaho, USA, 2014–2015. Nesting centroids are represented with brown points, and 3-km territory cores are shown in blue (single core) or orange (combined cores). The Snake River Canyon is in the southern portion of the NCA. Few Golden Eagles nest on the benchlands north of the canyon.

of nestlings in nests that could be climbed safely. We collected dietary data from 27 (~85%) historical Golden Eagle territories occupied during the pre-burn period and collected post-burn dietary data from 15 of the 27 territories in 2014 and 2015. Territories we did not sample in post-burn years were either vacant ( $n = 6$ ), had pairs that did not produce young that reached 2 weeks of age ( $n = 2$ ), had inaccessible nests ( $n = 2$ ), or were used in another concurrent study ( $n = 2$ ). Three vacant territories (2 of which had been sampled in pre-burn years) were used by pairs at adjacent historical territories in post-burn years. We considered these amalgamated historical territories as one nesting territory for analyses (Figure 1; Supplementary Material Table S1). Burn extents in the territories sampled in both periods did not differ from those of territories samples in the pre-burn years only (Supplementary Material Figure S1). We sampled diet by entering each nest on average every 5.7 days (SD = 5.3) in pre-burn years and every 4.0 days (SD = 0.2) in post-burn years. We used standard rappelling and climbing techniques (Pagel and Thorstrom 2007) to reach nests, starting when young eagles were old enough to thermoregulate (~3 weeks; Katzner et al. 2020) until young

were approaching the age of fledging (~8 weeks). We did not enter nests during inclement weather to ensure the safety of the young eagles and the climber.

We collected all inedible prey remains and pellets following the protocols described in Steenhof and Kochert (1985, 1988) and Marti et al. (2007). We identified fresh prey; marked them by removing the head, feet, and tail; and left them in the nest. We used the same collection procedures in pre-burn and post-burn years to ensure that methodological differences between the 2 time periods did not contribute to experimental error. However, we recognize that the methods we used were biased against the detection of smaller prey items (Collopy 1983, Harrison et al. 2019), and small prey items were probably more common than we recorded in eagle diets during both periods.

We examined samples in the laboratory and identified prey remains to species whenever possible. We recorded the size and sex of prey when possible by comparison with images and taxonomic keys and tallied the number of individual prey items by calculating a maximum count of body parts (Mollhagen et al. 1972, Steenhof and Kochert 1985,

1988). We compared prey remains to fresh prey identified during previous nest visits to correct for duplicate counts, following Steenhof and Kochert (1985). We assigned weights to individual prey according to their species, size, and sex based on average weights reported by Steenhof (1983) and the U.S. Department of the Interior (1979). For 3 bird species not previously recorded in NCA nests, we used weights from Birds of the World species accounts (Yellow-rumped Warbler [*Setophaga coronata*], Hunt and Flaspohler 2020; Gadwall [*Mareca strepera*], Leschack et al. 2020; Double-crested Cormorant [*Phalacrocorax auritus*], Dorr et al. 2020).

### Nestling Survivorship

We assessed nestling numbers, health, and status from visits to the nest and ground observations. During prey collections, we inspected nestling eagles for signs of plaques indicative of the disease trichomonosis (Dudek et al. 2018). If plaques were present, we treated nestlings with an anti-fungal drug (Spartix or Emtryl) to prevent further growth of plaques and to reduce nestling mortality (Amin et al. 2014, Dudek et al. 2018). We categorized these birds as mortalities in analyses (see below).

In addition, we installed motion-activated cameras at some nests ( $n = 9$ ) to assess nestling status in 2014 and 2015 (Harrison et al. 2019). We defined nestling survivorship as the number of young that reached 51 days of age at each nest. This age represents the 80th percentile of average fledging age and the minimum acceptable age for assessing Golden Eagle nesting success (Steenhof 1987, Steenhof et al. 2017). We visually inspected carcasses to determine the cause of death if we found dead nestlings. We considered missing nestlings as deceased if the number of nestlings decreased between subsequent observations or visits and searches below the nest did not reveal carcasses. We used the number of days exceeding 32°C between May 15 and June 21 to represent extreme heat (SpringHeat) during the eagle brood-rearing season (Kochert et al. 2019).

### Analysis

We used a generalized linear model with a beta distribution and logit link (Douma and Weedon 2019) to assess the relationship between the proportion of unburned shrub within territory cores in 2014 (response) and burn extent (predictor). We used a generalized linear mixed model (GLMM) with a beta distribution and logit link and a random variable for territory identity to assess changes in the proportion of unburned shrub between pre-burn and post-burn periods.

We quantified Golden Eagle diet diversity by calculating Levin's Index (Marti et al. 2007) for each territory in each year and used a linear mixed model to examine whether

time period (pre-burn or post-burn) explained diet diversity. All diet models had a random effect for territory identity. We focused our frequency and biomass analyses on the 6 most common prey species in 2014 and 2015 because they were well represented across focal nesting territories and made up most of the items (73%) and biomass (70%) of diets. The remaining items and biomass consisted of small numbers of many species. We did not statistically test whether there was a time period effect on Mallards (*Anas platyrhynchos*) or American Coot (*Fulica americana*) frequency or biomass because their frequency and biomass were close to zero during pre-burn years. We used a GLMM with a negative binomial distribution and an offset for the total number of prey items collected each year in each territory to examine whether the frequency of common prey items changed between pre-burn and post-burn periods in the *glmmADMB* package (Skaug et al. 2016) for R (R Core Team 2020). We used zero-inflated GLMM with a gamma distribution and an offset for the total biomass of prey collected at each territory to examine whether the proportion of biomass from common prey items changed between pre-burn and post-burn periods in the *glmmTMB* package (Brooks et al. 2017) for R (R Core Team 2020). The zero-inflation sub-model contained a fixed effect for time period and the random effect for territory identity.

We examined whether the proportion of black-tailed jackrabbits or Rock Pigeons, or weather (SpringHeat), explained nestling survivorship at our 15 focal nests. We did not include one nesting attempt where young were added to a nest for fostering in the survivorship analysis. We considered 23 nestlings (pre-burn:  $n = 12$  and post-burn:  $n = 11$ ) as mortalities because they showed plaques indicative of trichomonosis and were treated with an anti-fungal pill. One of these nestlings was treated with an anti-fungal pill even though it did not have plaques, but its sibling did, and given the proportion of Rock Pigeon in the diet, it likely would have become infected with *Trichomonas gallinae* (Dudek et al. 2018). Nestlings with trichomoniasis were considered mortalities because, if left untreated, the mortality rate of infected Golden Eagle nestlings approaches 100% (J.A.H., M.N.K., and K.S., personal observation) and is 100% for some other raptor species (Cooper and Petty 1988). We used zero-inflated GLMM with a generalized Poisson distribution and log link to evaluate candidate model sets for predicting nestling survivorship in the *glmmTMB* package (Brooks et al. 2017, 2019). These models have 2 sub-models: a conditional sub-model to fit the count data and a sub-model to fit the zero-inflation. We did not build candidate models that contained the proportion of black-tailed jackrabbits and the proportion of Rock Pigeons in the same model because these variables were inversely correlated. Otherwise, candidate models in both the

conditional sub-model and the zero-inflation sub-model included all combinations of the main effects: the proportion of black-tailed jackrabbits in the diet, the proportion of Rock Pigeons in the diet, and the number of days exceeding 32°C. All models contained a random effect of territory identity in the zero-inflation sub-model. The weather covariate was scaled and centered to aid with model convergence. We used a step-wise approach to find the best model by evaluating candidate models for the zero-inflation sub-model first and then used the best-supported zero-inflation sub-model to evaluate candidate models for the conditional sub-model. Separately, we evaluated whether there was evidence of an effect of time period in both the zero-inflation and conditional sub-models. We examined dispersion and residuals of the most parsimonious models using the *DHARMA* package (Hartig 2020) to check model assumptions.

We evaluated all models using an information-theoretic approach and compared the models using Akaike's information criterion corrected for small sample size ( $AIC_c$ ). We considered the candidate models  $< 2 \Delta AIC_c$  to be informative (Burnham and Anderson 2002). We estimated 85% confidence intervals (CIs) for model parameters to be compatible with model selection criteria (Arnold 2010), and we considered effects statistically unclear if CIs overlapped zero (Dushoff et al. 2019). We did all analyses in R (R Core Team 2020). We report descriptive statistics as mean  $\pm$  standard deviations (SD) unless otherwise stated and parameter estimates with their 85% CIs.

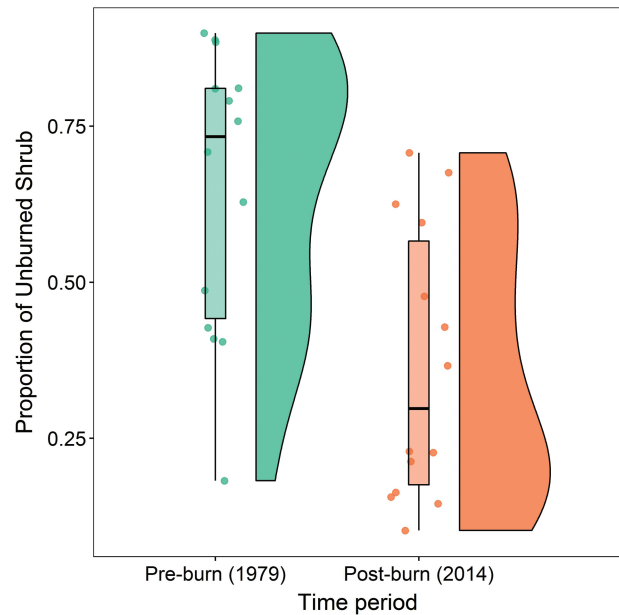
## RESULTS

### Fire and Vegetation

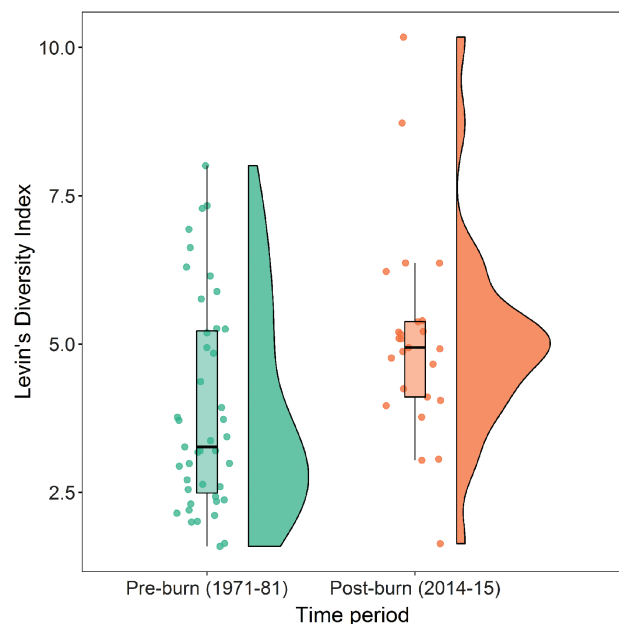
Fires burned 29,775 ha within the 15 focal Golden Eagle territory cores between 1981 and 2013 and resulted in large-scale loss of shrub ( $\beta$ :  $-1.8$ , 85% CI:  $-2.2$  to  $-1.5$ ). The proportion of unburned shrub in eagle territory cores decreased from a median of  $0.73 \pm 0.22$  per territory core in 1979 to  $0.22 \pm 0.22$  per territory core in 2014 (post-burn effect  $\beta$ :  $-1.5$ , 85% CI:  $-1.9$  to  $-1.2$ ; Figure 2; Supplementary Material Table S2).

### Diet

We identified 1,325 and 1,164 individual prey items from 418 and 233 collections in pre-burn and post-burn periods, respectively (Supplementary Material Tables S1 and S3). Eagle diets in the post-burn period (2014–2015) differed in diversity and composition from eagle diets in the pre-burn period (1971–1981). Diets were more diverse in post-burn years compared with pre-burn years: post-burn period diets had a higher Levin's Index compared with pre-burn diets (post-burn effect  $\beta$ :  $1.3$ , 85%



**FIGURE 2.** The proportion of unburned shrub in 15 Golden Eagle territory cores in 1979, before wildfires, and in 2014, after wildfires in the NCA. It was common for territory cores to consist of at least half shrub vegetation in 1979 but uncommon to have that much shrub in 2014. The points represent values from each territory core; the box plot shows the 25th, 50th, and 75th quartiles; and the half violin plot shows the distribution of the proportion of area containing unburned shrub.



**FIGURE 3.** Levin's Index of diet diversity from 15 Golden Eagle nesting territories in the Morley Nelson Birds of Prey NCA, Idaho, USA. Dietary data were collected in 1971–1981 (pre-burn) and again from the same territories in 2014–2015 (post-burn). Diet diversity was higher in post-burn years. Points represent values from each territory in each year; the box plot shows the 25th, 50th, and 75th quartiles; and the half violin plot shows the distribution of Levin's Index scores.



**TABLE 1.** Candidate model sets evaluating the effect of pre-burn and post-burn periods on the frequency of the most common prey items in the diets of Golden Eagles breeding in the NCA. Frequency models had an offset for the total number of prey items identified per territory per year and a random effect of territory identity. Models with the lowest AIC<sub>c</sub> scores were used to estimate parameters and CIs reported in results. The table shows model, number of parameters estimated (*k*), AIC<sub>c</sub>, ΔAIC<sub>c</sub> and AIC<sub>c</sub> weights (*w<sub>i</sub>*).

Candidate models	<i>k</i>	AIC <sub>c</sub>	ΔAIC <sub>c</sub>	<i>w<sub>i</sub></i>
Black-tailed jackrabbits				
Time period	5	411.2	0	0.99
Intercept-only	4	446.3	35.1	0.00
Mountain cottontails				
Time period	5	330.4	0	0.99
Intercept-only	4	352.2	21.8	0.00
Piute ground squirrels				
Time period	5	387.3	0	0.58
Intercept-only	4	387.9	0.6	0.42
Rock Pigeons				
Time period	5	236.7	0	0.86
Intercept-only	4	240.3	3.6	0.14

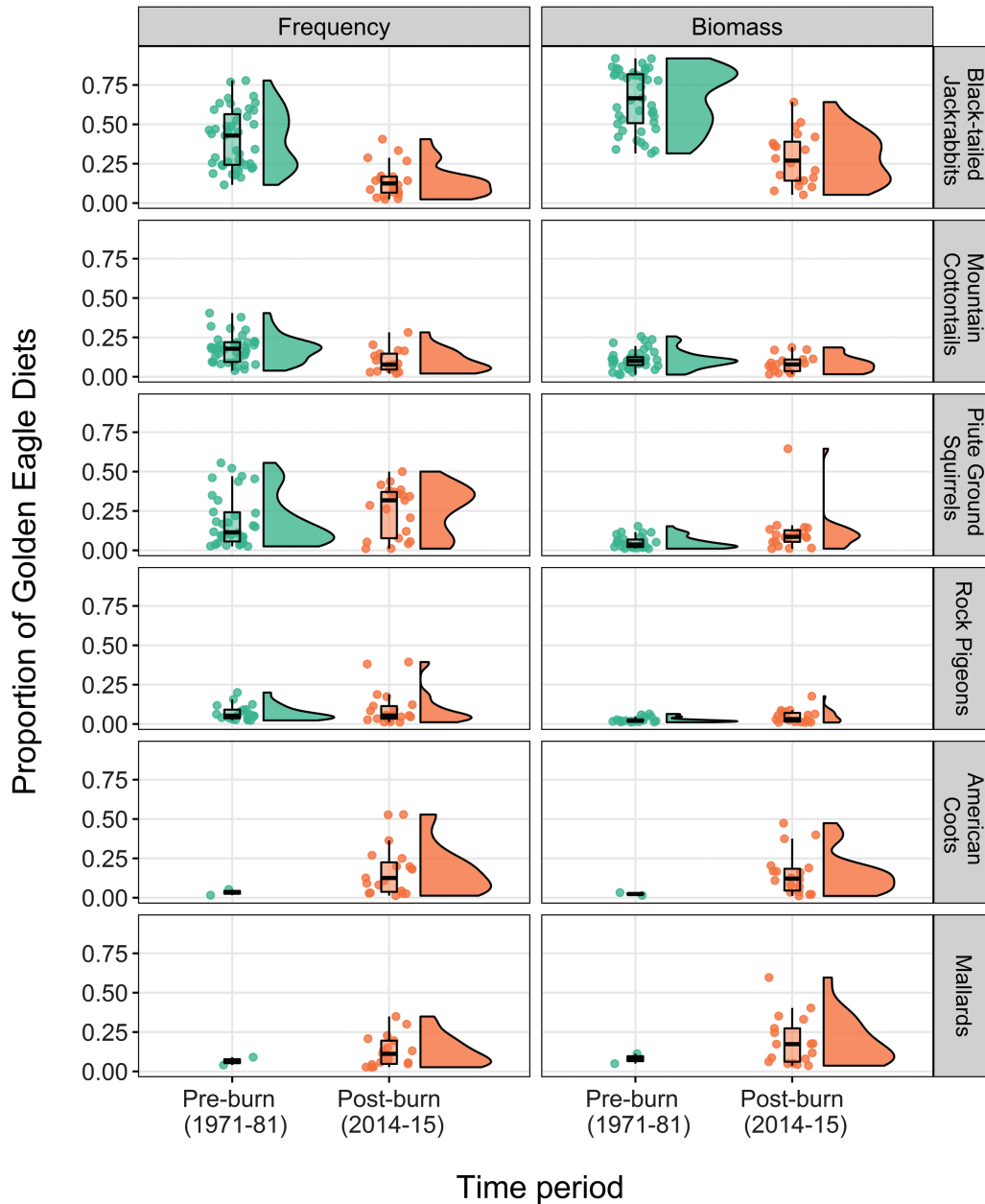
**TABLE 2.** Candidate model sets evaluating the effect of pre-burn and post-burn periods on the biomass of the most common prey items in the diets of Golden Eagles breeding in the NCA. Models had an offset for the total biomass of prey collected per territory per year and a random effect of territory identity within the zero-inflation portion of the model. Models with the lowest AIC<sub>c</sub> scores were used to estimate parameters and CIs reported in results. The table shows model, number of parameters estimated (*k*), AIC<sub>c</sub>, ΔAIC<sub>c</sub> and AIC<sub>c</sub> weights (*w<sub>i</sub>*).

Candidate models	<i>k</i>	AIC <sub>c</sub>	ΔAIC <sub>c</sub>	<i>w<sub>i</sub></i>
Black-tailed jackrabbits				
Time period	6	1,309.9	0	0.99
Intercept-only	5	1,343.1	33.2	0.00
Mountain cottontails				
Time period	6	1,076.8	0	0.56
Intercept-only	5	1,077.3	0.5	0.44
Piute ground squirrels				
Time period	6	995.9	0	0.97
Intercept-only	5	1,002.9	7.0	0.03
Rock Pigeons				
Time period	6	730.2	0	0.73
Intercept-only	5	732.2	2.0	0.27

CI: 0.6–1.9; [Figure 3](#); [Supplementary Material Table S4](#)). The frequency of prey items changed between time periods. Eagles were only a third (0.3) as likely to prey on black-tailed jackrabbits or mountain cottontails (*Sylvilagus nuttallii*) in post-burn years compared with pre-burn years (post-burn effect  $\beta$ : -1.2, 85% CI: -1.4 to -0.9, [Table 1](#), [Figure 4A](#);  $\beta$ : -1.1, 85% CI: -1.4 to -0.8, [Table 1](#), [Figure 4C](#), respectively). Conversely, eagles were 1.6 times more likely to forage on Piute ground squirrels (*Urocyon mollis*) (post-burn effect  $\beta$ : 0.5, 85% CI: 0.1–0.9; [Table 1](#); [Figure 4E](#)) and 2.2 times more likely to forage on Rock Pigeons ( $\beta$ : 0.7, 85% CI: 0.3–1.2; [Table 1](#); [Figure 4G](#)) in post-burn years compared with pre-burn years. Consumption of waterfowl represented a major shift in prey species between pre-burn and post-burn years. American Coots were found only twice in 1,348 prey items collected between 1971 and 1981, but American Coots were a substantial proportion (range: 0–0.53 per pair) of prey items collected in 2014–2015 ([Figure 4I](#)). Similarly, there were only 3 records of Mallards in 1,348

prey items collected between 1971 and 1981, but Mallards constituted up to 0.35 of items in diets during post-burn years ([Figure 4K](#)). Waterfowl species combined made up to 0.62 of prey items for 1 pair and were present in the diet of all 13 pairs nesting within 3 km of the Snake River. A pair that nested 8 km from the Snake River but <2 km from a creek and 3 small ponds also took Mallards. The only pair that did not take waterfowl in post-burn years nested 22 km from the Snake River.

Shifts in biomass between time periods were similar to shifts in frequency ([Figure 4](#)). The proportion of biomass from black-tailed jackrabbits and mountain cottontails was lower in post-burn years compared with pre-burn years (conditional model post-burn effect:  $\beta$ : -0.8, 85% CI: -1.0 to -0.7;  $\beta$ : -0.3, 85% CI: -0.6 to -0.1; [Table 2](#); [Figure 4B, D](#), respectively). The proportion of biomass from Piute ground squirrels (conditional model post-burn effect:  $\beta$ : 0.9, 85% CI: 0.5–1.3; [Table 2](#); [Figure 4F](#)) and Rock Pigeons (conditional model post-burn effect:  $\beta$ : 0.5, CI: 0.2–0.9; [Table 2](#); [Figure 4H](#)) increased in post-burn years. Finally,



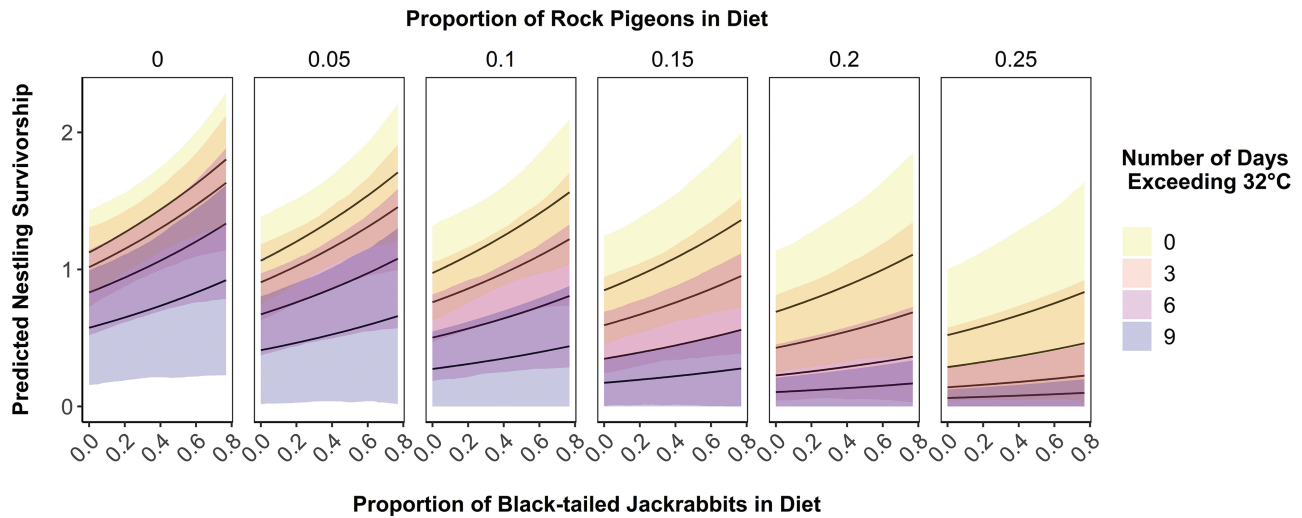
**FIGURE 4.** Frequency (left) and biomass (right) proportions of the most common prey items of 15 Golden Eagle pairs in the Morley Nelson Birds of Prey NCA, Idaho, USA, collected in 1971–1981 (pre-burn) and again from the same territories in 2014–2015 (post-burn). There were significant shifts in both frequency and biomass with fewer shrub-reliant leporids and more Piute ground squirrels and avian prey. Points represent values from each territory in each year; the box plot shows the 25th, 50th, and 75th quartiles; and the half violin plot shows the distribution of data.

the proportion of biomass from waterfowl increased in post-burn years. American Coot (Figure 4) and Mallard (Figure 4L) biomass combined represented <1% of the biomass consumed by eagles during the pre-burn period, but the same 2 species represented 25% of the biomass in the post-burn period.

#### Nesting Survivorship

We monitored 67 broods (Supplementary Material Table S1) containing a total of 123 nestlings (pre-burn:  $n = 78$ ; post-burn:  $n = 45$ ). Brood size ranged from 1 to 3. At least 1 nestling died in 32 monitored broods (48%), and all nestlings died in 22 monitored broods (33%); thus, 10 broods





**FIGURE 5.** Nestling survivorship depended on the proportion of the diet consisting of black-tailed jackrabbits (x-axis), Rock Pigeons (horizontal grid), and number of days exceeding 32°C (color) during the brood-rearing period in both the pre-burn and post-burn periods. There was a positive association between the proportion of black-tailed jackrabbits in Golden Eagle diets and nestling survivorship. High proportions of Rock Pigeons and the number of hot days increased the likelihood of all nestlings within a brood dying.

**TABLE 3.** Candidate models for predicting nestling survivorship of Golden Eagles at focal nesting territories in the Morley Nelson Snake River Birds of Prey NCA for the years 1971–1981 and 2014–2015. All models had a random effect of territory identity in the zero-inflation sub-model. Explanatory variables were number of days >32°C (SpringHeat), proportion of diet consisting of black-tailed jackrabbits, or proportion of diet consisting of Rock Pigeons. Models with the lowest AIC<sub>c</sub> scores were used to estimate parameters and CIs reported in results. The table shows model, number of parameters estimated (*k*), AIC<sub>c</sub>, ΔAIC<sub>c</sub>, and AIC<sub>c</sub> weights (*w<sub>i</sub>*).

Candidate models	<i>k</i>	AIC <sub>c</sub>	ΔAIC <sub>c</sub>	<i>w<sub>i</sub></i>
Zero-inflated sub-models (conditional sub-model: intercept-only)				
SpringHeat + Rock Pigeons	6	163.6	0	0.37
Black-tailed jackrabbits	5	164.2	0.6	0.26
SpringHeat + Black-tailed jackrabbits	6	164.9	1.3	0.19
Rock Pigeons	5	165.8	2.2	0.12
SpringHeat	5	167.7	4.2	0.05
Intercept-only	4	169.5	5.9	0.02
Conditional sub-models (zero-inflated sub-model: SpringHeat + Rock Pigeons)				
Black-tailed jackrabbits	7	160.2	0	0.61
Black-tailed jackrabbits + SpringHeat	8	162.7	2.6	0.17
Intercept-only	6	163.6	3.4	0.11
SpringHeat	7	164.8	4.6	0.06
Rock Pigeons	7	165.9	5.7	0.04
Rock Pigeons + SpringHeat	8	167	6.9	0.02

lost nestlings but still fledged young. Field inspections indicated that 27 mortalities were due to trichomoniasis, 5 were due to heat prostration, 4 were due to falls from nests, 4 were due to starvation or siblicide, and 12 were unknown or missing. Seventy-one nestlings (pre-burn: *n* = 49; post-burn: *n* = 22) within 45 broods survived to reach 51 days of age.

We evaluated whether diet (the proportion of jackrabbits or Rock Pigeons) or the number of days >32°C affected nestling survivorship. The top model showed a positive relationship between the number of nestlings surviving and the proportion of black-tailed jackrabbits in the diet (condition sub-modal β: 0.6, 85% CI: 0.3–0.9).

The proportion of Rock Pigeons (zero-inflated sub-model β: 11.2, 85% CI: 3.7–18.8) and the number of days >32°C during brood-rearing (zero-inflated sub-model β: 0.7, 85% CI: 0.2–1.2; Figure 5; Table 3) were positively associated with nestling mortality. The support for the time period candidate models on nestling survivorship was equivocal. The top candidate model was an intercept-only model. However, models with time period in the zero-inflated sub-model or conditional sub-model were within 2 ΔAIC<sub>c</sub> of the top model (Table 4). The 85% CI for time period in the zero-inflated sub-model did not cross zero (post-burn effect: 0.01–1.9), but the 85% CI for time period in the condition model did cross zero

**TABLE 4.** Candidate model set evaluating the effect of time period (pre-burn or post-burn) on Golden Eagles nestling survivorship in the NCA. All models had a random effect of territory identity in the zero-inflated sub-model. Models with the lowest  $AIC_c$  scores were used to estimate parameters and CIs reported in results. The table shows model, number of parameters estimated ( $k$ ),  $AIC_c$ ,  $\Delta AIC_c$ , and  $AIC_c$  weights ( $w_i$ ).

Candidate models (conditional, zero-inflated sub-models)	$k$	$AIC_c$	$\Delta AIC_c$	$w_i$
Intercept-only, intercept-only	4	169.5	0	0.33
Intercept-only, time period	5	169.6	0.1	0.31
Time period, intercept-only	5	170.4	0.9	0.21
Time period, time period	6	171.1	1.6	0.15

(post-burn effect:  $-0.4$  to  $0.02$ ). The time period effect in the zero-inflated sub-model suggests that nesting attempts were more likely to fail (all young die) in the post-burn period compared with the pre-burn period and is consistent with the temporal trends in diet composition, specifically an increase in Rock Pigeons, and field observations of more frequent nestling mortality.

## DISCUSSION

Golden Eagle diets became more diverse, and composition shifted after extensive fires and significant decreases in shrublands within eagle territory cores. Specifically, eagles ate fewer black-tailed jackrabbits and mountain cotton-tails, and more Piute ground squirrels, waterfowl, and Rock Pigeons in post-burn years. Golden Eagles in the NCA made a similar shift in diversity and composition from black-tailed jackrabbits to Piute ground squirrels during years of low jackrabbit abundance in the pre-burn period (Steenhof and Kochert 1988). However, the increased frequency of waterfowl from nearly zero in pre-burn diets to a major portion of the post-burn diet is a novel finding and suggests a substantial change from historical diet patterns during jackrabbit population cycles. Black-tailed jackrabbits remained an important component of Golden Eagles diets, despite the reduced frequency of jackrabbits in post-burn diets, because they were positively associated with nestling survivorship. Further, the proportion of Rock Pigeons in Golden Eagle diets and the number of days exceeding  $32^\circ\text{C}$  during brood-rearing were positively associated with nestling mortality. Together, these results suggest that eagles may be resilient to some bottom-up effects of large-scale habitat alteration, but threats from dietary exposure to disease or warming climate (Christensen et al. 2007) may increase the vulnerability of Golden Eagles in the NCA.

Wildfires in the NCA led to changes in vegetation communities, from a shrub-dominated landscape to extensive invasive grasslands (Kochert and Pellant 1986, Paprocki et al. 2015). The median proportions of unburned shrub vegetation within eagle territory cores declined from 0.73 to 0.22. This decline had negative effects on black-tailed

jackrabbits and other shrub-reliant species (MacCracken and Hansen 1982, Knick and Dyer 1997). Unfortunately, we do not have estimates of prey abundance in 2014 and 2015 to compare densities in pre-burn and post-burn periods. Long-term black-tailed jackrabbit monitoring in the NCA indicated that pre-burn years included 2 peaks and 1 low phase of the jackrabbit population cycle and suggested a declining trend in jackrabbit peaks between 1971 and 1994 (Figure 1 in Steenhof et al. 1997). Anecdotal evidence from field observations suggests that peaks in black-tailed jackrabbit population cycles have not been as high in subsequent years.

Diet diversity was higher in post-burn years compared with pre-burn years, when populations of black-tailed jackrabbits were presumably higher. This is consistent with patterns observed in Golden Eagles breeding in Wyoming, where diet breadth increased as leporid abundance decreased (Preston et al. 2017). Shifts in dietary biomass were similar to shifts in frequency between pre-burn and post-burn years. The proportion of biomass from leporid prey decreased, and the proportion of biomass from alternative prey, particularly waterfowl, increased.

Our findings support the conclusion of Bedrosian et al. (2017) that Golden Eagles are an opportunistic predator and that the presence of primary prey other than leporids in the diet may indicate depressed or absent populations of leporids. Dietary shifts of Golden Eagles have been documented in other areas and other time periods (Steenhof and Kochert 1988, Watson and Davies 2015, Preston et al. 2017). Steenhof and Kochert (1988) concluded that shifts in diets of Golden Eagles nesting in the Snake River Canyon during pre-burn years were consistent with optimal foraging theory (Pulliam 1974), in that the inclusion of alternative prey in the diet should depend not on their own abundance but on the abundance of the more profitable prey.

Eagle pairs that nested in extensively burned territories with only small islands of intact shrub communities still included black-tailed jackrabbits in their diets in post-burn years. Eagles in these territories may have focused on remnant shrub patches to capture leporids (Marzluff et al. 1997). Golden Eagles ranged over larger areas following fires in the NCA (Marzluff et al. 1997), and pairs in burned

areas were more successful if they could expand their range into adjacent vacant territories (Kochert et al. 1999). Our results suggest that Golden Eagles likely foraged in shrub and non-native grasslands for Piute ground squirrels, cliffs for Rock Pigeons, and riparian and riverine areas for waterfowl during post-burn years.

Mallards and American Coots were common in Golden Eagle diets in post-burn years, averaging ~25% of the total prey items and biomass. Waterfowl were the most abundant prey item at 3 nesting territories, contributing to more than half of the biomass and frequency. These findings were surprising given that mammalian species (i.e. leporid or sciurid) are typically the primary prey of Golden Eagles in western North America (Bedrosian et al. 2017, Katzner et al. 2020) and because waterfowl were rarely observed in diets of Golden Eagles in the NCA during the pre-burn period (Steenhof and Kochert 1988). Golden Eagles take many avian species (Olendorff 1976), but, in most of the areas, each bird species is taken in relatively low numbers. Birds become more common in Golden Eagle diets in areas where or years when typical mammalian prey populations are low (Marr and Knight 1983, Steenhof and Kochert 1988, Preston et al. 2017, Herzog et al. 2019).

Golden Eagles take waterfowl as alternative prey throughout their range (Katzner et al. 2020). Also, ducks and geese occur in relatively high proportions in Golden Eagle diets in areas where eagles nest in close proximity to water (e.g., Högstrom and Wiss 1992). Waterfowl were important in the diet of Golden Eagles nesting in coastal areas of western Alaska (Herzog et al. 2019), and waterfowl, particularly Canada Geese (*Branta canadensis*) and eider (*Somateria* spp.), formed ~40% of the eagle diet in the Central Canadian Arctic (Poole and Bromley 1988). These patterns are consistent with our finding that every Golden Eagle pair nesting within 3 km of the Snake River captured waterfowl in 2014, 2015, or both years. The Snake River attracts thousands of ducks each winter and early spring (Werner and Knetter 2010), when Golden Eagles are breeding and raising young. The availability and biomass of waterfowl may make them viable alternative prey for Golden Eagles, but they may not be as profitable, from a caloric standpoint, as leporids. Adult jackrabbits weigh nearly twice as much (2,114 g) as Mallards (1,185 g) and 3 times as much as American Coots (654 g; Steenhof 1983). Compared with leporids, the profitability of waterfowl as a dietary item for Golden Eagles remains to be seen and will depend partly on searching and handling costs as well as biomass.

The shift to waterfowl during the post-burn period may be due to declines in alternative prey species that were important in the pre-burn period. Shrub habitats provide a more favorable and stable environment for Piute ground squirrels than grass habitats (Steenhof et al. 2006), so squirrel abundance may have been lower in post-burn

years and not at densities high enough to compensate for rabbit declines. Additionally, populations of Ring-necked Pheasants (*Phasianus colchicus*), the fourth most frequently occurring prey item in the pre-burn period, have suffered dramatic declines in Idaho since the 1970s due to changes in agricultural practices (Midwest Pheasant Study Group 2013). In contrast, Breeding Bird Survey data and Christmas Bird Count data suggest that Mallard and American Coot populations have remained stable from the early 1970s through 2015 (Sauer et al. 2020, Meehan et al. 2020), and waterfowl populations are probably unaffected by terrestrial landscape change (i.e. shrub loss and agriculture change).

The proportion of black-tailed jackrabbits in the diet was positively associated with nestling survivorship. Schmidt et al. (2018a) concluded that Golden Eagle reproduction is driven largely by bottom-up processes. Previous studies in the NCA have shown a positive association between black-tailed jackrabbit abundance and the proportion of Golden Eagle pairs that lay eggs, the proportion of pairs that raised young, mean brood size at fledging, and number fledged per pair (Steenhof et al. 1997). Golden Eagle nesting success also closely paralleled jackrabbit abundance in Utah (Murphy 1975) and Oregon (Thompson et al. 1982). Our results bring new evidence about the links between preferred prey, diets, and nestling survivorship that add to these previous findings, and they confirm that jackrabbits continue to be important prey for Golden Eagles. The ecology and status of black-tailed jackrabbits have not received much research attention for more than 2 decades (Simes et al. 2015). Given the role of jackrabbits in trophic systems and widespread changes in the population dynamics of herbivores in ecosystems experiencing landscape and climate change (Schmidt et al. 2018b), future work on the once common and cyclic jackrabbit is warranted.

The proportion of Rock Pigeons in Golden Eagle diets and the number of days exceeding 32°C were positively associated with nestling mortality, confirming findings from earlier studies (Dudek et al. 2018, Kochert et al. 2019). Furthermore, the likelihood of all nestlings within a brood dying was higher in the post-burn years compared with pre-burn years. Together, these results suggest that threats from dietary exposure to disease or a warming climate may increase the vulnerability of eagles in the NCA. Rock Pigeon populations in Idaho have increased between the pre-burn and post-burn periods (Sauer et al. 2020). Consumption of Rock Pigeons increases the probability that young eagles develop trichomonosis (Dudek et al. 2018), a disease that likely leads to death (Cooper and Petty 1988, Amin et al. 2014). Trichomonosis was found in up to 42% of nestling eagles during pre-burn years when NCA jackrabbit abundance was low but rarely in years of high jackrabbit abundance (U.S. Geological Survey, unpublished data). In 2015,

41% of the nestlings in the NCA and surrounding areas tested positive for *T. gallinae*, the protozoan that causes trichomonosis (Dudek et al. 2018).

Decreased availability of preferred prey, like jackrabbits, and increased reliance on alternative prey, like Rock Pigeons, may be an emerging threat for Golden Eagles. This threat may worsen if changes in climate lead to increased frequency or magnitude of wildfires and shrub loss (Creutzburg et al. 2015). Warming temperatures could have both a direct effect on stressors through increased maximum temperatures during brood-rearing and an indirect effect through increased consumption of Rock Pigeons as shrublands and preferred prey decrease. Golden Eagle nestling survival could decrease and may result in population-level changes. Restoration and maintenance of shrubs that provide habitat for preferred prey should be a priority for NCA managers to restore the productivity of Golden Eagles, but this goal may be difficult to achieve in a changing climate. Access to alternative prey such as waterfowl and Piute ground squirrels may be essential for eagles to successfully raise young. Future work that focuses on the profitability of waterfowl and ground squirrels relative to leporids would be valuable for assessing the resiliency of this system.

## SUPPLEMENTARY MATERIAL

Supplemental material is available at *Ornithological Applications* online.

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**Data availability:** Analyses reported in this article can be reproduced using the data provided by Heath et al. (2021).

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