RECREATION, FIRE AND DISEASE CREATE A MOSAIC OF THREATS FOR GOLDEN EAGLES IN SOUTHWESTERN IDAHO

by

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DEDICATION

To my mentor and friend, Jerry Liguori.

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ABSTRACT

Anthropogenic stressors have resulted in ecosystem impoverishment and biodiversity loss worldwide. As the strength and reach of the human footprint increases, investigation of the additive or interactive effects of synergistic stressors on the landscape is imperative for conserving ecosystems and species within them. Apex predators can reflect how stressors impact ecosystems because of bottom-up effects. Golden eagles (*Aquila chrysaetos*) are apex predators of North American sagebrush-steppe ecosystems that are impacted by a suite of stressors, including wildfire, outdoor recreation disturbance, and habitat loss. We investigated whether multiple threats had additive or interactive effects on golden eagle occupancy, reproduction, and diet. We used a before-after-control-impact (BACI) design to study the effects of fire and recreation on eagle reproduction at 22 historical territories in southwestern Idaho. In 2015, the Soda wildfire burned 14 historical eagle territories, and 8 territories were unburned. We collected data on recreation and eagle territory occupancy, confirmed egg-laying rates, young fledged per egg-laying pair, and diet in 2017 and 2018 and compared these data to pre-fire levels of recreation and eagle reproduction in 2013 and 2014. Off-road vehicle (ORV) use, as well as total use, increased in unburned areas after the fire and remained the same in burned areas. ORV use was negatively associated with eagle territory occupancy, regardless of whether the time period was before or after the fire, or whether an area had burned. Conversely, early season pedestrian use decreased in burned areas after the fire and the effect of early season pedestrian use depended on fire. Before the Soda fire, pedestrian use was negatively associated with the rate of confirmed egg-laying. In burned territories after the Soda fire, pedestrian use decreased and the rate of confirmed egg-laying increased, suggesting that the decrease in pedestrian use had an interactive, positive effect on eagle reproduction. Diet composition differed between burned and unburned territories, but overall diet diversity and prey delivery rates were similar across fire and recreation gradients. In burned areas, eagles brought less leporid prey (rabbits and hares) and more sciurid prey (ground squirrels and marmots) to nests than in unburned areas. Additionally, eagle diets included more leporid prey and less rock pigeons (*Columba livia*) in areas with higher recreation use. This result may indicate diet shifts in areas with less leporids to eating more rock pigeons, which are vectors for disease. Combined our results suggest that recreation is a significant threat to eagle occupancy and reproduction, even compared to large-scale wildfires that can have massive effects on shrub-steppe ecosystems. Together, these results reveal a mosaic of stressors that threaten eagles across the southwestern Idaho landscape. It is therefore imperative that we understand the additive or interactive effects of synergistic stressors acting on ecosystems so that we can best manage lands and conserve biodiversity in a time of rapid global change.

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LIST OF ABBREVIATIONS

BSU	Boise State University
GC	Graduate College
TDC	Thesis and Dissertation Coordinator
ORV	Off-road Vehicle
BLM	Bureau of Land Management
OFO	Owyhee Field Office
GLMM	Generalized linear mixed model

INTRODUCTION

In the Anthropocene, wildlife populations are limited by changes in the magnitude and frequency of natural disturbances, like drought and fire, and novel stressors, like noise pollution, that arise from the accumulating human footprint. Anthropogenic stressors such as land use, climate change, and biological invasions have resulted in ecosystem impoverishment and the loss of biodiversity worldwide (Butchart 2010, Barnosky et al. 2011). As human populations grow and pressures on the landscape increase, multiple stressors are likely affecting wildlife (Steffen et al. 2011, Geldmann, Joppa and Burgess 2014). However, it is increasingly difficult for conservationists to mitigate individual threats to wildlife because of the potential complex effects of concurrent stressors on ecosystem processes (Brook, Sodhi and Bradshaw 2008, Côté, Darling and Brown 2016). Therefore, researchers must consider the additive or interactive effects of synergistic stressors acting on ecosystems so that we can understand how best to manage lands and conserve biodiversity in a time of rapid global change.

Apex predators reflect how different stressors affect ecological relationships because of bottom-up effects of ecosystem change on predators and stressors that accumulate in long-lived species (Sergio et al. 2008). Functional and physical loss of habitat can decrease predator abundance on the landscape both directly, from structural changes or avoidance (Romero-Muñoz et al. 2019), and indirectly, from the reduction of preferred prey (Holbrook et al. 2016). Fluctuations in prey resources are linked to changes in predator vital rates such as reproduction (Schmidt et al. 2018) and population dynamics (Millon, Nielsen, Bretagnolle, and Møller 2009). Additionally, predators can reveal the presence of detrimental environmental contaminants (Serieys et al. 2019) and the spread of disease (Dudek et al. 2018) acquired from prey experiencing ecosystem disturbances at lower trophic levels. Therefore, studying predator demography and reproductive parameters can be useful in identifying the compounding effects of synergistic stressors on ecosystems.

Golden eagles (*Aquila chrysaetos*) are apex predators of sagebrush-steppe ecosystems of western North America, and their populations are limited by the availability of suitable nesting sites within habitat that supports prey populations (Newton 1979, Watson 2010). Sage-steppe ecosystems are experiencing increasing, concurrent stressors because of their utility and accessibility for multiple uses including natural resource exploitation, agriculture, and outdoor recreation (Noss, LaRoe III, and Scott 1995, Knick et al. 2003, Davies et al. 2011). Much of the historical shrub dominant habitat has been converted to exotic grasslands, which has resulted in a decline in sagebrush obligate wildlife across taxa (Suring, Rowling and Wisdom 2005a, Suring et al. 2005b, Wisdom et al. 2005). Habitat alterations, coupled with the changing climate, also have led to an increase in the rate and magnitude of wildfire (Marlon et al. 2009, Balch, Bradley, D’Antonio and Gómez-Dans 2013). These accumulating, synergistic anthropogenic stressors within this system may cause cascading effects, which could ultimately affect eagles at the top of the trophic hierarchy.

Motorized and non-motorized recreation is increasing as human populations increase and can affect ecosystem structure and dynamics. Recreation can have direct physical impacts to systems, such as soil compaction or direct mortality, that can alter species distributions and abundance (review in Switalski 2018). Wildlife-human interactions also can include human disturbance, resulting in an animal changing its normal behavior (Knight and Cole, 1991, Frid and Dill 2002). This can have physiological costs (Creel et al. 2002, Thiel et al. 2008, Arlettaz et al. 2015), cause habitat avoidance (Taylor and Knight 2003, Rodríguez-Prieto and Fernández-Juricic 2005, Kangas et al. 2010), and impact reproduction of animals (Barton and Holmes 2007, Watson, Bolton, and Monaghan 2014, Spaul and Heath 2016). Golden eagles are known to be sensitive to human disturbance (Kochert, Steenhof, McIntyre and Craig 2002, Watson 2010). For example, Steenhof, Brown and Kochert (2014) documented a decline in occupancy and success rates at territories near motorized trails and parking areas and no change in reproduction at territories that had little or no motorized recreation. Additionally, Spaul and Heath (2016) found a negative association with off-road vehicle (ORV) use and occupancy rates and found that the level of pedestrian use within an eagle territory, early in the breeding season, correlated negatively with the probability that eagles will lay eggs or fail early. Recreation effects on eagle reproduction can have population-level consequences, where marginal territories become vacant and reproductive potential in high-use areas is lowered (Pauli, Spaul and Heath 2017). Chronic disturbance also may cause changes in predator-prey dynamics. For example, it can cause habituation or sensitization of prey species (Geffroy, Samia, Bessa and Blumstein 2015), and can change species' daily spatiotemporal patterns for things like foraging (Wheat and Wilmers 2016, Ziege et al. 2016). Behavioral shifts of prey species can alter hunting success of predators, which may ultimately impact reproductive success.

Wildfire is a major driver of ecological processes in the sage-steppe ecosystem because it alters shrub habitat and accelerates the invasion of exotic annual grasses such as cheatgrass (*Bromus tectorum;* D'Antonio and Vitousek 1992, Balch, Bradley, D'Antonio and Gómez-Dans 2013). Habitat alterations after wildfire may affect the distributions of shrub-reliant prey for top predators such as eagles (Smith and Nydegger 1985, Yensen and Quinney 1992, Steenhof, Yensen, Kochert and Gage 2006). In one study, golden eagles experienced decreased nesting success in burned territories immediately following fire, most likely due to the reduction of prey (Kochert, Steenhof, Carpenter and Marzluff 1999). Wildfire has reduced the abundance and diversity of small mammals (Groves and Steenhof 1988), reptiles and amphibians (Rochester et al. 2018), and birds (Knick et al. 2005, Coates et al. 2016). Additionally, important prey for eagles including black-tailed jackrabbits (*Lepus californicus*; Smith and Nydegger 1985) and ground squirrels (*Urocitellus mollis*; Yensen et al. 1992, Steenhof, Yensen, Kochert and Gage 2006) occur at lower densities within non-native grasslands: a consequence of wildfire. Eagles shift to alternative prey resources and increase diet diversity when preferred prey populations are low (Steenhof and Kochert 1988, Bedrosian et al. 2017, Preston, Jones and Horton 2017), which could be an important adaptation after wildfire. However, shifts in preferred prey abundance can affect golden eagle reproduction (Steenhof, Kochert and Mcdonald 1997, Tjernberg 2016, Schmidt et al. 2018), and alternative prey use may result in the transmission of disease. If eagles use rock pigeons (*Columba livia*) for more than 10% of their diet, nestlings are more likely to contract *Trichomonas gallinae*, a protist that causes the disease avian trichomonosis which can cause nestling death (Dudek et al. 2018).

Wildfires can also alter human decisions, specifically recreation, which may create even more complex impacts to wildlife and system processes. Recreationists are likely to respond to wildfire depending on the location and type of recreation, pre-fire habitat conditions, fire characteristics, and post-fire restoration (Englin, Boxall, Chakraborty and Watson 1996, Kline 2004). Recreationists may avoid burned areas and shift to adjacent unburned areas (Brown et al 2008). This may cause relief from recreation pressure on wildlife in burned areas, but recreation pressure could expand elsewhere. Recreation also may increase following fire because recreationists are drawn to novel ecosystem attributes found in burned landscapes (Englin, Loomis and González-Cabán 2001), which may cause additive negative pressure in burned systems. However, recreationists reported that they did not change visitation patterns after a forested area of Oregon burned; they enjoyed areas despite being burned (Brown et al 2008). Thus, recreation patterns may remain unchanged, which may cause additive, negative effects on wildlife in burned areas following a wildfire.

This project aimed to investigate how wildfire may add to or alleviate the effects of outdoor recreation on trophic interactions in the sagebrush steppe by investigating reproduction and diet of golden eagles. In August 2015, the Soda Fire burned 112,966 hectares of land in southwestern Idaho. The burned area included 14 golden eagle territories where we had conducted research on recreation patterns and eagle responses to recreationists (Spaul and Heath 2016). We used a before-after-control-impact (BACI) design, where we leveraged pre-fire data collected from this area in 2013-2014 with data collected post-fire in 2017 and 2018 on recreation use, eagle occupancy, apparent non-egg-laying, and eagle productivity, to test hypotheses about the interactions between wildfire and recreation on eagle reproduction. We hypothesized that wildfire will differentially affect the amount and location of various types of recreation activities, and that this shift in stressors on the landscape will affect eagle occupancy and reproduction. We also studied eagle diets during brood-rearing in 2017 and 2018 to examine whether fire or recreation affected the composition and delivery rates of prey brought to nests.

METHODS

Study Area

We conducted our study along the northeastern front of the Owyhee Mountains in southwestern Idaho. The area consists of rolling hills punctuated by isolated rocky buttes and canyons and is characteristic of a sagebrush-steppe plant community, covered by a patchy mixture of forbs, bunch grasses and shrub species, including big sagebrush (*Artemisia* spp.), rabbitbrush (*Chrysothamnus* and *Ericameria* spp.), bitterbrush (*Purshia tridentata*), greasewood (*Sarcobatus vermiculatus*), and saltbushes (*Atriplex* spp.; U.S. Department of the Interior, 1979, U.S. Department of the Interior, Bureau of Land Management 1996). A large proportion of this area is covered by introduced and invasive species, including exotic annual grasses such as cheatgrass (*Bromus tectorum*) and medusahead (*Taeniatherum caput-medusae*), which also dominates the landscape in the wake of wildfire (Kochert et al 1999). Much of this area is managed by the Bureau of Land Management (BLM), and it provides opportunities for multiple uses including livestock grazing and extensive networks of roads and trails for both motorized and non-motorized recreation. Agricultural areas and livestock feedlots line the eastern edge of the range and are dispersed in valleys throughout. Between 10 and 23 August 2015 the Soda Fire burned areas that included 72,697 hectares within BLM-administered lands in the Owyhee Field Office (OFO) of southwestern Idaho (BLM 2015).

Recreation Monitoring

We followed the recreation monitoring methods described in Spaul and Heath (2016) to facilitate comparison of pre- and post-fire recreation data. We installed motion-activated trail cameras (Bushnell HD ® Trophy Cameras) along one trail per survey within 1200 m of focal nests, which included either the occupied nest or the most recently used nest within the territory. We chose the same or similar camera locations as those used in 2013-2014. We analyzed trail camera photos and categorized recreationists into 4 groups: 1) off-road vehicles (any motorized recreation not including road vehicles, including all-terrain vehicles, utility task vehicles and dirt bikes.), 2) road vehicles (including cars, trucks, jeeps and other sport utility vehicles) 3) non-motorized (bike and horseback riders), 4) pedestrians (hikers or runners on foot), and 5) unknown (the image only captured evidence of a recreationist). We calculated an index of recreation use for each territory on an average per trail, per day basis for each type of recreation as well as total average recreation per trail, per day. We defined early season (relative to the eagle breeding season) recreation as the average use from 15 January to 16 March, which was set to include 90% of the egg-laying dates in the study area for the four years studied.

Eagle Territory Monitoring

Along the Owyhee front golden eagles are year-round residents and nest primarily on canyon cliffs and rocky buttes (USDI 1979, Steenhof, Kochert and Moritsch 1984). In 2017 and 2018, we followed the same monitoring methods in the same historical eagle territories as those used by Spaul and Heath (2016) in 2013 and 2014 (before the Soda fire). We surveyed territories for occupancy and nesting activity from mid-January to mid-June. Observations were usually made > 400m from focal nests to avoid observer disturbance (Pagel, Whittington and Allen 2010). We considered territories to be occupied by eagles if we observed territorial behavior, courtship, incubation, brood-rearing, or other signs of eagle pairs (e.g. newly built or decorated nests; Steenhof, Kochert, McIntyre, and Brown 2017). We considered territories to be vacant if no adult eagles were detected after three, 4-hour observations, spaced approximately 30 days apart (Pagel, Whittington and Allen 2010). In occupied territories, we considered pairs as 'confirmed egg-laying' by observing an incubating adult, eggs or young in a nest. At four occupied territories we did not observe incubating adults, eggs, young, nor a completed nest bowl (Kochert, Steenhof, McIntyre and Craig 2002), however there was uncertainty in whether or not pairs laid eggs. We classified these pairs as 'apparent non-laying' because either they did not lay eggs, or they laid eggs but abandoned the eggs between observation dates. We considered young to have successfully fledged if they were observed at ≥ 51 days of age (80% of typical fledging age; Steenhof 1987). We also calculated the total number of young that successfully fledged per egg-laying pair. We considered individual nestlings that were treated for the disease trichomonosis (see below) as dead (not successful) in our analysis because these nestlings likely would have died before fledging (Dudek et al. 2018).

We estimated the extent of burned area within each territory by using average centroids of known nest locations (McGrady, Grant, Bainbridge, and McLeod 2002) and calculating the proportion of burned area within a 3-km radius (28.27 km^2), which encompasses the mean home range size of breeding eagles (McGrady, Grant, Bainbridge, and McLeod 2002, Marzluff et al. 1997). We categorized territories as "burned" if the extent of the burn was > 60% (range 61.82- 100%) and "unburned" if the extent of the burn was < 25% (range 0- 21.09%). There were no territories with a burned extent of 22-60%. When creating model sets, we initially considered both the numerical representation of proportion burned and the categorical representation of burned. The categorical variable burned had the most evidence for support in most model sets, and therefore we took the numerical variable of proportion burned out of our analysis.

Eagle Diet

We assessed eagle diets during brood-rearing using images of prey brought to the nest by adults to feed nestlings. We installed motion-activated Bushnell 14MP HD Aggressor Trophy ® cameras at 9 nests in 2017 and Reconyx HyperFire HC600 ® cameras at 11 nests in 2018. We used different cameras in 2018 because we wanted a better image quality with smaller image sizes, where more high-quality images could fit onto one memory card. We posted cameras on cliffs using swivel mounts bolted and secured with epoxy putty. We chose camera locations around the nest that captured the largest proportion of the nest and that were the least conspicuous to avoid disturbance to eagles (Harrison, Kochert, Pauli and Heath 2019). We camouflaged cameras to the best of our ability with tan spray paint and camouflage-patterned tape. We set cameras at medium to high sensitivity depending on the distance from the nest and to take two simultaneous photos when the camera was triggered, with a 30-second delay. We entered nests once to install cameras when nestlings were 2.5 to 5.5 weeks old to minimize disturbance. During nest visits, we thoroughly examined the oral cavities of each nestling to check for visible plaques indicative of *Trichomonas gallinae* infections. We treated infected individuals with Spartrix ® tablets, an antiprotozoal medication for captive birds (Dudek et al. 2018). We re-entered nests to retrieve cameras after young fledged from the nests or died. We reviewed images and identified prey items to the lowest taxonomic level. Items were grouped into 13 biologically meaningful categories for our analysis (Robinson, Booms, Bechard and Anderson 2019) including corvids, galliformes, ground squirrels, leporids, lizards, marmots, other birds, other mammals, rock pigeons, raptors, rodents, snakes, and waterbirds. We estimated prey biomass using an average weight for each animal, regardless of the percentage of the carcass that was brought to the nest. We used average weights from Steenhof (1983), Sibley (2014) (birds), and Kays and Wilson (2009) (mammals). Biomass of items that could not be identified to species but could be sorted into a category were estimated by comparing the size of the item to the size of a known species. We disregarded completely unidentified items when calculating prey proportions and diversity indices but included all items to determine prey delivery rates. The number of unidentified items was 13% in 2017 and 7% in 2018, though this difference was most likely attributed to better camera placements in our second year, and not camera function. We calculated diet diversity using prey categories for each nest using the Standardized Levins (1968) formula, where diversity ranged from 0-1.

Standardized Levin's Index:

$$B_i = \frac{1}{(n-1)}\left[\frac{1}{(\sum_j p_{ij}^2)} - 1\right]$$

n = number of prey items

p = proportion of an individual prey category

Statistical Analysis

We created generalized linear mixed models (GLMMs) with a negative binomial distribution to determine the effects of the variables "burned" (burned and unburned) and "time period" (before and after fire) on recreation use. We included temporal variation in model sets because Spaul and Heath (2016) reported a polynomial relationship of week of the year + week^2 as well as a weekend effect on recreation in the region. They reported that recreation use changed over the course of the breeding season with peaks mid-season from March through May, and use was higher on weekends than on weekdays. We created GLMMs for total recreation as well as individual recreation types using combinations of the variables, week, week^2, weekend, burned, and time period with the random effect of individual territory. We focused on total recreation use and the specific recreation types (ORV and early season pedestrian use) because they were associated with eagle occupancy and egg-laying in previous work (Spaul and Heath 2016).

We used recreation metrics that affected eagle occupancy, egg-laying, and productivity in Spaul and Heath's (2016) study with the variables "burned" and "time period" to examine whether fire changed the effect of recreation on eagle reproductive rates. We used a GLMM with a binomial distribution to evaluate whether average ORV use across the breeding season, burned, and time period explained eagle occupancy. We used separate GLMMs with a binomial distribution to evaluate whether early season pedestrian use, burned, and time period explained whether eagles were categorized as apparent non-egg-laying or egg-laying. We also used GLMMs with a Poisson distribution and a log link to evaluate whether average ORV use across the breeding season, early season pedestrian use, average total recreation use across the breeding season, burned, and time period explained the number of young that fledged successfully from nests of egg-laying pairs.

Finally, we used linear and generalized mixed models to evaluate the influence of fire and recreation on eagle diet characteristics. We investigated the effects of whether a territory burned and total average recreation use on prey delivery rates, biomass delivered per day, and diet diversity using a normal distribution and a random effect of territory. We included nestling age in days and whether or not it was a weekend day to account for possible variation associated with these parameters. We found no difference in prey delivery rates on weekends compared to weekdays, so we did not account for this variable in diet models. Additionally, we used GLMMs with a negative binomial distribution, a random effect of territory, and an offset for the total number of items brought to the nest to evaluate whether burned, average total recreation use, or the interaction between the two explained the proportion of leporids or the proportion of rock pigeons in eagle diets. We focused our analysis on leporid species as a group because both black-tailed jackrabbits and mountain cottontail (*Sylvilagus nutalii*) are primary prey for eagles in this region and because diet diversity has been inversely associated with the proportion of leporid prey (Steenhof and Kochert 1988, Preston, Jones and Horton 2017). Jackrabbit abundance has been positively associated with eagle egg-laying and the number of young fledged per occupied territory (Steenhof, Kochert and Mcdonald 1997), and cottontail abundance has been positively associated with eagle nesting success (Preston, Jones and Horton 2017). We focused on rock pigeons because they have been associated with lower nestling survival likely due to the transmission of disease (Dudek et al. 2018).

We performed all analyses in the program R version 3.5.2 (R Core Team 2016). We created negative binomial models using the glmer.nb function in the package lme4.

We used the glmer and lmer functions from the package lme4 for binomial and normal distributions, respectively (Bates, Mächler, Bolker and Walker 2014). All continuous variables were centered and scaled before running models. We evaluated all possible combinations of variables within candidate sets using Akaike's Information Criterion adjusted for small sample size (AICc) during model selection and considered the model with the lowest AICc to have the most support given the data (Burnham and Anderson 2002). In some model sets, there was more than one model within 2 ΔAICc suggesting evidence for more than one model. In these situations, we considered whether 85% confidence intervals overlapped zero as providing reliable estimates of an effect (Arnold 2010). We reported descriptive statistics as the mean ± the standard deviation.

RESULTS

We surveyed recreationists on trails within golden eagle territories for 53 ± 10 days per territory from January-June of 2017 and 2018 and compared recreation use to pre-fire use within the same territories. The best supported model to explain ORV use included the polynomial effects of week of the year, whether or not it was a weekend day, and the interaction between whether a territory was burned and time period (Table 1). ORV use changed throughout the breeding season, with a peak in early May and was higher on weekends than weekdays (see Appendix A). After the fire, ORV use remained the same in burned areas, but increased in unburned areas (post-fire effect of burn: β= -0.42, 85% CI = -0.67, -0.17; Figure 1).

Similarly, the best supported model to explain early season pedestrian use included the polynomial effects of week of the year, whether or not it was a weekend day and the interaction between whether a territory burned and time period (Table 2). Total Early season pedestrian use was lower in burned territories after the fire but remained the same in unburned territories (post-fire effect: β= -0.69, 85% CI= -0.94, -0.43; Figure 2). Pedestrian use also changed throughout the breeding season and there were more pedestrians on weekends than weekdays (see Appendix A).

Total average recreation use was best explained by the polynomial effects of week, whether or not it was a weekend day, and the interaction between whether a territory was burned and time period (Table 3). Total recreation use changed during the breeding season, peaking from March to May, and was higher on weekends than weekdays (See Appendix A). After the fire, total recreation increased in unburned areas but remained the same in burned areas (post-fire effect of burn: β= -0.43, 85% CI= -0.57, -0.28; Figure 3).

Eagle territory occupancy was similar before and after the fire. Territory occupancy was best explained by average ORV use per trail, per day and whether or not a territory burned (Table 5). Territory occupancy was inversely associated with ORV use. As average ORV use increased, the probability of territory occupancy decreased (ORV_Avg: β= -1.27, 85% CI= -1.96, -0.59; Figure 4a). Additionally, eagle occupancy was lower in burned areas, regardless of time period (burned: β= -2.00, 85% CI= -3.89, -0.11; Figure 4b).

After the Soda fire, more eagle pairs were confirmed to lay eggs and the number of young that fledged per egg-laying pair was higher compared to before the fire (Table 4). Confirmed egg-laying was best explained by the interaction between time period and whether a territory burned, and average early season pedestrian use per trail, per day (Table 6). After the fire, the probability of confirmed egg-laying in burned areas was higher than before the fire and remained the same in unburned areas (post-fire effect of burn: β= 3.18, 85% CI=1.37, 5.01; Figure 5a). Early-season pedestrian use was negatively associated with the probability of confirmed egg-laying (PreLay_Ped: β= -0.76, 85% CI= -1.37, -0.15; Figure 5b). Finally, the number of young that successfully fledged per egg-laying pair was best explained by time period (Table 7). After the fire, the number of young fledged per egg-laying pair was higher than before the fire (post-fire effect: β= 0.62, 85% CI= 0.10 to 1.18; Figure 6). The number of young fledged was not related to whether or not a territory burned.

In 2016 and 2017, we installed cameras in 18 nests each for 23 ± 12 days between late April and late June and captured 846 prey deliveries: an average of 43 ± 23 identified prey items per nest. We identified 750 prey items to family and 30 prey items to order; 66 prey items were unidentified. Snakes were the most numerous prey item (23%), followed by ground squirrels (18%), leporids (15%), marmots (14%), and galliformes (11%). Eight other categories comprised the remaining 29%, but the contribution of each category to the total diet was small (0.5 to 5%, Figure 7). Estimated prey biomass ranged from 18g to 2700g, with an average of 599g. Marmots contributed more biomass to eagle diets (41%) than other groups, and leporids contributed the next most (22%). Galliformes, ground squirrels, and snakes each made up 7% of total prey biomass, and the 8 other categories comprised the remaining 16%, with biomass contributions ranging from 0.001% to 6%. Standardized Levins indices averaged 0.08 ± 0.08 (range 0.02-0.34).

We detected and treated *Trichomonas gallinae* infections in 4 of 37 nestlings in 2017 and 2018. We also found one nestling dead in the nest with thick plaques in its throat from a *T. gallinae* infection. Additionally, cameras revealed that 2 other nests had high Mexican chicken bug (*Haemetosiphon inodorus*) infestations that caused 3 nestlings to leave the nest before they could fly and they died.

Neither recreation use nor burn extent affected prey delivery rates in terms of number of individuals or biomass delivered per day, nor was there an effect on diet diversity (Table 10). Diet composition, however, was associated with burned areas and recreation use. In burned areas, eagles delivered fewer leporids and higher proportions of alternative prey including snakes, ground squirrels, marmots, and galliformes than in unburned areas (Figure 7). The proportion of leporids in eagle diets was best explained by whether a territory had burned (Table 8). The proportion of leporids was lower in burned areas (β= -1.61, 85% CI=-2.62, -0.58; Figure 8). In addition, a second competitive model showed evidence for the effect of total average recreation use. The proportion of leporids delivered to nests was positively associated with total recreation use (Avg_Total: β=0.44, 85% CI= 0.10, 0.79; Table 8). Lastly, total average recreation use best explained the proportion of rock pigeons in eagle diets (Table 9). The proportion of pigeons brought to eagle nests was inversely associated with recreation use (Avg_Total: β= -1.03, 85% CI= -1.78 to -0.38).

DISCUSSION

Multiple threats occur within the sage-steppe ecosystem in southwestern Idaho, and these threats can have both interactive and additive effects on eagle territory occupancy, apparent non-egg-laying, and diet, with consequences for reproduction. Despite relatively rapid and extreme landscape-level changes caused by wildfire, recreation within eagle territories continue to be one of the main drivers of eagle territory occupancy and the probability of confirmed egg laying. We found that eagles may be able to adapt to large-scale wildfires by shifting prey use, but they may not be able to cope with the effects of increasing human presence on the landscape. Our results suggest that wildfire may provide some short-term relief from increasing recreation disturbance, but this may come at the cost of increased recreation elsewhere, or reduction of preferred prey that may increase exposure of young eagles to disease. Recreation occurs against a backdrop of stressors that fluctuate across the landscape, and it may become increasingly difficult to tease apart the effects of individual threats to ecosystems.

To our knowledge, this is the first report of the effects of fire on recreation patterns in the sagebrush steppe ecosystem. Following wildfire, we saw differential changes in recreation use based on both the type of recreation and on whether or not the area burned. ORV use stayed the same in burned areas but increased in unburned areas following fire. Early season pedestrian use followed a different pattern after fire and decreased in burned areas but generally stayed the same in unburned areas. Additionally, total recreation use remained unchanged in burned areas and increased in unburned areas after the fire, a pattern that was most likely driven by the high ORV use in the area.

These shifting patterns in ORV use after fire suggests that ORV recreation increased but concentrated in unburned areas after the fire. This is consistent with reported trends of increased outdoor recreation associated with increasing human populations (Cordell 2012, Steenhof, Brown and Kochert 2014). The Boise City-Nampa metropolitan area is a fast-growing region in the United States, with an estimated 15.9% population increase (92,253 people) in Ada and Canyon counties from 2010 to 2017 (US Census Bureau). Increased human presence on the landscape also may hinder restoration efforts in burned areas and increase the odds of human-induced wildfires in unburned areas, further compounding impacts to lands and associated wildlife. More careful management would help mitigate these pressures after fire, where ORV users are monitored and regulated in both burned and adjacent unburned areas.

Pedestrians responded differently to wildfire than ORV users. Pedestrian use was highest inside the fire boundary both before and after the fire, which may be due to the types of and access to trails as well as the ecological characteristics of those particular areas. However, pedestrian use decreased significantly after the fire within both burned and unburned areas, suggesting that either pedestrian use is declining in the area, or that pedestrians were avoiding popular hiking areas that had burned. Because nature-based recreation is thought to be growing in the US (Cordell 2012), pedestrians most likely continued to recreate but shifted use outside of our study area to other popular areas for hiking or running. Press releases and signage posted by the BLM following the Soda fire starting in 2016 also may have added incentive to deter pedestrians from burned areas, though there were no new trail closures on monitored trails in our study area. Hiking in this area is generally motivated by viewing or photographing nature (Opdahl 2018); burned vegetation and reduced wildlife populations might diminish the value of nature-based recreation in these areas. Many alternative popular natural areas near Boise provide similar recreation opportunities. This includes the Snake River Canyon, which also supports a high density of wildlife and breeding raptors, including golden eagles (Kochert and Pellant 1986). In the future it may be worthwhile to monitor recreation within a larger buffer around urban centers to understand the effects of fire and shifting recreation patterns on systems at larger spatial scales.

We found a strong negative association with ORV use and golden eagle territory occupancy, before and after the fire. This result is consistent with previous studies that also reported decreased eagle occupancy with increased ORV use (Steenhof, Brown and Kochert 2014, Spaul and Heath 2016). Eagles may not occupy intensively used ORV areas because of chronic disturbance. Avoidance of areas with high ORV use is a common theme across taxa (review in Switalski 2018), and therefore these areas may have reduced abundance and diversity of species at all trophic levels. Additionally, habitat degradation and fragmentation associated with consistently high ORV use over time also may result in limited abundance and distribution of prey. The impacts of ORV use may be long-term, where chronic, high ORV use creates unsuitable habitat for eagles and their prey. Cumulative effects of ORV use over time need to be studied further to fully understand the mechanisms behind the effects of recreation on ecosystems and associated wildlife.

After the fire, confirmed egg-laying in unburned territories did not change, but increased significantly in burned territories. Decreased pedestrian recreation in burned areas after fire seem to be associated with an interactive, positive effect on eagles. Pedestrians cause eagles to flush from perches more than any recreation type (Spaul and Heath 2018), and eagles are more sensitive to disturbance early in the nesting season (Watson 2010). Our results support the hypothesis that early season pedestrian use may result in eagles not laying eggs or eagles abandoning nesting attempts soon after egg-laying perhaps because of increased risk perception or physiological response caused by increased disturbance (Spaul and Heath 2016). Alternately, previous studies also have shown that egg-laying is strongly correlated with winter weather and prey availability: eagles are more likely to lay eggs after milder winters and higher numbers of black-tailed jackrabbits (Steenhof, Kochert and Mcdonald 1997). It is difficult to make an association with weather with few years of data, but weather patterns do not suggest this is an underlying explanation for our results (see Appendix B). Temperatures in winters preceding egg-laying from November to February were lowest in the post-fire years of the study relative to pre-fire years (data sourced from NOAA online from Boise, ID at www.w2.weather.gov). Our results suggest that shifts in early season pedestrian use can have immediate, substantial effects on whether or not eagles will lay eggs or fail early, and therefore careful management may be successful in mitigating this disturbance.

The number of young fledged per egg-laying pair was higher after the fire, regardless if a territory was burned. Brood size at fledging has been reported to remain fairly stable and therefore the mechanisms driving this pattern remain unclear. In our study, both confirmed egg laying and number of young fledged per egg-laying pair were higher 3 and 4 years after the fire than before the fire. The number of young fledged may have been high as a result of increased confirmed egg-laying. This is consistent with Steenhof et al. (1997) who found a strong association with the proportion of pairs that laid eggs and annual reproductive output. Conversely, Spaul and Heath (2016) found that sudden intervals of high ORV use negatively impacted nest survival most likely from increased ORVs coming in close contact with nesting eagles and dismounting, creating pedestrian recreation. Because of the burned landscape, signage that is posted preventing travel off-trail in burned areas and less pedestrians in these areas after fire, this may be a factor affecting the survival of young.

Our information on diet composition was similar to that of other eagle studies in the same ecoregion due to the high frequency of leporids and sciurids (ground squirrels and marmots; Bedrosian et al. 2017), but it differed most notably because of the high contribution of snakes. Eagle diets in burned and unburned territories varied in the frequency of major prey types, and fire may be linked to these differences. Specifically, we found that the proportion of leporid species in eagle diets was best explained by whether or not a territory burned, with significantly lower proportions of leporids in burned areas. Fewer leporid prey in burned areas could reflect the loss of shrub cover after the fire (Knick and Dyer 1997) and supports the hypothesis that wildfire may have detrimental effects to eagles from shrub loss and the reduction of prey (Marzluff et al. 1997, Kochert et al. 1999). We remain cautious extrapolating information about prey populations from prey use because eagles preferentially select preferred prey even when densities are low (Steenhof and Kochert 1988), and eagles could be selecting prey such as sciurids instead of leporids. However, abundance estimates of preferred prey have been positively correlated with frequencies of preferred prey in eagle diets and inversely correlated with frequencies of alternative prey (Steenhof and Kochert 1988). Therefore, habitat loss in burned areas and the associated decrease in leporid prey use could explain a shift to alternative prey sources, which, in this case, were mostly sciurids, snakes, and galliformes. Alternately, marmots and ground squirrels also may be preferred by eagle pairs in these areas despite fire, which is consistent with other studies that found sciurids to be one of the most frequent prey types in eagle diets (Bedrosian et al. 2017). This is also supported by our findings that diet breath remained consistent between burned and unburned sites, which we would expect to increase if preferred prey populations changed (Steenhof and Kochert 1988). Loss of vegetation after fire may also provide increased access alternative prey resources such as ground squirrels and snakes, that may have been difficult to locate under shrub cover. Though the difference in the high use of snakes as prey in our study could be because we used modern techniques with motion-activated cameras as opposed to using prey remains and pellet sampling that can underestimate the proportion of snakes in eagle diets (Harrison, Kochert, Pauli and Heath 2019). However, the proportion of snakes brought to nests in burned areas was over 10 % more than that of unburned areas, suggesting that the overall shift in prey use may be associated with the fire.

The proportion of leporids delivered to nests by eagles was positively related to recreation use. The mechanisms driving this association are unclear and subject to speculation. Based on our findings with recreation shifts after the fire and the concentration of total recreation in unburned areas, this association with rabbits and high recreation may just be correlative with unburned areas. Alternately, leporids may be easier to find and hunt in areas with higher recreation use due to behavioral adaptations. European rabbits in urban areas with lower predation pressure had slower fleeing reactions to disturbance and longer times spent outside of burrows than those in rural areas with less human presence (Ziege et al. 2016). Additionally, disturbance may cause leporids to flush from cover, making them more vulnerable to predation (Steenhof, pers. comm.). Research is necessary to further investigate possible anthropogenic mechanisms controlling leporid abundance and demography, and behavioral adaptations of leporids in high and low recreation areas.

The proportion of pigeons in eagle diets was negatively associated with total average recreation use; more pigeons were brought to nests in areas with lower recreation use. Recreation probably did not displace pigeons, but eagles in high recreation areas may have shifted their diets towards more rock pigeons as a response to fewer leporids in areas with lower recreation use. The shift from preferred prey to rock pigeons has been seen in multiple studies (Marzluff et al. 1997, Real, Manosa and Munoz 2000, Palma, Beja, Pais, and Fonseca 2006, Heath and Kochert 2016) and can affect nestling survival directly and negatively (Dudek et al. 2018). However, if the shift to rock pigeons was a consequence of a decrease in preferred prey, we also would expect to see a positive association with the proportion of rock pigeons and burned areas. Multiple factors likely drive rock pigeon demography and the consumption of rock pigeons by eagles. Habitat associations of pigeons and other prey need to be assessed to mitigate this threat to eagles because rock pigeon populations may increase and expand following increased human development (Bonter et al. 2010). However, we often see particularly large flocks of pigeons inhabiting cliff faces of eagle nests in more remote sites, which warrants further investigation.

Neither diet breadth nor daily prey delivery rates were explained by fire or recreation use. This is contrary to previous studies that showed an increase in eagle diet diversity when the proportion of preferred prey in eagle diets decreased (Steenhof and Kochert 1988, Heath and Kochert 2016, Preston, Jones and Horton 2017). This suggests that eagles may have already been using alternative prey prior to wildfire, possibly due to regional differences in prey availability or eagles may have already adapted habitat shifts over time. Increased frequency and intensity of wildfires, over-grazing, recreation and development have been impacting vegetative characteristics of the region for at least 50 years, which have been simultaneously impacting prey populations over time. We may not have detected effects of recreation on diet because of the temporal pattern of recreation use in our study area. In this area, total recreation use decreased following a peak in early May (see Appendix A), and most of our diet information was collected after this peak. Diet data were also limited to a small snapshot during the nestling period, collected only after 3 years post-fire from eighteen nests, which included only 3 nests outside of burned areas. More diet sampling over time, as well as prey abundance estimates in both occupied and vacant territories are needed to track the effects of reduced shrub cover on prey availability, prey use, and eagle reproduction after fire.

CONCLUSION

Our study shows that fluctuations in anthropogenic stressors across the landscape are creating complex, additive and interactive effects on golden eagles and their prey in southwestern Idaho. Recreation pressure continues to be a major threat to eagles despite large-scale wildfires. As recreation pressure continues to increase, it is important that conservationists continue to monitor and understand the patterns and drivers of recreation use and its impact on wildlands, focusing not only on managing burned areas but the surrounding landscape. Though management of recreationists on the landscape is becoming increasingly hard in the open sagesteppe landscape, careful and informed management of both motorized and non-motorized recreation is essential in protecting golden eagles. More research is needed on the effects of synergistic stressors on wildlife demography and behavior, and the long-term impacts of shifting prey use and habitat degradation on eagle populations.

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Table 1. AICc table comparing candidate models used to explain off-road vehicle use per-trail, per-day on trails within 22 golden eagle territories in southwestern Idaho in 2013, 2014, 2017 and 2018. All models included the random effect of territory. Table includes the number of model parameters (K), delta AICc (ΔAICc), and model weights (AICcWt).

Model	K	ΔAICc	AICcWt
week + week^2 + weekend + period + burned + period:burned	9	0.00	0.87
week + week^2 + weekend + period + burned	8	3.75	0.13
weekend + period + burned + period:burn	7	63.33	0.00
week + week^2 + weekend + period	7	217.36	0.00
week + week^2 + weekend	6	218.54	0.00
weekend	4	289.71	0.00
week + week^2 + period + burned + period:burned	8	337.20	0.00
period + burned + period:burned	6	388.13	0.00
period + burned	5	395.12	0.00
burned	4	399.94	0.00
week + week^2	5	573.88	0.00
period	4	628.40	0.00
week	4	630.62	0.00
intercept only	3	632.71	0.00

Key: week = week of the year, weekend = weekday or weekend day, period = time period pre- and post-fire, burned = whether or not a territory was burned

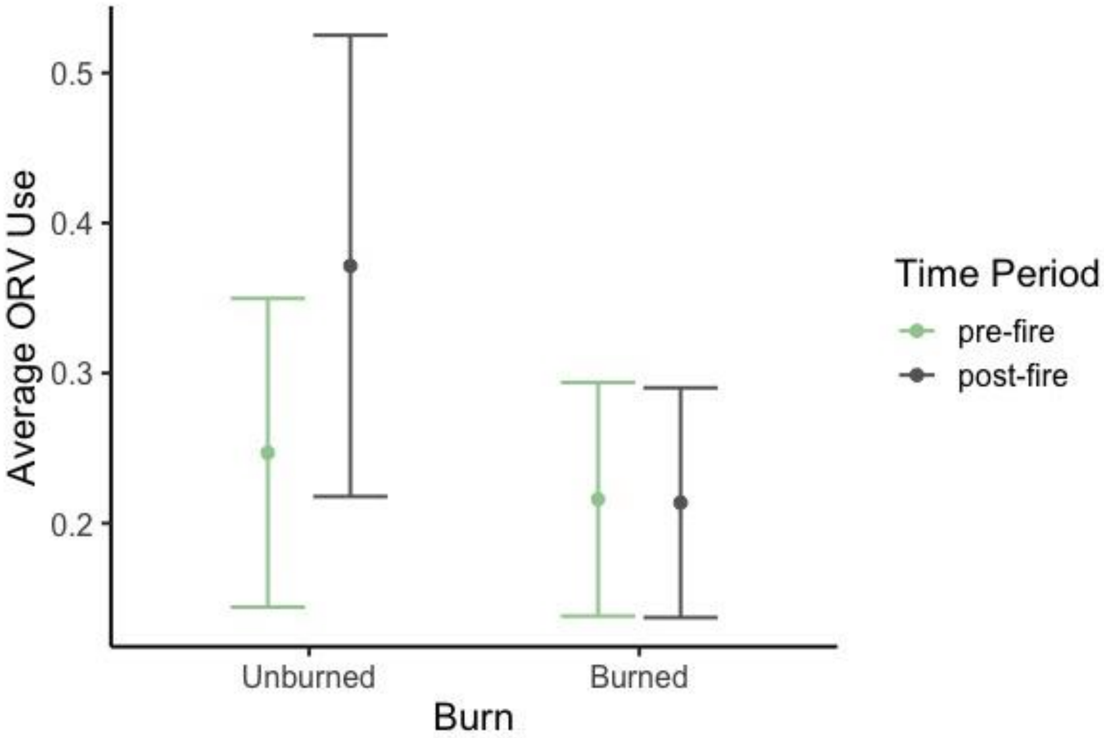

Figure 1. The interactive relationship between time period (pre- and post-fire) and whether or not an area burned on ORV use per-trail, per-day during the breeding season in 22 eagle territories along the Owyhee front of southwestern Idaho pre-fire (2013-2014) and post-fire (2017-2018). Post-fire, ORV use increased in unburned areas, but remained the same in burned areas.

Table 2. **AICc table comparing candidate models used to explain early season (15 January – 16 March) pedestrian use per trail, per day within 22 golden eagle territories in southwestern Idaho in 2013, 2014, 2017 and 2018. All models included the random effect of territory. Table includes the number of model parameters (K), delta AICc (ΔAICc), and cumulative model weights (AICcWt).**

Model	K	ΔAICc	AICcWt
week + week^2 + weekend + period + burned + period:burned	9	0.00	0.97
week + week^2 + period + weekend + burned	8	6.80	0.03
week + week^2 + period + burned + period:burned	8	22.23	0.00
week + week^2 + period + weekend	7	23.99	0.00
week + week^2 + weekend	6	25.65	0.00
period + burned + period:burned	6	31.67	0.00
period + burned	5	36.35	0.00
burned	4	38.90	0.00
weekend	4	42.41	0.00
week + week^2	5	46.25	0.00
week	4	54.56	0.00
period	4	55.00	0.00
intercept only	3	56.50	0.00

Key: week = week of the year, weekend = weekday or weekend day, period = time period pre- and post-fire, burned = whether or not a territory was burned

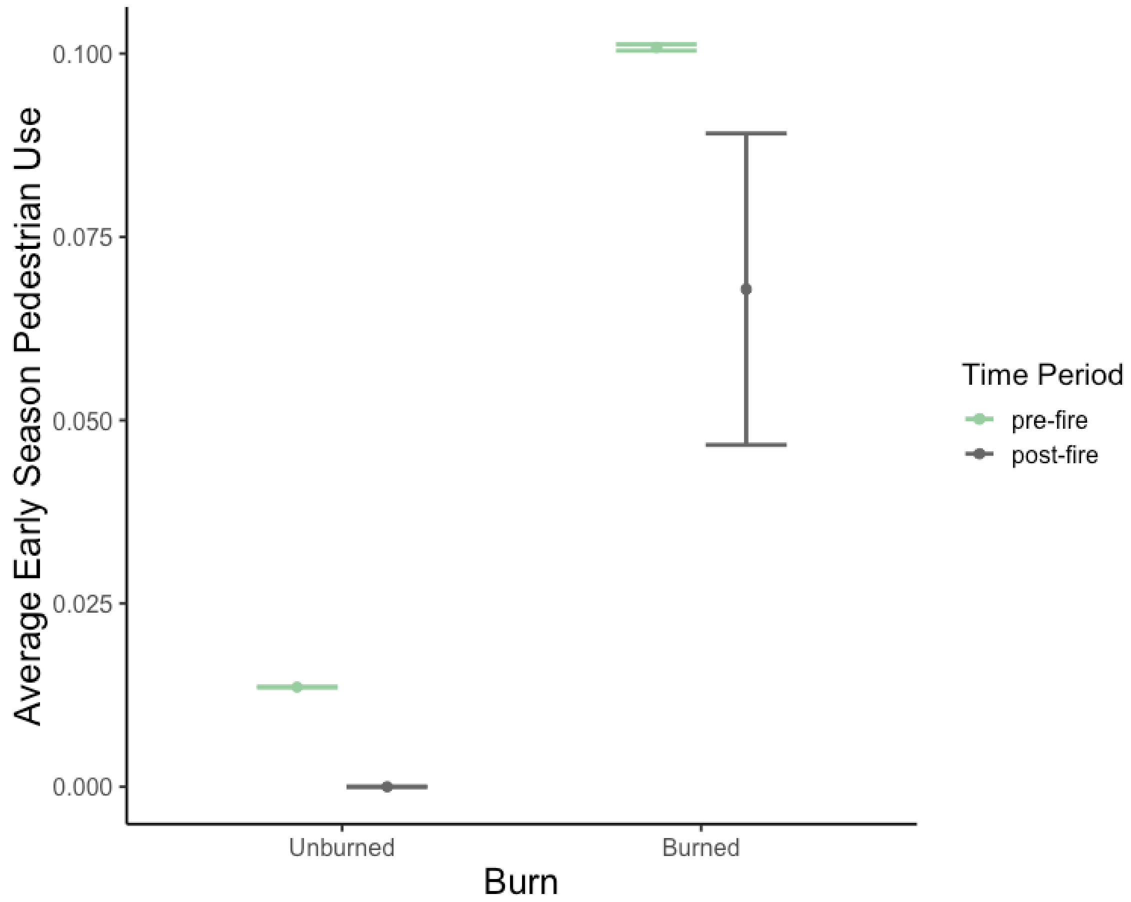

Figure 2. **The interactive relationship between time period (pre- and post-fire) and whether or not an area burned on average early season (15 January – 16 March) pedestrian use during the breeding season in 22 eagle territories along the Owyhee front of southwestern Idaho pre-fire (2013-2014) and post-fire (2017-2018). Post-fire, ORV use increased in unburned areas, but remained the same in burned areas.**

Table 3. AICc table comparing candidate models used to explain total recreation use per trail, per day within 1 km of 22 golden eagle territories in southwestern Idaho in 2013, 2014, 2017 and 2018. All models included the random effect of territory. Table includes the number of model parameters (K), delta AICc (ΔAICc), and cumulative model weights (AICcWt).

Model	K	ΔAICc	AICcWt
week + week^2 + weekend + period + burned + period:burned	9	0.00	1.00
week + week^2 + weekend + period + burned	8	15.67	0.00
weekend + period + burned + period:burned	7	93.49	0.00
week + week^2 + period + burned + period:burned	8	512.05	0.00
period + burned + period:burned	6	589.15	0.00
period + burned	5	606.49	0.00
burned	4	620.24	0.00
week + week^2 + weekend + period	7	126.49	0.00
week + week^2 + period	6	134.25	0.00
weekend	4	1236.14	0.00
week + week^2	5	1682.22	0.00
period	4	1749.86	0.00
week	4	1753.80	0.00
intercept only	3	1765.99	0.00

Key: week = week of the year, weekend = weekday or weekend day, period = time period pre- and post-fire, burned = whether or not a territory was burned

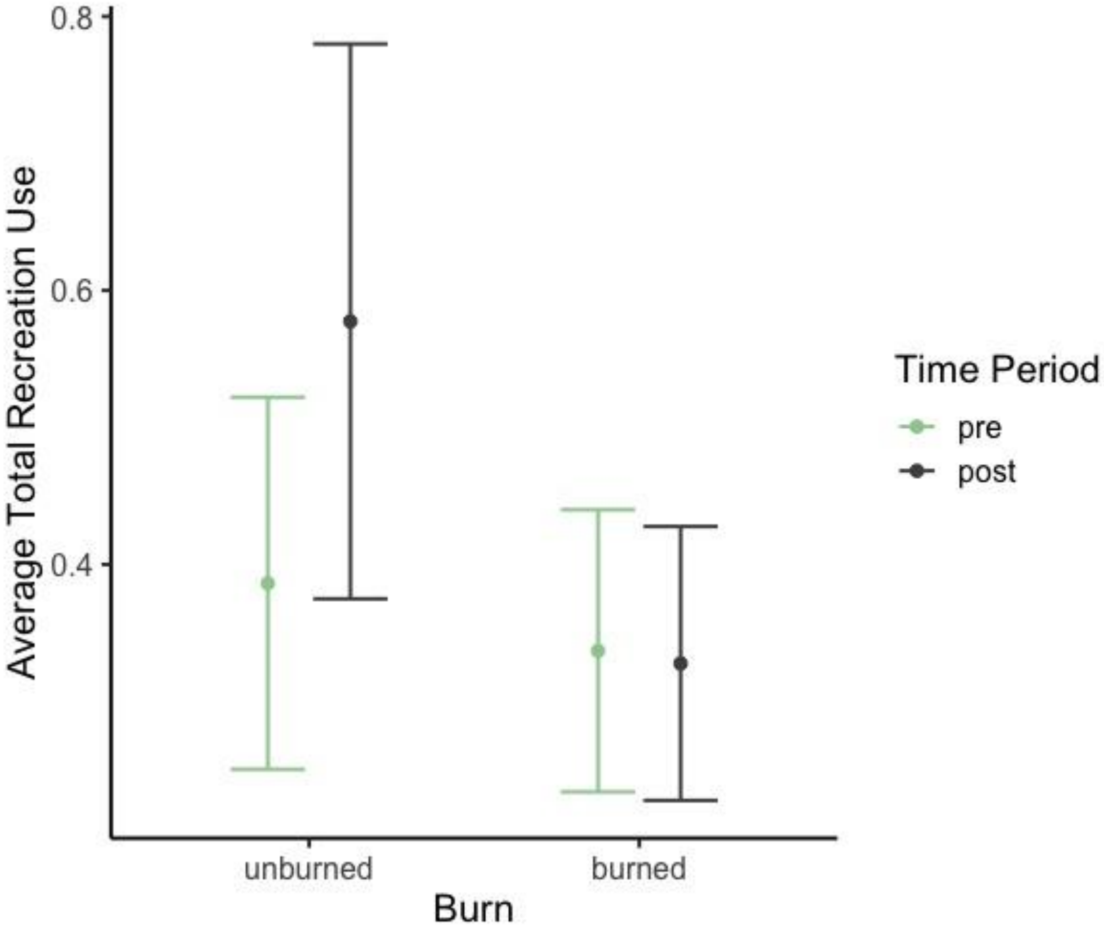

Figure 3. The interactive relationship between time period (pre- and post-fire) and whether or not an area burned on total recreation use per-trail, per-day during the breeding season in 22 golden eagle territories along the Owyhee front of southwestern Idaho pre-fire (2013-2014) and post-fire (2017-2018). After the fire, total recreation use increased in unburned areas, but remained the same in burned areas.

Table 4. Yearly summary of golden eagle territory occupancy, the proportion of confirmed egg-laying pairs and the average number of young fledged per egg-laying pair in 22 eagle territories monitored before and after wildfire burned 14 territories in 2015.

Time period	Year	Number of occupied territories	Number of confirmed egg-laying pairs	Confirmed egg-laying per occupied territory	Young fledged per egg-laying pair
pre-fire	2013	19	10	0.53	0.4
	2014	20	11	0.55	0.55
post-fire	2017	19	13	0.68	0.85
	2018	19	15	0.79	1.0

Table 5. AICc table comparing candidate models used to explain golden eagle territory occupancy in southwestern Idaho in 22 eagle territories monitored in 2013, 2014, 2017 and 2018. All models included the random effects of year and territory. Table includes the number of model parameters (K), delta AICc (ΔAICc), and cumulative model weights (AICcWt).

Model	K	ΔAIC	AICcWt
Avg_ORV + burned	5	0.00	0.25
Avg_ORV	4	0.05	0.25
intercept only	3	0.92	0.16
Avg_ORV + period	5	2.26	0.08
Avg_ORV + period + burned	6	2.28	0.08
period	4	2.89	0.06
burned	4	2.96	0.06
Avg_ORV + burned + period + burned:period	7	4.57	0.03
burned + period	5	4.99	0.02
burned + period + burned:period	6	6.90	0.01
Avg_ORV + burned + period + Avg_ORV:burned + burned:period + Avg_ORV:period + Avg_ORV:burned:period	10	10.28	0.00

Key: Avg_ORV= average off-road vehicle use per trail, per day, period= time period pre- and post-fire, burned= whether or not a territory was burned

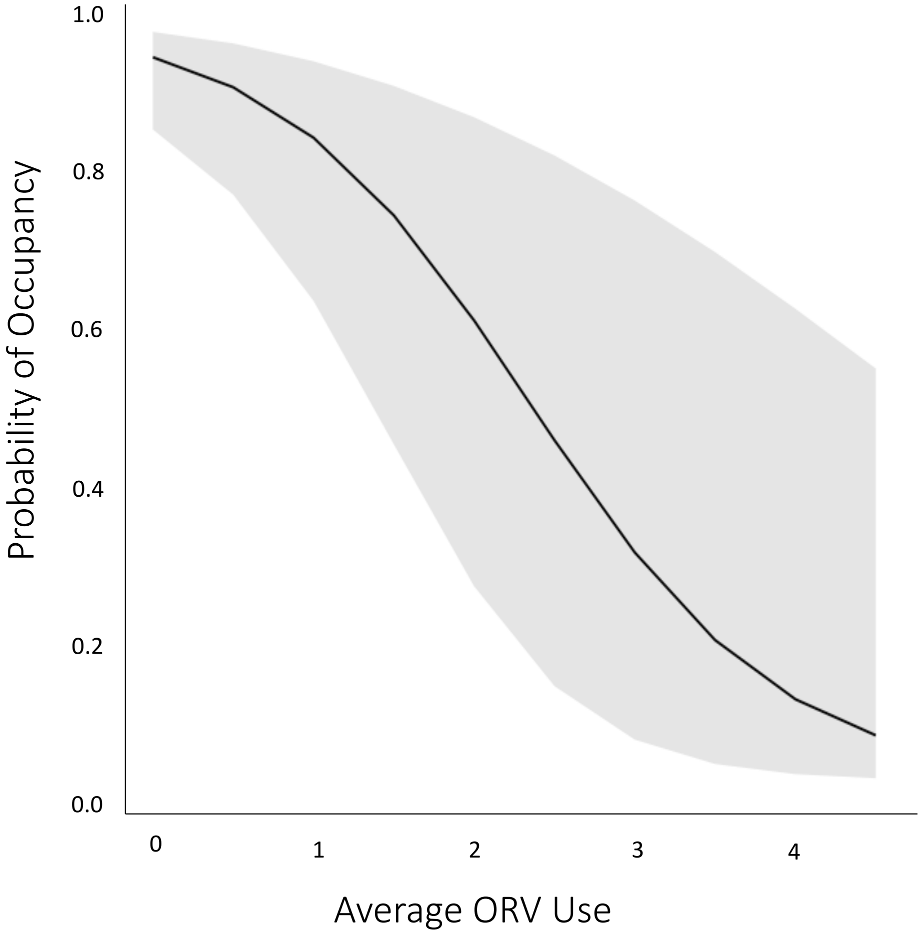

Figure 4a. **The relationship between average ORV use per trail, per day (Avg_ORV) and eagle territory occupancy during the breeding season in 22 golden eagle territories along the Owyhee front of southwestern Idaho in 2013, 2014, 2017 and 2018. ORV use was inversely associated with territory occupancy. Shaded area depicts 85% confidence intervals.**

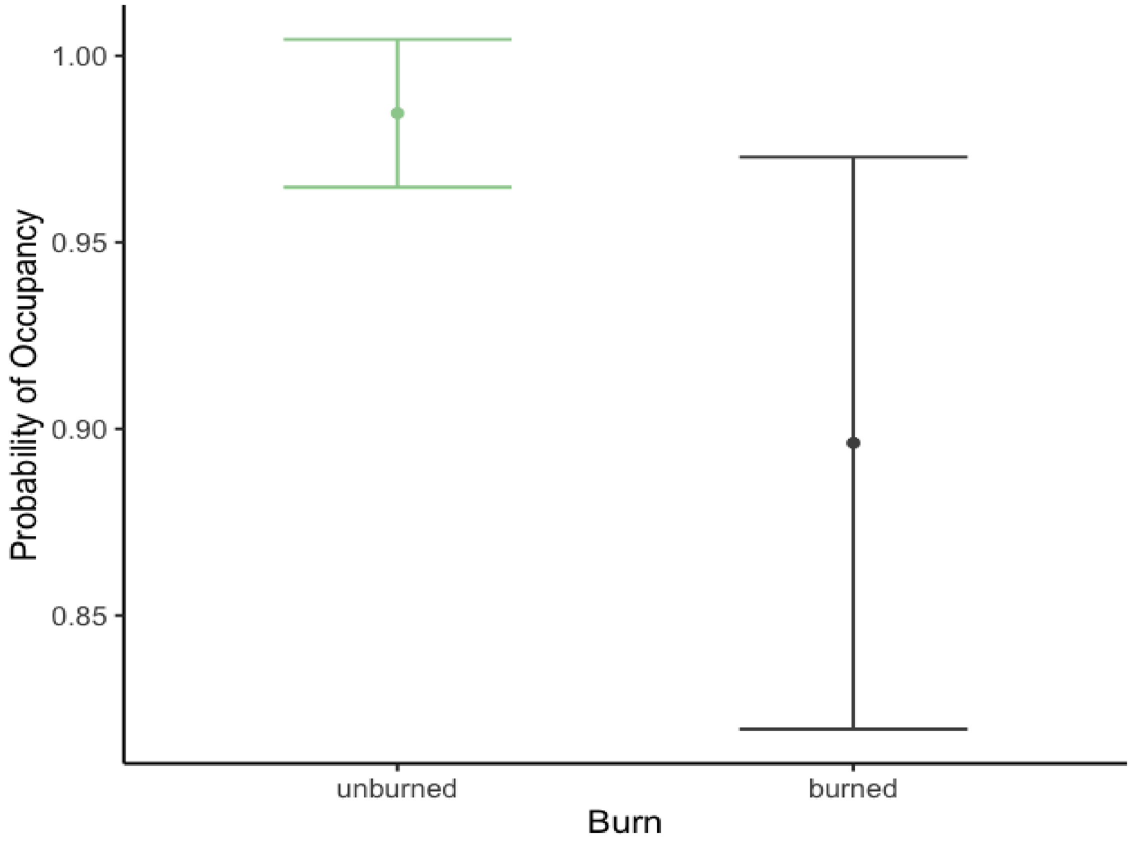

Figure 4b. **The relationship between the probability of eagle territory occupancy and whether or not an area burned in 22 golden eagle territories along the Owyhee front of southwestern Idaho before (2013-2014) and after (2017-2018) a large-scale wildfire. The probability of occupancy was greater in burned areas regardless of whether the time period was before or after the fire.**

Table 6. **AICc table comparing candidate models used to explain confirmed egg-laying of golden eagles in occupied territories in southwestern Idaho within 22 eagle territories monitored in 2013, 2014, 2017 and 2018. All models included the random effects of year and territory. Table includes the number of model parameters (K), delta AICc (ΔAICc), and cumulative model weights (AICcWt).**

Model	K	ΔAIC	AICcWt
PreLay_Ped + period + burned + period:burned	7	0.00	0.56
period + burned + period:burned	6	2.77	0.14
PreLay_Ped + burned + period + PreLay_Ped:burned + burned:period + PreLay_Ped:period + PreLay_Ped:burned:period	9	3.44	0.10
PreLay_Ped + period + burned	6	4.49	0.06
PreLay_Ped + period	5	4.86	0.05
PreLay_Ped + burned	5	6.10	0.03
period	4	6.62	0.02
PreLay_Ped	4	6.86	0.02
period + burned	5	7.31	0.01
intercept only	3	7.97	0.01
burned	4	8.37	0.01

Key: PreLay_Ped= average off-road vehicle use per trail, per day from 15 January to 16 March, period= time period pre- and post-fire, burned= whether or not a territory was burned

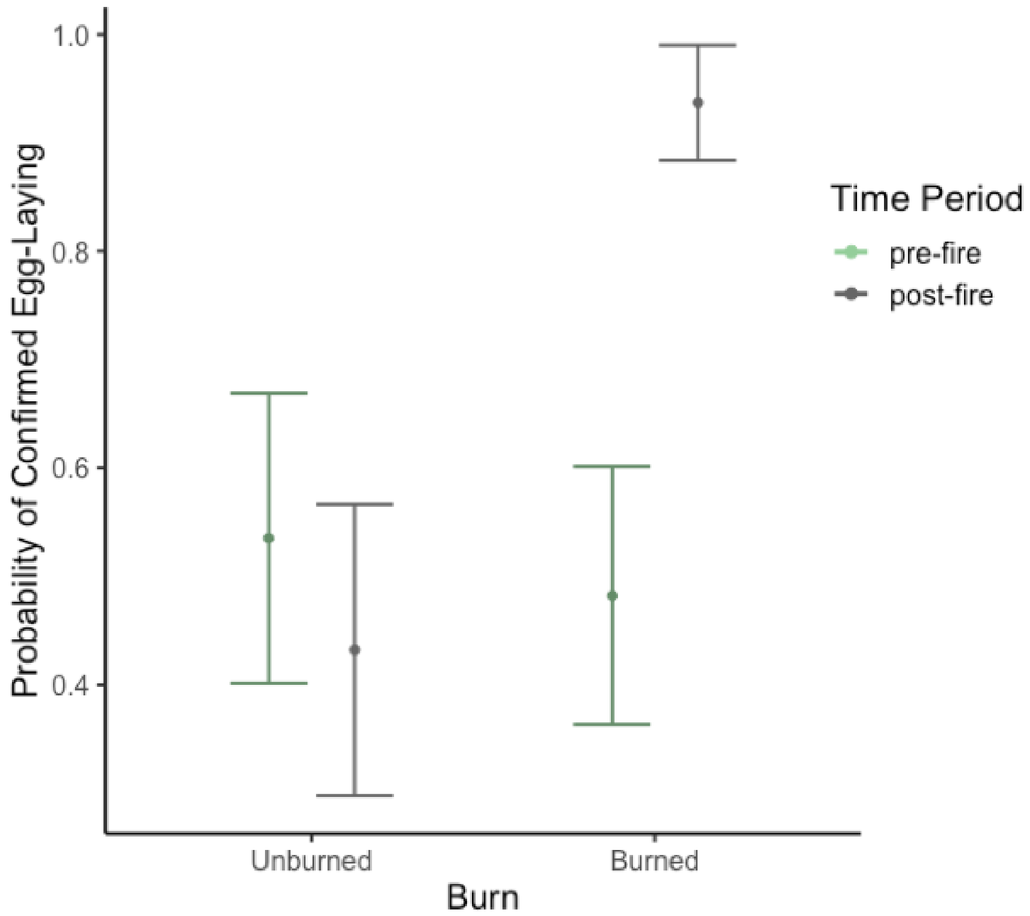

Figure 5a. **The interactive relationship between time period (pre- and post-fire) and whether or not a territory burned and the probability of confirmed egg laying within occupied golden eagle territories along the Owyhee front of southwestern Idaho pre-fire (2013-2014) and post-fire (2017-2018). In unburned areas, confirmed egg-laying did not significantly change pre- and post-fire, but in burned areas the probability of confirmed egg-laying increased post-fire compared to territories pre-fire.**

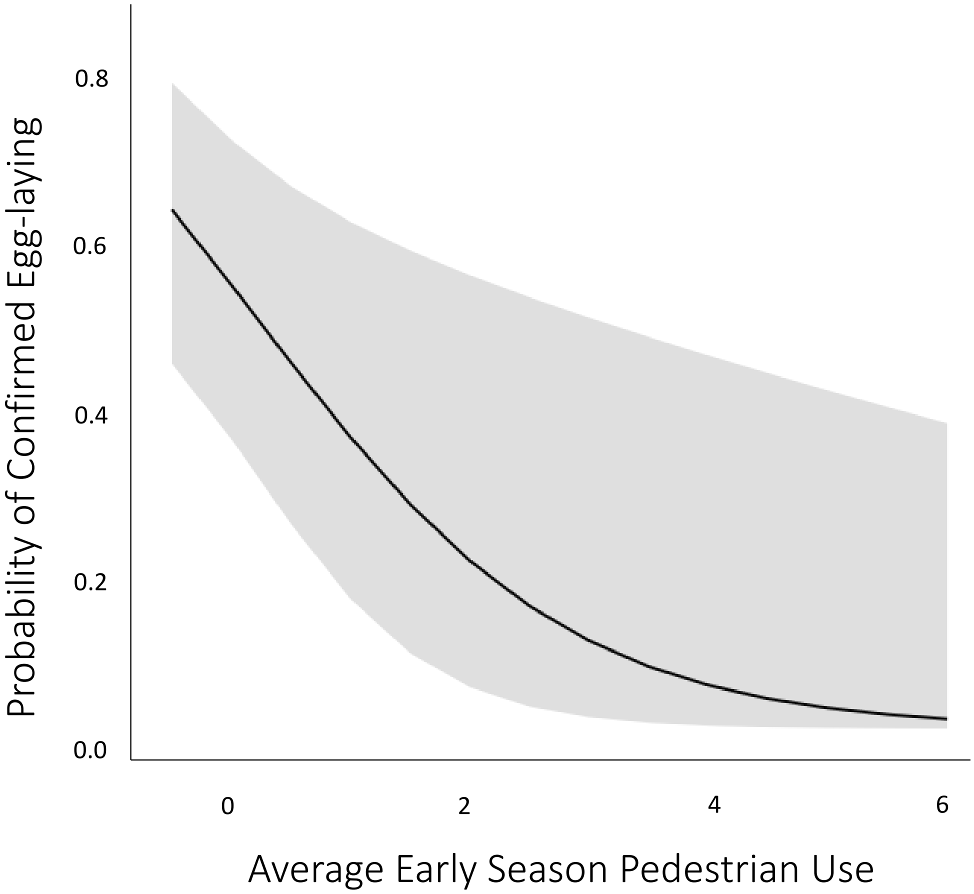

Figure 5b. The relationship between the probability of confirmed egg-laying in occupied golden eagle territories and average pedestrian use per-trail per-day before the mean egg-laying date (PreLay_Ped) in 22 eagle territories along the Owyhee front of southwestern Idaho in 2013, 2014, 2017 and 2018. Early-season pedestrian use was negatively associated with the probability of confirmed egg-laying. Shaded area depicts 85% confidence intervals.

Table 7. AICc table comparing candidate models used to explain the amount of young that successfully fledge from nests of egg-laying pairs in southwestern Idaho in 22 eagle territories monitored in 2013, 2014, 2017 and 2018. All models included the random effects of year and territory. Table includes the number of model parameters (K), delta AICc (ΔAICc), and cumulative model weights (AICcWt).

Model	K	ΔAIC	AICcWt
period	4	0.00	0.33
intercept only	3	0.61	0.24
Avg_Total + period	5	2.44	0.10
period + burned	5	2.46	0.10
Avg_Total	4	2.82	0.08
burned	4	2.97	0.07
Avg_Total + period + burned	6	4.99	0.03
period + burned + period:burned	6	5.06	0.03
Avg_Total + burned	5	5.31	0.02
Avg_Total + period + burned + period:burned	7	7.69	0.01
Avg_Total + burned + period + Avg_Total:burned + burned:period + Avg_Total:period + Avg_Total:burned:period	10	13.02	0.00

Key: Avg_Total= average total recreation use per trail, per day, period= time period pre- and post-fire, burned= whether or not a territory was burned

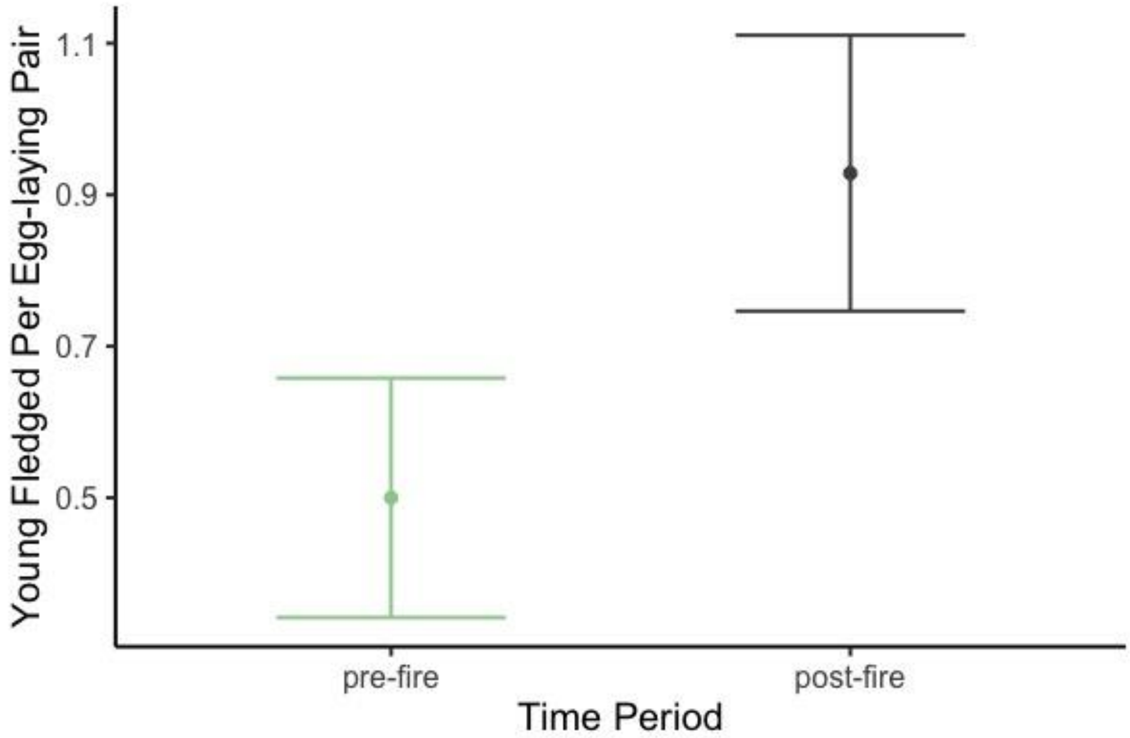

Figure 6. **The relationship between time period (pre- and post-fire) and the number of golden eagle young that successfully fledged from nests of egg-laying pairs in 22 eagle territories along the Owyhee front of southwestern Idaho pre-fire (2013-2014) and post-fire (2017-2018). The number of young that successfully fledged was higher post-fire than pre-fire.**

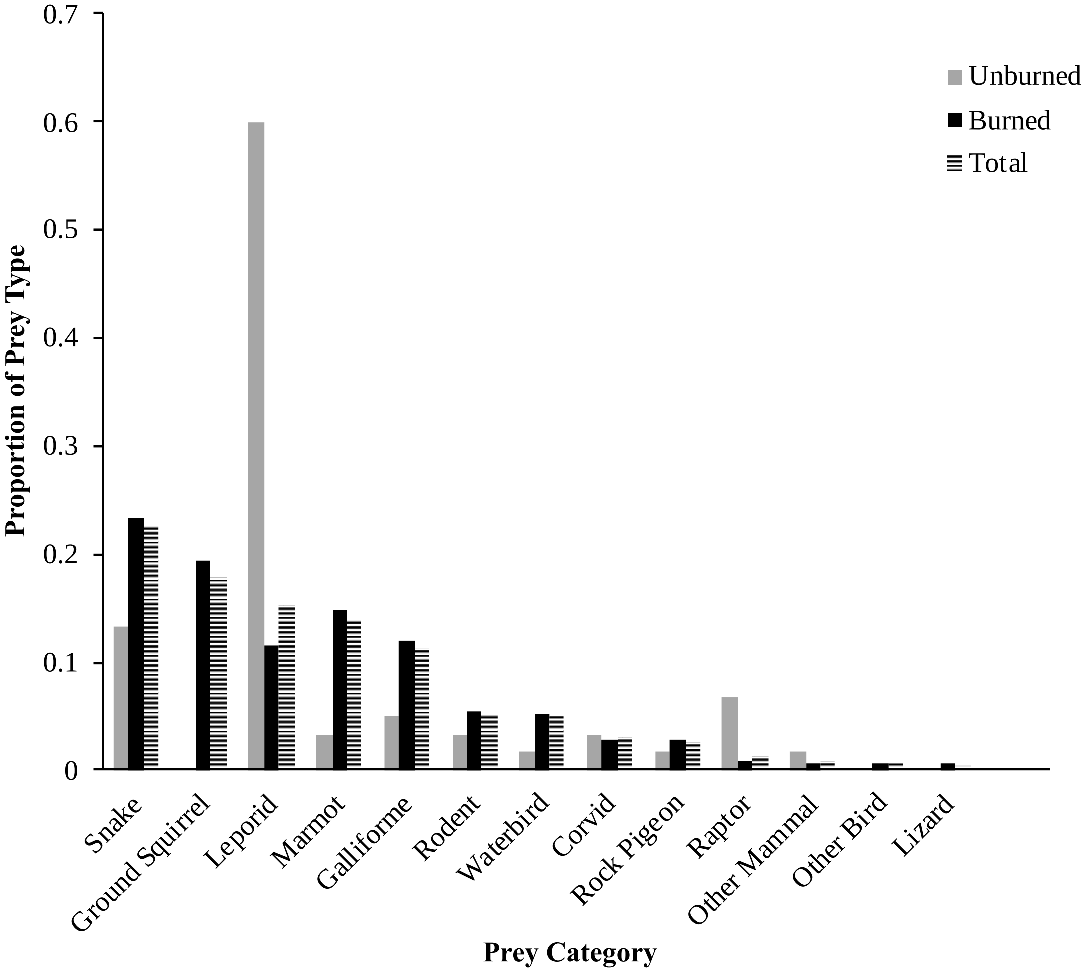

Figure 7. The proportion of prey categories brought to golden eagle nests identified from motion-activated cameras installed in 18 nests during brood-rearing in southwestern Idaho in 2017 and 2018.

Table 8. AICc table comparing candidate models used to explain the number of leporid species brought to golden eagle nests identified from motion-activated cameras installed in 18 nests during brood-rearing in southwestern Idaho in 2017 and 2018. All models included the random effects of year and territory. Table includes the number of model parameters (K), delta AICc (ΔAICc), and cumulative model weights (AICcWt).

Model	K	ΔAIC	AICcWt
burned	6	0.00	0.44
burned + Avg_Total	5	0.78	0.30
Intercept Only	4	2.01	0.16
Avg_Total	4	3.63	0.07
burned + Avg_Total + burned:Avg_Total	3	5.77	0.02

Key: Avg_Total= average total recreation use per trail, per day, burned= whether or not a territory was burned

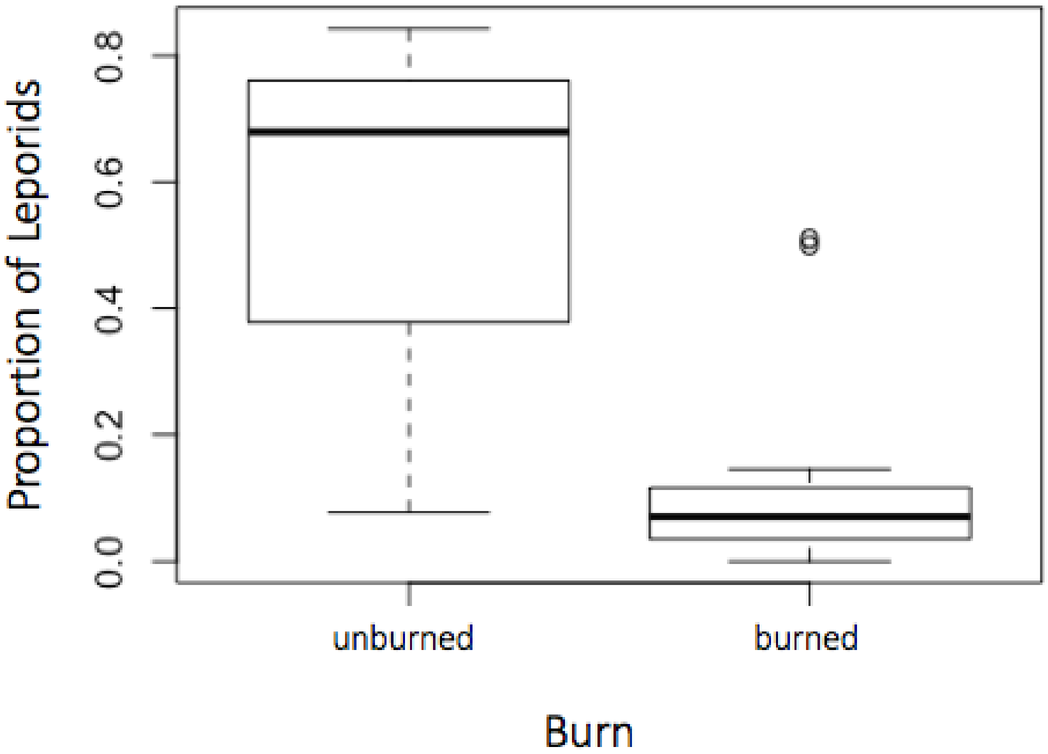

Figure 8. The proportion of leporid prey brought to golden eagle nests after the 2015 Soda fire documented from 18 nests within burned (15) and unburned (3) territories along the Owyhee front of southwestern Idaho in 2017 and 2018. Golden eagles brought a lower proportion of leporid prey in burned areas compared to unburned.

Table 9. AICc table comparing candidate models used to explain the number of rock pigeons brought to golden eagle nests identified from motion-activated cameras installed in 18 nests during brood-rearing in southwestern Idaho in 2017 and 2018. All models included the random effects of year and territory. Table includes the number of model parameters (K), delta AICc (ΔAICc), and cumulative model weights (AICcWt).

Model	K	ΔAIC	AICcWt
Avg_Total	4	0.00	0.58
intercept only	3	1.49	0.27
Avg_Total + burned	5	3.89	0.08
burned	4	4.78	0.05
burned + Avg_Total + burned:Avg_Total	6	7.97	0.01

Key: Avg_Total= average total recreation use per trail, per day, burned= whether or not a territory was burned

Table 10. AICc table comparing candidate models used to explain the number prey brought to golden eagle nests per day identified from motion-activated cameras installed in 18 nests during brood-rearing in southwestern Idaho in 2017 and 2018. All models included the random effects of year and territory. Table includes the number of model parameters (K), delta AICc (ΔAICc), and cumulative model weights (AICcWt).

Model	K	ΔAIC	AICcWt
age	4	0.00	0.64
age + age^2	5	1.90	0.25
age + weekend	5	4.22	0.08
age + age^2 + weekend	6	6.13	0.03
intercept only	3	14.50	0.00
burned	4	16.79	0.00
Avg_Total	4	17.39	0.00
weekend	4	18.73	0.00
burned + Avg_Total + burned:Avg_Total	6	21.45	0.00

Key: Avg_Total= average total recreation use per trail, per day, age= nestling age, in days, weekend= weekday or weekend day, burned= whether or not a territory was burned

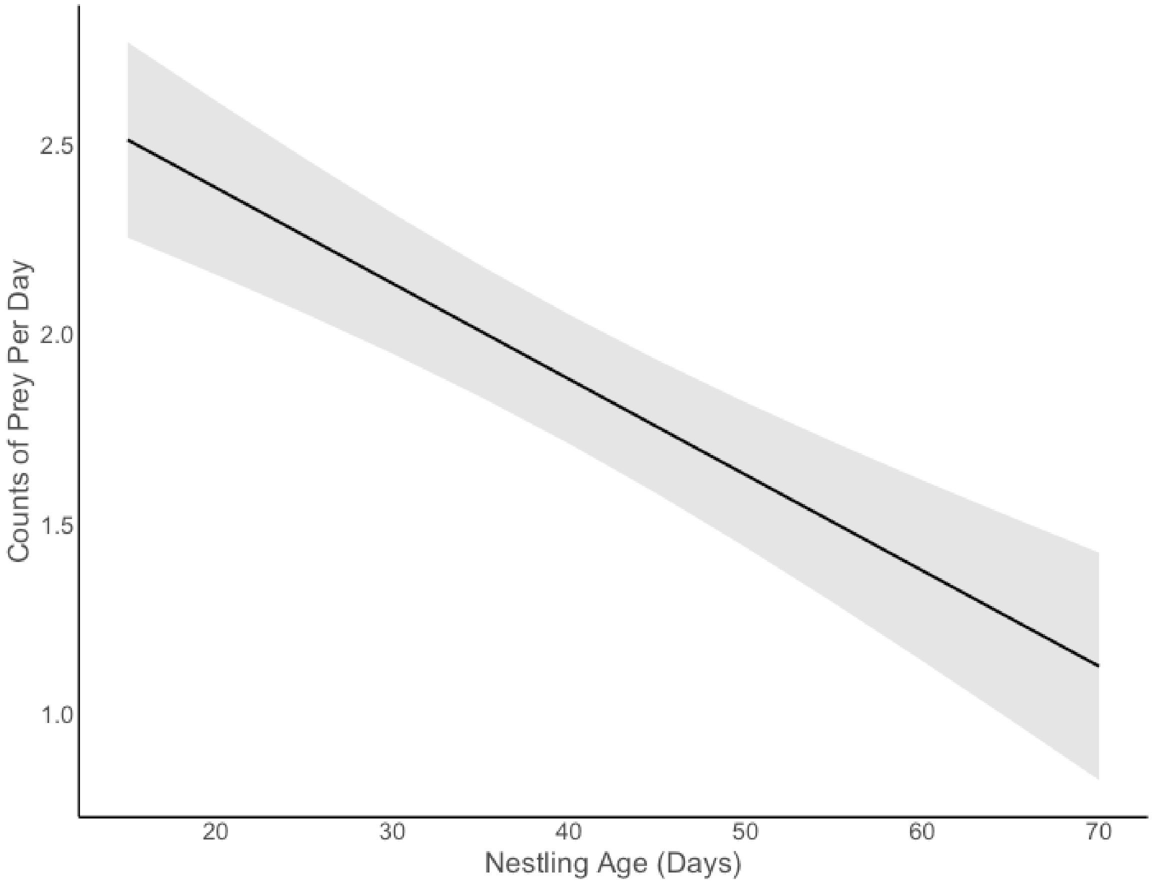

Figure 9. The inverse relationship between average nestling age (in days) and number of prey per day brought to golden eagle nests by adults in 18 nests along the Owyhee front of southwestern Idaho in 2017 and 2018.

APPENDIX A

Supplementary information on the effects of temporal variation and wildfire on recreation patterns in southwestern Idaho

Recreation patterns changed differentially after fire based on the type of recreationist and total recreation volumes varied temporally, where use changed throughout the eagle breeding season and there was more recreation use on weekends than on weekdays. We reported changes in ORV use and pedestrian use after fire because of past associations with these types of recreation on eagle reproductive biology. However, road vehicle users and other non-motorized users in our area (horseback riding and mountain biking) also add recreation pressure to the landscape and could respond to wildfire. Road vehicle use followed the same general temporal use pattern as other recreationists but did not seem to be affected by the wildfire. Whether a territory "burned" and the interactive effect of burned and time period affected road vehicles, but these effects are unreliable because confidence intervals for both overlapped zero. Non-motorized users were affected by the interaction between burned areas and time period: In unburned areas use remained unchanged after fire, but in burned areas non-motorized use decreased. Understanding the shifting recreation patterns of all recreation types may be important in the holistic management of these areas following wildfire.

Table A.1. AICc table comparing candidate models used to explain road vehicle use per-trail, per-day on trails within 22 golden eagle territories in southwestern Idaho in 2013, 2014, 2017 and 2018. All models included the random effect of territory. Table includes the number of model parameters (K), delta AICc (ΔAICc), and model weights (AICcWt).

Model	K	ΔAICc	AICcWt
week + week^2 + weekend + period + burned	8	0.00	0.62
week + week^2 + weekend + period + burned + period:burned	9	0.95	0.38
weekend + period + burned + period:burn	7	14.60	0.00
week + week^2 + period + burned + period:burned	8	135.02	0.00
burned	4	176.98	0.00
week + week^2 + weekend + period	7	314.26	0.00
week + week^2 + weekend	6	343.15	0.00
period	4	472.51	0.00
week + week^2	5	492.70	0.00
intercept only	3	507.40	0.00
week	4	508.69	0.00

Key: week = week of the year, weekend = weekday or weekend day, period = time period pre- and post-fire, burned = whether or not a territory was burned

Table A.2. AICc table comparing candidate models used to explain non-motorized use (mountain biking and horseback riding) per-trail, per-day on trails within 22 golden eagle territories in southwestern Idaho in 2013, 2014, 2017 and 2018. All models included the random effect of territory. Table includes the number of model parameters (K), delta AICc (ΔAICc), and model weights (AICcWt).

Model	K	ΔAICc	AICcWt
week + week^2 + weekend + period + burned + period:burned	9	0.00	1.00
week + week^2 + weekend + period + burned	8	12.70	0.00
weekend + period + burned + period:burn	7	23.68	0.00
week + week^2 + weekend + period	7	37.03	0.00
week + week^2 + weekend	6	40.61	0.00
week + week^2 + period + burned + period:burned	8	46.88	0.00
burned	4	84.16	0.00
week + week^2	5	89.87	0.00
week	4	104.08	0.00
period	4	107.74	0.00
intercept only	3	108.35	0.00

Key: week = week of the year, weekend = weekday or weekend day, period = time period pre- and post-fire, burned = whether or not a territory was burned

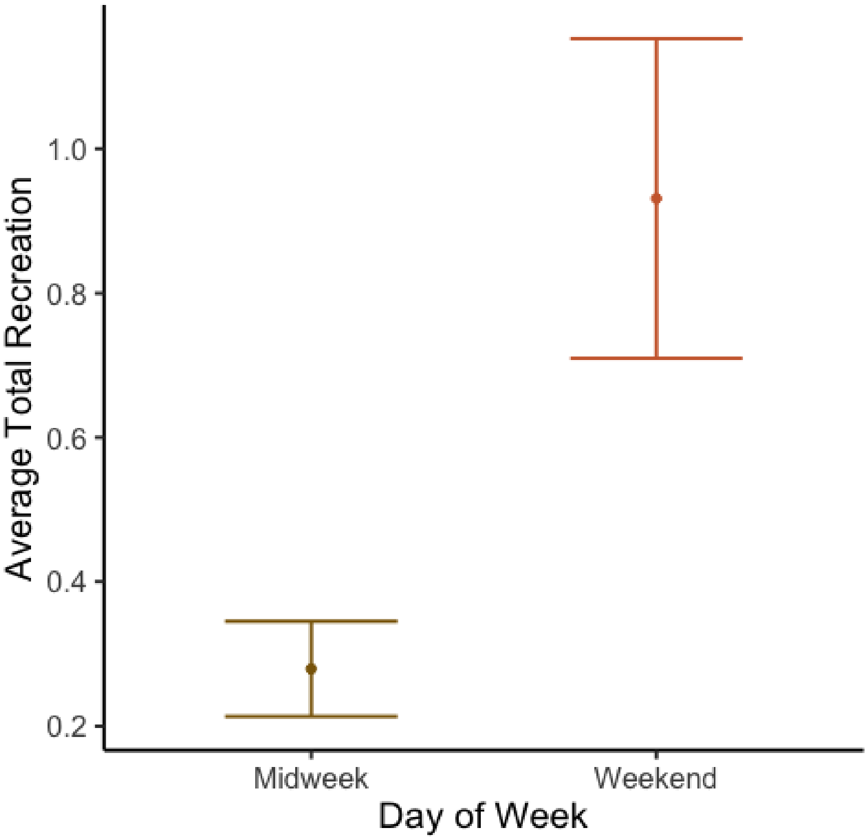

Figure A.1. Midweek and weekend day comparison of average total recreation use per-trail, per-day during the breeding season measured within 22 golden eagle territories along the Owyhee front of southwestern Idaho.

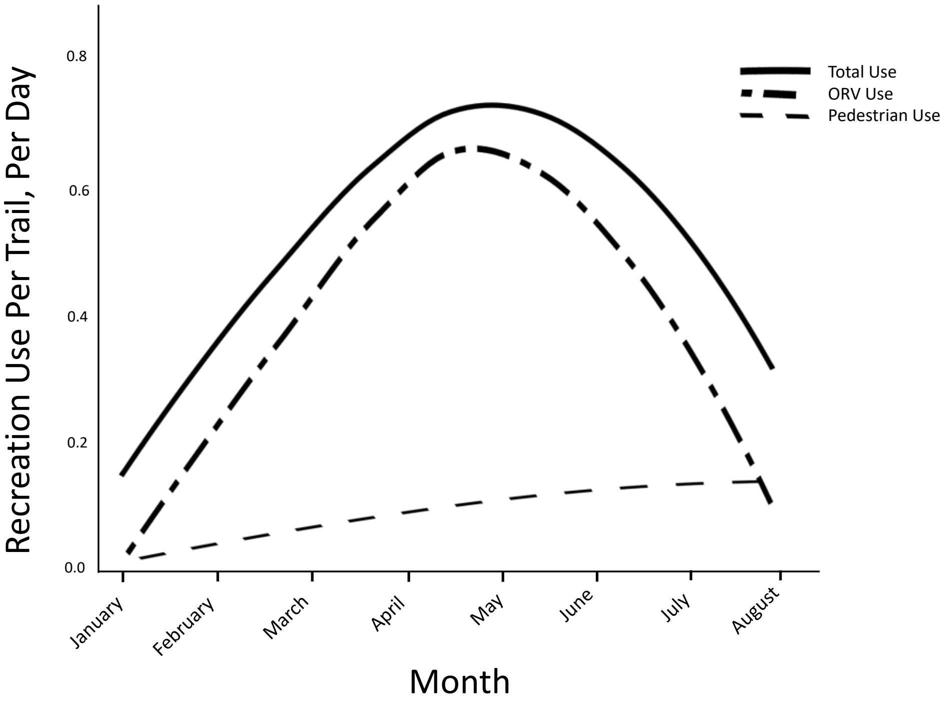

Figure A.2. Temporal variation of total recreation, ORV use and pedestrian use per-trail, per-day within 22 golden eagle territories along the Owyhee front of southwestern Idaho during the breeding season in 2013-2014 and 2017-2018.

APPENDIX B

Supplementary information on golden eagle reproduction and weather in southwestern Idaho

Table B.1. Extreme winter and summer weather before and after a large-scale wildfire, referenced from Boise, Idaho. The table includes winter severity prior to the timing of golden eagle egg-laying (Nov- Feb) measured in Heating Degree Days (HDD), and extreme weather during golden eagle brood-rearing (15 May- 15 Jun) measured in the number of days that reached > 32° C.

Period	Year	HDD	Days > 32° C
Pre-fire	2013	3722	4
	2014	3403	1
Post-fire	2017	3922	3
	2018	3408	4

APPENDIX C

Supplementary information on golden eagle diet during brood rearing in southwestern Idaho

Table C.1. Prey identified from motion-activated cameras placed in 18 golden eagle nests during brood-rearing in southwestern Idaho in 2017 and 2018. We grouped items together based on the lowest taxonomic level identified and sorted them into biologically meaningful categories (bold). Information includes the count of each prey type and subtotal for each category, the percent of the total count, total biomass contributions and the percent of the total biomass. Items that could not be assigned to a category were not included in total counts.

Prey Types	Count	% Total Count	Biomass	% Total Biomass
Ground squirrels				
Urocitellus spp.	120	0.154	29472	0.061
Urocitellus beldingi	10	0.013	3150	0.007
Callospermophilus lateralis	9	0.012	2232	0.005
Subtotal Ground Squirrels	139	0.178	34854	0.073
Leporids				
Leporid spp.	55	0.071	31203	0.065
Sylvilagus nuttallii	42	0.054	27300	0.057
Lepus californicus	22	0.054	46508	0.097
Subtotal Leporids	128	0.153	105011	0.218
Marmots				
Marmota flaviventris	115	0.138	280113	0.406
Subtotal Marmots	115	0.138	280113	0.406
Rodents				
Rodent spp.	22	0.028	1828	0.004
Neotoma cinerea	8	0.010	2216	0.005
Neotoma lepida	7	0.009	868	0.002
Neotoma spp.	4	0.005	1124	0.002
Subtotal Rodents	41	0.053	6031	0.013
Other Mammals				
Canis latrans	3	0.004	6129	0.013
Antilocapra americana	2	0.003	5400	0.011
Felis catus	1	0.001	1800	0.004
Subtotal Other Mammals	6	0.008	13329	0.028
Galliformes				
Callipepla californica	21	0.026	3400	0.007
Alectoris chukar	63	0.076	29494	0.061
Galliforme spp.	6	0.008	1107	0.002
Perdix perdix	4	0.005	1556	0.003
Subtotal Galliformes	94	0.114	35557	0.074
Waterbirds				
Larus californicus	16	0.021	9760	0.020

Anas platyrhynchos	12	0.015	13135	0.027
Larus spp.	8	0.010	5064	0.011
Fulica americana	1	0.001	654	0.001
Numenius americanus	1	0.001	590	0.001
Anas spp.	1	0.001	767	0.002
Subtotal Waterbirds	42	0.050	31380	0.062
Corvids				
Corvus corax	18	0.022	12632	0.026
Pica hudsonia	7	0.008	1020	0.002
Subtotal Corvids	25	0.029	23311	0.028
Pigeons				
Columba livia	21	0.027	6972	0.015
Subtotal Pigeons	21	0.027	5790	0.015
Raptors				
Tyto alba	4	0.005	2100	0.004
Buteo regalis	2	0.003	990	0.002
Bubo virginianus	1	0.001	1310	0.003
Asio otus	1	0.001	260	0.001
Buteo spp.	1	0.001	513	0.001
Owl spp.	1	0.001	260	0.001
Subtotal raptors	13	0.013	5433	0.011
Other Birds				
Sturnella neglecta	4	0.005	380	0.001
Zenaida macroura	1	0.001	134	0.000
Subtotal Other Birds	6	0.006	514	0.001
Snakes				
Pituophis catenifer	162	0.208	32724	0.068
Coluber constrictor	8	0.010	616	0.001
Masticophis taeniatus	4	0.005	408	0.001
Colubrid spp.	2	0.003	267	0.001
Subtotal Snakes	178	0.226	60252	0.071
Lizards				
Lizard spp.	2	0.003	36	0.000
Gambelia wislizenii	1	0.001	23	0.000
Phrynosoma platyrhinos	1	0.001	18	0.000
Subtotal lizards	4	0.005	100	0.000
Unknown Mammals	20	--	--	--
Unknown Birds	12	--	--	--
Unknown	36	--	--	--

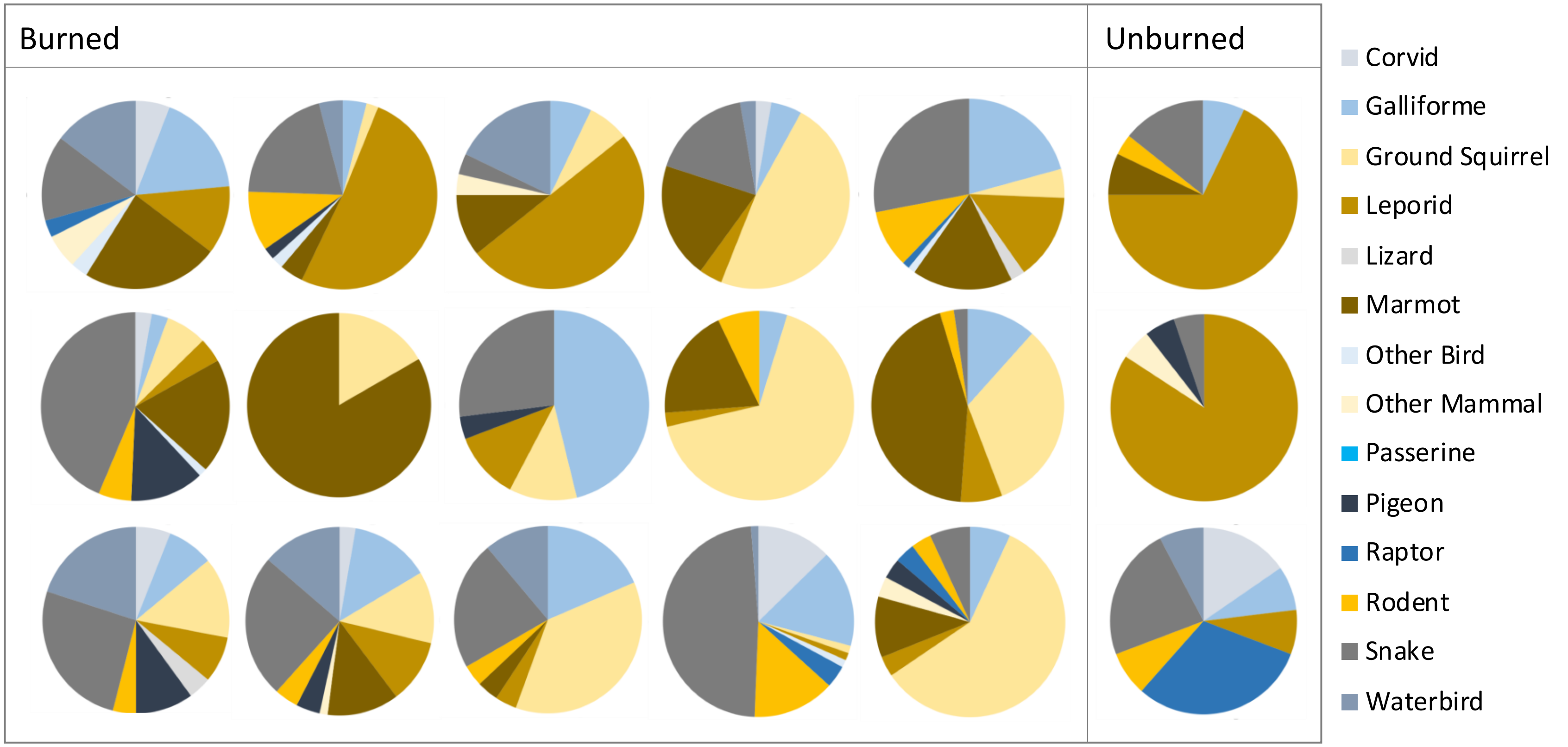

Figure C.1. **The proportion of prey categories brought to golden eagle nests identified from motion-activated cameras installed in 18 nests during brood-rearing in southwestern Idaho in 2017 and 2018 after a large-scale wildfire. Pie charts represent the diet composition of individual nests within burned (n = 15) and unburned (n = 3) eagle territories.**

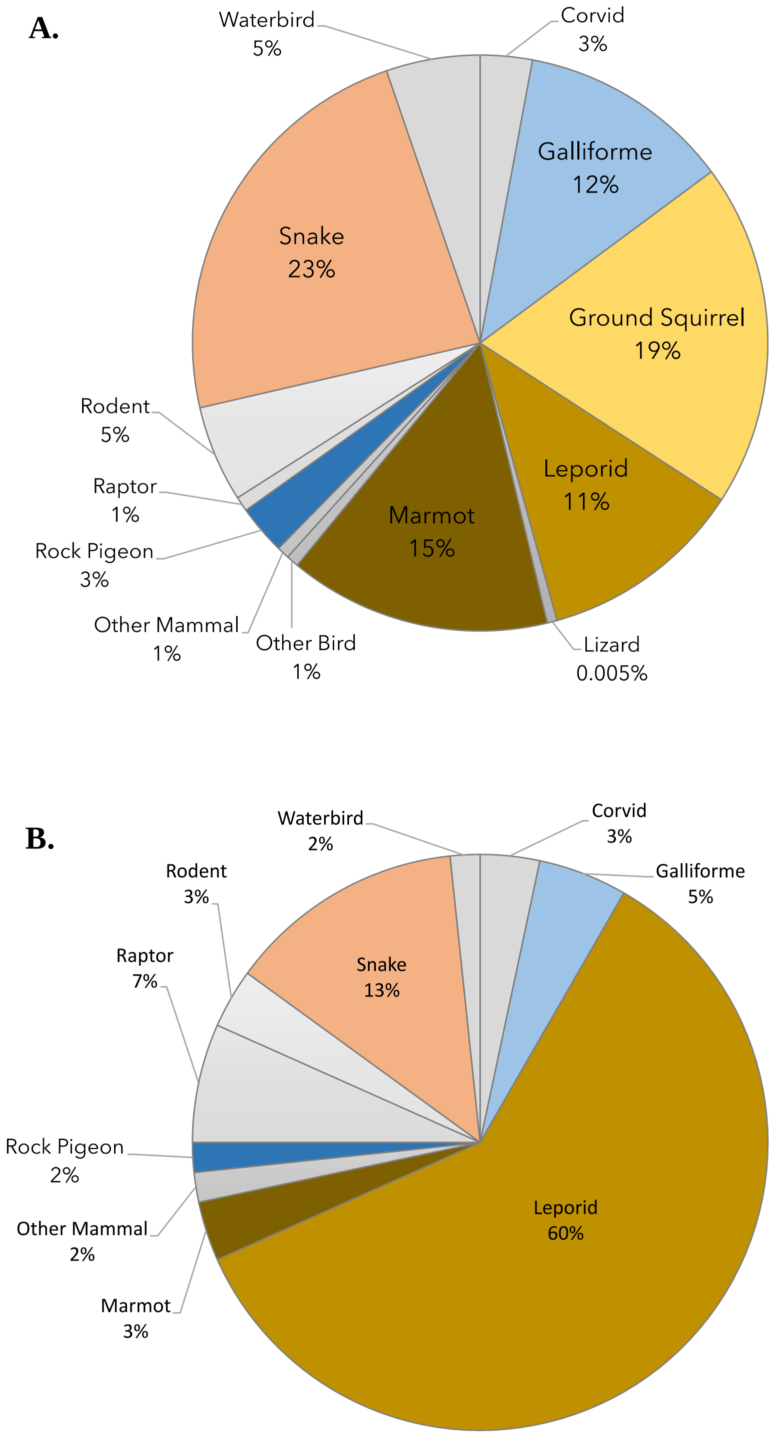

Figure C.2. **The proportion of prey categories identified from motion-activated cameras installed in eagle nests during brood-rearing in southwestern Idaho in 2017 and 2018, 3 and 4 years after a large-scale wildfire. Pie charts represent prey items from nests within A) burned (n = 15) and B) unburned (n = 3) territories.**

Table C.2. Prey identified by motion-activated cameras installed in 18 eagle nests during brood-rearing in southwestern Idaho in 2017 and 2018, 3 and 4 years after a large-scale wildfire within both burned (15) and unburned (3) territories. Identified prey that could be sorted into 13 biologically meaningful categories were used to calculate the Levin's index of diet diversity and Standardized Levin's index for each nest.

	2017				2018			
Territory	No. Prey Items	Survey Length (days)	Levin's Index	Standardized Levin's	No. Prey Items	Survey Length (days)	Levin's Index	Standardized Levin's
Con Shea	16	10.19	5.12	0.34	--	--	--	--
Hart Creek	19	7.72	1.39	0.02	--	--	--	--
Hardtrigger*	45	30.32	6.57	0.17	62	33.03	3.14	0.04
Poison Creek*	--	--	--	--	74	38.93	3.89	0.04
Rats Nest*	--	--	--	--	12	5.27	1.38	0.03
Red Canyon*	57	20.95	6.38	0.11	77	37.24	6.89	0.08
Rock Cabin Springs	--	--	--	--	29	11.05	2.03	0.04
Reynolds Canyon*	--	--	--	--	33	25.04	3.27	0.08
Reynolds Lower*	--	--	--	--	27	22.71	3.19	0.09
Sage Creek*	30	12	4.21	0.12	85	37.08	3.38	0.03
Squaw Creek*	48	13.84	2.05	0.02	75	39.02	3.26	0.03
Upper Hardtrigger*	--	--	--	--	84	39.67	5.4	0.05
Wilson Creek*	30	12.66	2.7	0.06	43	16.72	3.12	0.05

***** > 60% of territory within the Soda fire boundary