EFFECTS OF HABITAT DISTURBANCES ON REPTILES IN SAGEBRUSH STEPPE

by

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The following individuals read and discussed the thesis submitted by student Kristina Joan Parker, and they evaluated the student's presentation and response to questions during the final oral examination. They found that the student passed the final oral examination.

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DEDICATION

I would like to dedicate my thesis to my nuclear family and my chosen family. Thank you for all the support, love, guidance, and laughter that has kept me pushing and never giving up.

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I cannot begin to express my thanks and appreciation for my committee, you all have encouraged me, pushed me, but most of all supported me every step of the way. Thank you for always being ready to ‘bat’ for me, knowing that gave me the confidence to keep progressing. I’m grateful for the wide spectrum of advice and knowledge you have shared with me. I have learned a great deal academically, professionally, and personally from you all; thank you David, Jay, and Sven. I am thankful for the John Cossel and Chuck Peterson for trusting me to continue the legacy. I appreciate the long conversations and days ‘herping’ with you both.

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ABSTRACT

Reptiles inhabiting shrub-steppe ecosystems of the Intermountain West have adapted to harsh, unpredictable desert conditions, yet recent changes in disturbance regimes may put species at risk. In southwest Idaho, cheatgrass (*Bromus tectorum*) has altered the fire regime resulting in a vast conversion of shrub-steppe to mostly annual grasslands that burn too frequently to allow shrublands to recover. Southwest Idaho has the highest reptile diversity in the Pacific Northwest, yet we know little about reptile community dynamics in response to the cheatgrass-fire cycle. We hypothesized that wildfires and cheatgrass negatively affect reptile communities directly (i.e., mortality during fires) and indirectly through changes in the quality of reptile habitats at multiple spatial scales. We used trapping and visual encounter survey data to quantify the effect of previous wildfires, cheatgrass, and other habitat metrics on reptile richness, diversity, occupancy, and abundance at local (i.e., trapping array) and landscape levels. We found that vegetation cover, distance to a rock outcrop, and wildfire frequency were essential predictors c reptile abundance at both spatial scales. We found that many reptile species were not affected by cheatgrass cover but were affected by wildfire frequency. Lizard richness decreased with the number of times an area immediately around a trapping array burned. Our models indicated that occupancy for many reptile species declined in areas that burned, especially in areas with repeated burns at the local level. We found that only gophersnake abundance was significantly negatively affected by wildfire at the local level. Our research contributes to the growing body of evidence that the cheatgrass-fire cycle in the western U.S. negatively impacts many species, including reptiles. However, the effect on communities is nuanced, with winners and losers depending on a combination of habitat associations, life history, and environmental sensitivities.

Continual surveying efforts, via live-trap or visual encounter, are important for the survival of reptiles in southwest Idaho, especially for the species of concern. We further examined the occupancy of Great Basin rattlesnake (*Crotalus oreganus lutosus*) by assessing the genetic differentiation among and between highly occupied locations throughout the Morley Nelson Birds of Prey National Conservation Area (NCA). In addition to the cheatgrass-fire cycle, *C.o. lutosus* faces targeted persecution from vehicles and recreational shooters. These factors contribute to a decline in *C.o. lutosus* occupancy probability, which is potentially problematic— an understanding of the population genetics is powerful from a conservation standpoint. We predicted the presence of at least two subpopulations, due to the geography and urbanization of the area. The NCA encompasses a large area of land vital to wildlife, however, from a genetics standpoint it is a small landscape. Therefore, we used restriction site-associated DNA sequencing (RADSeq) to establish the genetic diversity and gene flow of *C.o. lutosus* subpopulations. To help identify genetic differentiation within the NCA, we included DNA samples from populations in southeast Idaho and central Nevada on the boarder of Utah. In addition, we used the prairie rattlesnake (*Crotalus viridis*) as a reference genome to assist the sequence alignment process. The inclusion of samples from distant populations within the *C.o. lutosus* range assisted our principal component analysis, which allowed us to identify two distinct clusters within the NCA. There are several possible reasons for two subpopulations to occur within the NCA; we examined the gene differentiation of *C.o.*

lutosus to establish current gene flow. Our results can assist land managers in maintaining the connectivity of subpopulations to prevent habitat fragmentation and enhance conservation efforts.

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LIST OF ABBREVIATIONS

NCA	Morley Nelson Snake River Birds of Prey National Conservation Area
SEID	southeastern Idaho
GBNP	Great Basin National Park
VES	Visual Encounter Survey
BLM	Bureau of Land Management
RMP	Resource Management Plan
OCTC	Orchard Combat Training Center

CHAPTER ONE: EFFECTS OF THE CHEATGRASS-FIRE CYCLE ON REPTILES IN SAGEBRUSH STEPPE

Abstract

Reptiles inhabiting shrub-steppe ecosystems of the Intermountain West have adapted to harsh, unpredictable desert conditions, yet recent changes in disturbance regimes may put species at risk. In southwest Idaho, cheatgrass (*Bromus tectorum*) has altered the fire regime resulting in vast conversion of shrub-steppe to mostly annual grasslands that burn too frequently to allow shrublands to recover. Southwest Idaho has the highest reptile diversity in the Pacific Northwest, yet we know little about reptile community dynamics in response to the cheatgrass-fire cycle. We hypothesized that wildfires and cheatgrass negatively affect reptile communities directly (i.e., mortality during fires) and indirectly through changes in the quality of reptile habitats at multiple spatial scales. We used a combination of trapping and visual encounter surveys to quantify the effect of previous wildfires, cheatgrass, and other habitat metrics on reptile richness, diversity, occupancy, and abundance at local (i.e., trapping array) and landscape scale. We found that vegetation cover, distance to a rock outcrop, and wildfire frequency were essential predictors of reptile abundance at both spatial scales. We found that many of the reptile species were not directly affected by cheatgrass cover but were affected by wildfire frequency. Lizard richness decreased with the number of times an area immediately around a trapping array burned. Our models indicated that occupancy for many reptile species declined in areas that burned, especially in areas with repeated burns at the local level. We found that gophersnake abundance, but not occupancy, was significantly negatively affected by wildfire at the local level. Our research contributes to the growing body of evidence that the cheatgrass-fire cycle in the western U.S. negatively impacts many species, including reptiles. However, the effect on communities is nuanced, with winners and losers depending on a combination of habitat associations, life history, and environmental sensitivities.

Introduction

Shrub steppe ecosystems of the western United States support diverse but secretive fauna that are understudied and potentially at risk because of a legacy of human land use and recent changes in disturbance regimes. Initial wildlife habitat alterations occurred because of overgrazing by cattle and sheep, intentional conversion of shrublands to grasslands to improve livestock forage, and drainage of valley bottoms for agriculture (West, 1999). Insidious habitat changes occurred with the arrival of non-native grasses and forbs (Knapp, 1996). Particularly, cheatgrass (*Bromus tectorum*) is an invasive annual that outcompetes native perennials and shrubs after wildfires by obtaining nutrients necessary for rapid germination to emerge early in the growing season. Also, its' early senescence results in dry vegetation by peak wildfire season, and cheatgrass-invaded habitats burn more frequently than native vegetation (Balch et al., 2013, Pilliod et al., 2017). In some areas, the fire regime, mainly the frequency of wildfires, has been altered by cheatgrass to the point where native shrub species cannot recover (Davies et al., 2012, Mahood & Balch, 2019, Ellsworth et al., 2020). This cheatgrass-fire cycle was particularly evident in the northern Great Basin and Intermountain West starting in the 1980s (Balch et al., 2013, Bradley et al., 2018). In southwestern Idaho, USA for example, the cheatgrass-fire cycle is burning so frequently that the area has experienced a vast conversion of shrub-steppe to mostly annual grasslands intermixed with some fire-resistant perennial bunchgrasses, such as Poa secunda (Knick & Rotenberry, 1997, Davies et al., 2012, Shi et al., 2018, Barker et al., 2019). This widespread shrubland to grassland conversion has altered plant diversity, vegetation structure, soil crusts, and bare ground to such an extent that habitats and microhabitats of most sagebrush steppe-associated wildlife are now fundamentally different (Freeman et al., 2014, Dumroese et al., 2015, Coates et al., 2016, Holbrook et al., 2016).

Reptile species vary greatly in their habitat preferences, home range sizes, and vagility, and thus their susceptibility and responses to disturbance. There are generalist reptiles that occupy grasslands and shrublands alike, whereas others are specialists that occupy specific features or microhabitats (e.g., rock structures or riparian), and still others that might be restricted to native shrub-steppe while avoiding exotic grasslands (Segura et al., 2007). Wildfires and invasive plants can affect the quality of reptile habitats at multiple spatial scales, including landscapes where habitat loss leads to habitat fragmentation. For example, native shrub-bunchgrass communities typically have interspaces that are devoid of vegetation, which is important for ground-dwelling animals to travel through the environment. These interspaces also provide basking and foraging locations that are adjacent to vegetative cover from predators and shade for thermoregulation (Esque et al., 2003, Howey et al., 2016). In contrast, habitat quality for many reptiles deteriorates when these open interspaces become choked with dense cheatgrass (Hall et al., 2009, Rieder et al., 2010, Germano et al., 2011) or when shrubs are lost to wildfire (Jenkins & Peterson, 2008, Klug et al., 2010).

Lizards and snakes play an integral role in shrub-steppe ecosystems as both predator and prey (Diller & Johnson, 1988, Steenhof & Kochert, 1988, Etzel et al., 2014) and yet are often understudied and underappreciated, which hampers their conservation. Although the cheatgrass-fire cycle represents the greatest threat to shrub-steppe ecosystems in North America, there are no studies to date that have examined the effects of the cheatgrass-fire cycles on reptile communities. Southwest Idaho has the highest reptile diversity in the Pacific Northwest because of suitable geology, climate, and ecotones (Jeffries, 2019, Pilliod et al., 2020). Although reptiles have been studied in southwestern Idaho since 1977 (Diller & Johnson 1982), little is known about their community dynamics, or the habitat changes associated with the cheatgrass-fire cycle (Cossel, 2003).

The objectives of our study were to assess how wildfire and cheatgrass affect reptile community composition and the occupancy and relative abundance of specific reptile species in the context of local and landscape-level factors. We defined local level as an area delineated by a 50 m radius around a trapping array and landscape-level as the average home range size for our seven lizard species and seven snake species, separately (Burkholder & Walker 1973, Burkholder & Tanner, 1974, Schorr et al., 2011, Hirth et al., 1969, Bauder et al., 2015). We predicted that wildfire and cheatgrass would not affect reptile richness because we expected that the mosaic of habitats created by the cheatgrass-fire cycle across the landscape might benefit some species while harming others, and thus local richness would be equivocal. The conversion of shrublands to grasslands may remove some shrubland-associated species, but grassland-associated species may colonize; thus, we hypothesized that alpha diversity, species richness at each trapping location, would be equivalent at the local scale, whereas beta diversity would vary at the local scale because of differences in species composition. To further assess possible causal mechanisms leading to these patterns, we predicted that the occupancy and abundance of shrubland-associated species would be negatively associated with the loss of shrubland habitat at local and landscape levels. Conversely, we expected grassland species or habitat generalists to have higher occupancy and abundance in landscapes now dominated by cheatgrass or where cheatgrass has invaded heavily into shrubland habitats (Table 1.1).

Table 1. 1 A list of associated habitat type for the reptiles observed at the Morley Nelson Snake River Birds of Prey National Conservation area (NCA) during 2018 and 2019 field season. We use standard taxonomy for species and subspecies (Crother, 2017).

Common Name	Genus	Species	Associated Habitat	Citations
Lizards				
Tiger whiptail lizard	Aspidoscelis	tigris	Shrublands	Pianka 1966, Burkholder & Walker 1973, Nussbaum et al. 1983
Great Basin collard lizard	Crotaphytus	bicinctores	Rock Outcrop, Shrublands	Pianka 1966, Setser et al. 2002
Long-nosed leopard lizard	Gambelia	wislizenii	Shrublands	Setser et al. 2002, Schorr et al. 2011
Desert horned lizard	Phrynosoma	platyrhinos	Shrublands, Grasslands	Pianka 1966, Pianka 1975, Setser et al. 2002
Sagebrush lizard	Sceloporus	graciosus	Shrublands	Burkholder & Tanner 1974, Green et al. 2001, Setser et al. 2002
Western fence lizard	Sceloporus	occidentalis	Rock Outcrop, Shrublands	Nussbaum et al 1983, Davis and Verbeek 1972, Marcellini and Mackey 1970
Side-blotched lizard	Uta	stansburiana	Shrubland, Grasslands, Rock Outcrop	Parker & Pianka 1975, Nussbaum et al 1983, Pianka 1989

Common Name	Genus	Species	Associated Habitat	Citations
Snakes				
North American racer	Coluber	constrictor	Grasslands	Fitch 1963, Fleet et al. 2009, Klug et al. 2011
Striped whipsnake	Coluber	taeniatus	Shrublands	Hirth et al. 1969, Parker & Brown 1980
Great Basin rattlesnake	Crotalus	oreganus lutosus	Shrubland, Rock Outcrop	Diller & Wallace 1984, Diller & Wallace 1996, Glaudas et al. 2008
Desert nightsnake	Hypsiglena	chlorophaea	Rock Outcrop	Diller & Wallace 1981, Diller & Wallace 1986, Cossel 2003
Gophersnake	Pituophis	catenifer	Shrublands, Grasslands, Rock Outcrop	Parker & Brown 1980, Diller & Wallace 1996, Setser et al. 2002, Edkins et al. 2018
Western groundsnake	Sonora	semiannulata	Rock Outcrop, Grassland, Shrubland	Diller & Wallace 1981, Nussbaum et al. 1983, Cossel 2003
Western terrestrial gartersnake	Thamnophis	Elegans	Riparian	Nussbaum et al. 1983, Rossman et al. 1996, Bronikowski & Arnold 1999,

Common Name	Genus	Species	Associated Habitat	Citations
				Weaver et al 2010

Methods

Study Area

The Morley Nelson Snake River Birds of Prey National Conservation Area (hereafter "NCA") in southwestern Idaho was historically an area with extensive sagebrush steppe habitat, but it is now a mosaic of native shrublands, and exotic annual grasslands fragmented by roads, fences, and periodic wildfire scars (Whisenant, 1990, Knick & Rotenberry, 1997, Mutz et al. 2004). The NCA is 195,746 hectares of public land, providing a wide range of resources. The NCA is a protected area for nesting and foraging raptors, but it is also used for military training, livestock grazing, and recreational activities (Mutz et al., 2004, USDI, 2008, pp. 1.1-1.2). Encompassed within the NCA, the Orchard Combat Training Center (OCTC) is 55,846 hectares of land used by the Idaho Army National Guard for military training since 1953 (USDI, 2008). The NCA was established in 1993 under Public Law 103-64 to "…provide for the conservation, protection, and enhancement of raptor population and habitats, and the natural and environmental resources and values associated", however, some protections began nearly 20 years earlier (USDI 2008, p. 2.3). In 1971 the raptor nesting habitats along the cliffs of the canyon were protected. Between 1975 and 1980, the protected area was expanded greatly after the Bureau of Land Management (BLM) observed the extent of raptor foraging habitat use to be much larger than previously estimated. A Resource Management Plan (RMP) was prepared for the NCA and finalized in 1995, with the addition of recreational shooting and access management. In BLM's NCA RMP, they have committed to conserve and restore the raptor populations and habitats, but also the prey that raptors depend on (USDI, 2008). Raptors in this area typically prey on rodents, lagomorphs, lizards, and snakes that inhabit shrublands and grasslands (Steenhof & Kochert, 1988, Marzluff et al., 1997).

The Snake River and the steep canyon walls formed by basalt talus slopes are major topographic features bisecting the southern portion of the NCA. The canyon and northwestern portion of the NCA are easily accessible to Boise, Idaho's largest city, making them popular recreation areas (Pauli et al., 2019, Katzner, 2020). From north to south, the NCA's topography and shrublands vary. The flat plains are punctuated by basalt buttes further south (USDI 2008). The shrublands are predominantly Wyoming big sagebrush (*Artemisia tridentata wyomingensis*) and green rabbitbrush (*Chrysothamnus viscidiflorus*) in the north, transitioning into shadscale (*Atriplex confertifolia*), winterfat (*Krascheninnikovia lanata*), and greasewood (*Sarcobatus vermiculatus*) further south. The native shrublands currently cover only about 10% of the NCA (Enterkine, 2019). Majority of the native grasslands are Sandberg's bluegrass (*Poa secunda*), covering around 9% of the NCA. Meanwhile, exotic annuals, mostly a combination of cheatgrass and mustards (e.g., tall tumble mustard, *Sisymbrium altissimum*), now cover roughly 37% of the NCA. The remaining 44% is comprised of bare ground, cliffs, and the Snake River.

Besides recreation, livestock grazing and wildfire are two dominant, and actively managed, disturbances on the landscape. The majority of the NCA is grazed by sheep and cattle, and the grazing allotments vary by season and quantity of livestock (USDI, 2008). Over 60% of the NCA has burned at least once since 1957 (Welty & Jeffries, 2020). The

BLM has administered wildfire prevention through fuel breaks, including green strips where native vegetation is removed and replaced by non-native vegetation that has higher moisture content and a lower tendency to burn, including crested wheatgrass (*Agropyron cristatum*), Russian wildrye (*Psathyrostachys juncea*), and forage kochia (*Bassia prostrata*) (Pilliod & Welty, 2013). BLM also conducts post-fire rehabilitation land treatments by treating non-native forbs and grasses with herbicides (typically Imazapic and Glyphosate) and drill, broadcast, and aerial seeding of native grasses, forbs, and shrubs to restore sagebrush steppe vegetation (Pilliod & Welty, 2013, Pilliod et al., 2019). The wildfire prevention treatments also include prescribed burns targeting areas of excessive tumbleweed accumulations, especially along fence lines. The Idaho Army National Guard has conducted post-fire restoration projects by implementing similar treatments as the BLM and hand planting of shrubs (Z. Tinkle, personal communication, June, 2020). These treatments attempt to restore vegetation back to its pre-fire state by seeding native grasses and forbs in combination with sagebrush plugs. Protecting unburned shrublands and restoring shrublands after wildfires is a challenge for managers (Knutson et al., 2014, Shriver et al., 2018). An annual loss of shrublands to wildfire is anticipated to continue from increased fire frequency and climate change (Abatzoglou & Kolden, 2011, Ellsworth et al., 2020, USDI, 2008).

Reptile Surveying

2018 Trapping

Over a forty-year time span, from 1977 to 2017, a total of 104 reptile trapping locations had been established at the NCA and sampled at irregular intervals (Diller & Johnson, 1982, Beck, 1997, Cossel, 2003, Peterson et al., 2002). In 2018, we trapped lizards and snakes at 48 of the 104 historic trapping locations in the NCA (**Figure 1.** 1). We chose historical locations to contribute our data to a long-term trend analysis we plan to publish. We chose the 48 locations for our study based on accessibility (e.g., road conditions and land ownership) and drive time from Boise. In 2018, we established trapping arrays at 36 locations within the OCTC and 12 locations in northwest parts of the NCA. When originally established, the primary factor that determined trap locations was vegetation. The NW NCA trapping locations include arrays distributed across the major cover types (big sagebrush, canyon rim, riparian, shadscale, grasslands, and talus) found in the study area (Diller & Johnson, 1982, Cossel, 2003). The OCTC trapping arrays were originally placed using a random design, stratified on vegetation and topography (Peterson et al., 2002). Vegetation was classified into three categories (big sagebrush/rabbitbrush, shadscale/winterfat, and native grass/annuals) and topography was subdivided into three categories based on aspect and slope: flat (slope < 5 degrees with no aspect), northeast (slope > 5 degrees, aspect = 315-135 degrees), and southwest (slope > 5 degrees, aspect = 135-315 degrees). The original sampling design installed four trapping arrays for each combination of vegetation and topography categories.

We used the historical configuration of the trapping arrays, a cross-shaped array at the OCTC locations, and a linear array for the other NCA locations (**Figure 1.** 1) to ensure utility in long-term monitoring. These two array configurations consist of funnel traps attached to a metal drift fence. For the cross-shaped arrays, we used a four-pronged funnel trap; extending from the funnels were four 7.5 m drift fences with a funnel trap at each end. For the linear arrays, we installed a 15 m drift fence with a funnel trap on both ends, and an additional 7.5m drift fence laterally from each funnel trap.

We live-trapped lizards and snakes from 7 May – 30 June 2018 and checked all active traps daily. Due to technician shortages that arose early in the season, we kept the 36 OCTC arrays open 7 days a week, while the 12 NW NCA arrays were opened 5 days and 4 nights a week. The trapping arrays were opened gradually at the beginning of the season to ensure we properly trained the technicians. We recorded the dates that traps were opened to calculate trap nights, to include effort by array in our models. We processed trapped reptiles one at a time. We recorded morphological information and marked individuals with a passive integrated transponder (PIT) tag subcutaneously. This allowed us to identify individuals captured more than once and individuals that moved to new locations.

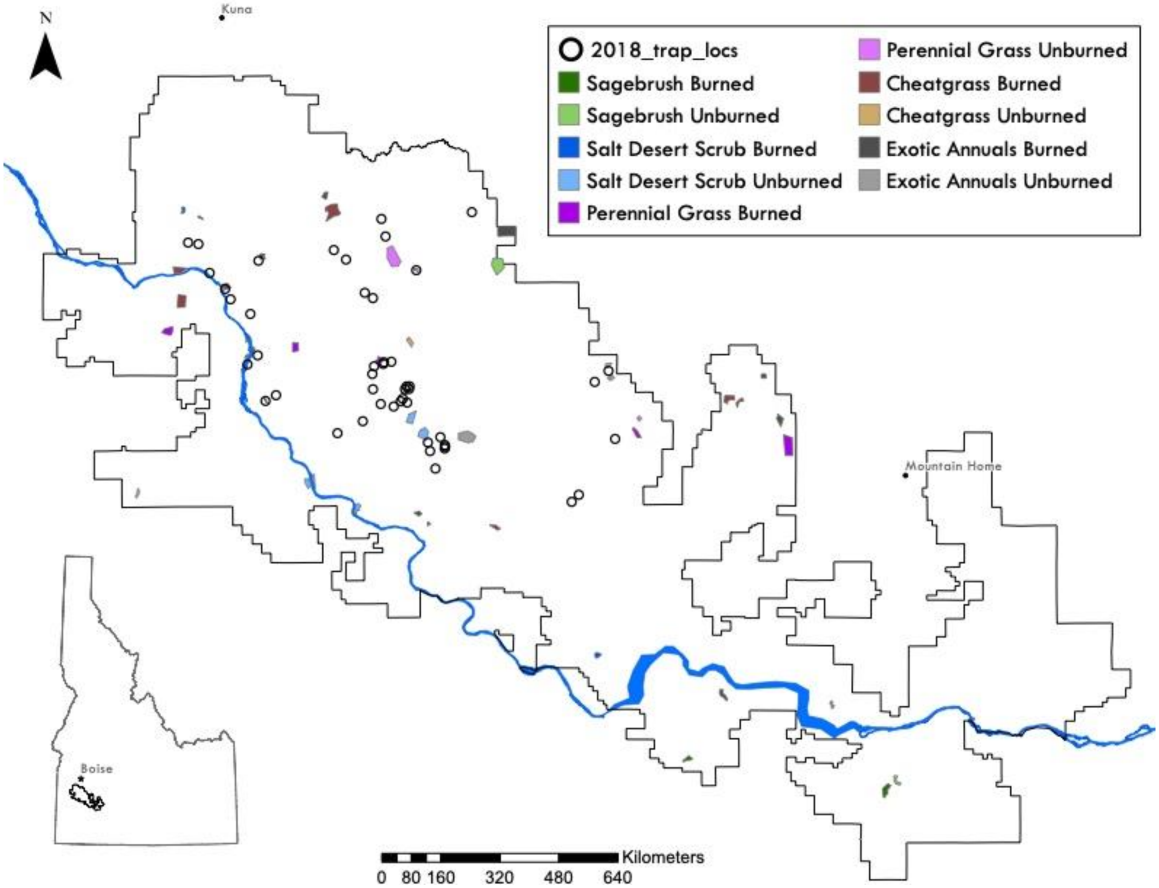


Figure 1. 1 Map of the 48 reptile trapping locations ("2018_trap_locs") in the Morley Nelson Snake River Birds of Prey National Conservation Area (NCA) surveyed in 2018. The 2019 areas surveyed are color coordinated based on major cover types (cheatgrass, sagebrush, salt desert shrubs, exotic annuals, and perennial grasses) and fire history (burned or unburned).

2019 Visual Encounter Surveys

Drift fence trapping is a common reptile survey method, and we recognize the biases toward capturing highly mobile species (Willson & Gibbsons, 2010). To complement the 2018 trapping effort, we took a different approach to survey reptiles that would add information on the distribution and relative abundance of additional species. In 2019 we conducted visual encounter surveys, which consist of walking systematically through a survey area (Furnas et al., 2019). We selected locations to survey based on cover types (sagebrush, salt desert scrub, cheatgrass, exotic annuals, and perennials) and fire history (burned or unburned). We generated multiple novel survey areas for each category in ESRI ArcGIS Pro. Of all the survey areas generated, we randomly selected areas to survey from each category. Three of these survey areas happened to encompass trapping locations surveyed in 2018 whereas the rest were in non-overlapping areas. From 13 May – 19 July 2019, we surveyed 74 survey areas, covering approximately 2,500 hectares (**Table 1.** 2, **Figure 1.** 1). There were multiple survey areas with the same treatment type (cover type and fire history), and we visited each survey area on a single day during the season. To minimize sampling bias due to environmental temperatures at the time of our visit, we varied the time of surveys to ensure we visited the survey areas of each treatment type during a mix of morning, midday, and afternoon visits throughout the season.

Table 1. 2 The 74 areas we surveyed at the NCA at five different cover types (sagebrush, salt desert scrub, cheatgrass, exotic annuals, and perennials) that previously burned or have not burned.

Vegetation Category	Burned	Not Burned
Sagebrush	2	20
Salt Desert Scrub	6	5
Perennials	6	4
Cheatgrass	22	9
Exotic Annuals	6	3

We surveyed each survey area by lining up a team of surveyors along an edge with ~10 m spacing between observers. The team walked slowly from one edge to the other and, if shrub density was high, we meandered through the interspaces between shrubs. We repeated this method until we completely searched each survey area. For each survey, we recorded a start and end time and temperature. Surveyors recorded track logs using Collector software (ESRI Corp., Redlands, CA). When we detected a reptile, a surveyor would determine if capturing it was feasible. If not, an observation point was recorded (with a picture of the individual if possible). When we captured individuals, we inserted a PIT tag and collected morphological data for all species. To assess differences in observer detection abilities, we recorded the surveyor for each reptile observation.

Wildfire and Habitat Cover

At the local scale, we calculated vegetation and bare ground percent cover from line-point intercept (LPI) data that we collected at each trapping array. We collected LPI data along three 50 m long lines; the first line was designated by a random azimuth, and the other two were 120 degrees apart (Herrick et al., 2018). The ground was slightly disturbed when installing the trapping arrays, so to ensure we sampled areas undisturbed by our arrays we started each line 5 m from the center of each trapping array. We calculated vegetation and bare ground percent cover at the landscape level using land cover data generated from 2016 Sentinel-2 and Landsat satellite imagery (Enterkine, 2019, Rigge et al., 2020). To ensure reliable landscape-level cover, we selected these images by comparing the percent cover from multiple rasters to the LPI data. In ArcGIS Pro, we extracted a 50-m radius around the trapping locations to compare the vegetation percent cover of the remotely sensed data to the LPI dataset. We ran a Spearman's rank correlation test for each habitat variable, and we selected the raster datasets with the highest correlation to the LPI. Enterkine (2019) had the highest correlation for all vegetation percent covers and Rigge et al. (2020) for bare ground percent cover. Enterkine (2019) used K-Means clustering to classify the percent cover of vegetation communities of the NCA at a 20-m resolution. Rigge et al. (2020) used a fractional component approach to classify a continuous percent cover of bare ground for the western U.S. rangelands at a 30-m resolution. For the two raster datasets, we extracted the cover percentages for the landscape scale radii needed for richness, occupancy, and abundance.

For many reptiles, a suitable retreat site is critical to thermoregulation for behavioral and physiological processes (e.g., prey capture, predator protection, digestion, locomotion; Huey et al., 1989, Peterson et al., 1993). Typically, rock outcrops are retreat sites as they have a variety of rock thicknesses and the degree of shading (Huey et al., 1989). In ArcGIS Pro we predicted rock outcrops using 1/3 arc-second resolution Digital Elevation Models (DEMs) raster (USGS, 2019a, USGS, 2019b). We converted the DEMs into a Terrain Ruggedness Index (TRI) raster using the TRI tool from the ArcGIS Pro Arc Hydro build. We calculated TRI by measuring the elevation difference from a central cell to its adjacent cells. We grouped the expressed elevation of the cells into 0.5 meters increments. Cells that were less than a meter were removed, and we clustered the remaining cells into rock outcrops. We determined cells with 2 meters or less elevation change captured the subtle changes in elevation and not the drastic difference in elevation rock outcrops create. We considered the canyon rim and talus as rock outcrops. We were not able to ground truth all rock outcrops predicted with TRI. We generated predictor variables as distance to the nearest rock outcrop and the number of rock outcrops at our two spatial scales of analysis (i.e., local and landscape).

We used several variables to quantify important aspects of the cheatgrass-wildfire cycle. Cheatgrass makes wildfires burn more frequently. Thus, our wildfire variables included the number of times an area had burned. We generated these variables from a compiled wildfire raster dataset (Welty & Jeffries, 2020) for the local and landscape level around each trapping array and for each visual encounter survey area. We quantified percent cover of cheatgrass, along with native herbaceous, shrubs, and bare ground, from LPI or satellite imagery (Enterkine, 2019, Rigge et al., 2020).

Analysis

Richness

We generated models to quantify how habitat, cheatgrass, and wildfire affect the richness, diversity, occupancy, and abundance of reptiles at local and landscape scales. We delineated the local scale as a circular area with a 50-m radius centered on each trapping array. We delineated the landscape scale as a circular area with a radius of 3,560 m approximating the average home range size of each lizard species (~10 sq km; Burkholder & Walker, 1973, Burkholder & Tanner, 1974, Schorr et al., 2011) and with a radius 13,580 m approximating the average home range size of each snake species (~145 sq km) in our study area (Hirth et al., 1969, Bauder et al., 2015), centered on each trapping array. Hence, the local scale is nested within the landscape scale, and they are not completely independent.

We modeled the effects of wildfire and cheatgrass on lizard and snake richness and diversity using a Poisson (richness) and linear (diversity) generalized linear models. We chose to model lizards and snakes separately because they have different movement patterns and ecology. We calculated lizard and snake species richness at each trapping array as a cumulative count over the entire 2018 trapping season. We also calculated a Shannon’s Wiener diversity index for each trapping array using the equation:

$H = -\sum_{i=1}^{S} p_i \log_b p_i$. Since trap nights were not equal across all trapping locations, we included it as an offset in the models (Appendix 2).

Occupancy

Occupancy models model the occurrence of a species as a mixture of two probabilities; one which describes the ecological process giving rise to the presence (or absence) of a species and which describes the likelihood of detecting a species (given that it is present). Such models are particularly important for cryptic species and species with differential susceptibility to trapping (Mackenzie et al., 2009)

We included covariates in the detection model, to ensure the occupancy model considered the uncertainty from imperfect detection (Equation 1). We used the detection model as a nuisance parameter in the occupancy model (Equation 2). We evaluated the detection probability, varying intercepts, and covariates when reviewing model convergence and diagnostics. We report and infer results of the occupancy probability and our covariates of interest; refer to Appendix 2 for the parameters: surveyor detection, air temperature, time of year and survey area size.

2018 Trapping

We fit a Bayesian occupancy model to assess how wildfire frequency and cheatgrass affect occupancy of reptiles based on the trap locations throughout the NCA (Mordecai et al., 2011). Our attempt to explain imperfect detection from the trapping effort we included the date a trap was open (TN_ij) and the daily average air temperature (AT_ij). We determined the covariates for the occupancy model were habitat type; we used cheatgrass (C_i), native herbaceous (NH_i), and shrub (S_i) percent cover at the local level. We are also interested in the effect repeated burns (TB_i) had on occupancy probability of reptiles. The shifts that cheatgrass cover or number times burned had on occupancy probability are insightful alone. However, together these covariates showed the effects of the cheatgrass-fire cycle.

$$logit(p_{ij}) = \beta_0 + \beta_1 * AT_{ij} + \beta_2 * TN_{ij} + \beta_4 * TN_{ij}^2 \quad \text{Equation 1}$$

$$logit(\psi_i) = \alpha_0 + \alpha_1 * TB_i + \alpha_2 * C_i + \alpha_3 * S_i + \alpha_4 * NH_i \quad \text{Equation 2}$$

2019 Visual Encounter Surveys

We modeled occupancy for the most frequently observed species (> 20 individuals captured). To avoid violating a key assumption of occupancy models, repeated surveys at a site, we considered each surveyor a replicate at the site (surveyors visited the survey areas one time). However, this includes an additional variability to the probability of detection. We accounted for surveyor detection probability by setting it as a varying intercept (obs_ij) whereas time of year (date_ij) and air temperature (temp_ij) remained fixed variables for detection probability. The occupancy model used the probability of reptile detection and surveyor detection to calculate the probability estimates. Although trapping and VES occupancy covariates of interest are identical, we included survey area (area_i) to the VES occupancy model.

To fit the occupancy models, we applied Hamiltonian Monte Carlo sampling using Stan through the package `rstan` (Stan Development Team, 2020) in R (R Core Team, 2020). We used non-informative priors for all the predictor variables and probabilities calculated in the model (Northrup & Gerber, 2018). We gained further inference on the probability estimates by examining the credible intervals. The credible intervals calculated by the model help us determine certainty of the probability estimate.

Abundance

We modeled abundance for the most frequently captured species, the same selection method used for the occupancy analysis. We calculated abundance as the sum of new individuals captured at a trap array all season; we removed recaptured individuals from a trap's dataset before analysis. We used a negative binomial distributed GLM because of the overdispersion of captures across the trapping arrays (Blasco-Moreno et al., 2018). The predictor variables we used to predict occupancy of Great Basin rattlesnakes, gophersnake, striped whipsnake, and tiger whiptail were number of times burned, number of rock outcrops, distance to nearest rock outcrop, and percent cover of shrub, bare ground, native herbaceous, and cheatgrass. The cheatgrass-fire cycle is an interaction of factors over time and, thus, we used the number of times burned to represent it. We also included a variable for cheatgrass even though we know there is a relationship between cheatgrass abundance, fine fuel accumulation, and subsequent wildfire (Pilliod et al., 2017). This relationship, however, is time-lagged by 1-2 years and is strongly dependent upon antecedent precipitation. Hence, we could include both cheatgrass cover and the number of times burned in the models and be independent.

We chose the variables based on habitat preferences; for example, Great Basin rattlesnake, striped whipsnake, and tiger whiptail models included shrubs and open corridors (bare ground) due to their foraging behaviors (Burkholder & Walker, 1973, Diller & Johnson, 1982, Setser et al., 2002). Native herbaceous covariate was used for gophersnakes because the detections vary across multiple habitats (Diller & Johnson, 1982, Diller & Wallace, 1996, Kapfer et al., 2010). Although all the predictor variables do not align with the habitat preferences of the four species, we decided to include them because any negatively associated variables would also be informative for explaining the variance of the species abundance. We accounted for unequal trap nights (effort) using an offset, similarly to the richness analysis.

We generated multiple hypothesis-based models with assorted grouping of the compiled predictor variables for all response variables. We ran GLMs for snake and lizard diversity, richness, and species abundance at the local and landscape levels. We ran the a priori models, then used AIC to select the best model to infer results. The AIC tables for all response variables can be found in Appendix 1.

Results

During the 2018 trapping efforts, we documented seven lizard species and seven snake species, and we trapped a total of 142 lizards and 200 snakes across the NCA. The most abundant snake species in our traps was the gophersnake (n=134), followed by the Great Basin rattlesnake (n=30) then the striped whipsnake (n=26). Among lizards, the tiger whiptail (n=109) was most abundant, followed by the common side-blotched lizard (*Uta stansburiana*, n=19) and the sagebrush lizard (*Sceloporus gracious*, n=11). We also detected 3 of the 5 reptile species (two lizard and three snake species) listed as species of concern by BLM and Idaho Department of Fish and Game: Great Basin collared lizard (*Crotaphytus bicinctores*), desert nightsnake (*Hypsiglena chlorophaea*), and western groundsnake (*Sonora semiannulata*).

For the visual encounter surveys conducted in 2019, we observed six lizard species (487 individuals) and four snake species (174 individuals) across the 74 survey areas, all of which were also detected in the trapping effort during 2018. The common side-blotched lizard was the most frequently observed species with 241 observations, followed by 116 sagebrush lizard and 94 tiger whiptail observations. The most observed snake species were the Great Basin rattlesnake (n=93), then the gophersnake (n=38) and the striped whipsnake (n=31). We did not detect any rare reptile species or the terrestrial gartersnake (*Thamnophis elegans*).

Richness

We assessed reptile richness and diversity at a local and landscape level. Our models for diversity had difficulty converging, thus we won't report on these models. Although the richness models converged, the lizard richness models (Table A.2. Table A.3) fitted moderately and the snake richness models (Table A.4, Table A.5) fitted weakly. We determined the top richness models had weak predictive power based on pseudo R2 McFadden value (Table 1. 3). The variables selected for lizard richness explained a moderate amount of variation. For the top model at the local scale, we noted that the time since the last fire was the only significant predictor variable ($p = 0.04$). We determined locations that never burned had a higher probability of trapping more lizard species (Figure 1.2). Our evaluation at the landscape scale determined the number of rock outcrops influenced the number of lizard species trapped ($p = 0.001$, Figure 1.2). We determine locations with more than 30 rock outcrops increased the likelihood of trapping more than one lizard species. The top model for snake richness at both spatial scales fitted poorly to the data (Table 1.3). We will not discuss the estimates produced; however, the coefficients for all hypothesized models can be found in the Appendix.

Table 1. 3 The top model for lizard and snake richness at the local scale (area of a trapping array) and landscape scale (area around a trap the average dispersal range of lizards and snakes). We evaluated pseudo R2 value for goodness of fit for the top AICc models.

	Lizard Richness		Snake Richness	
	Local	Landscape	Local	Landscape
(Intercept)	-0.88 *** [-1.33, -0.42]	-0.59 ** [-0.99, -0.20]	0.08 [-0.17, 0.32]	0.37 ** [0.12, 0.61]
Bare ground cover	0.29 [-0.10, 0.68]			
Native herbaceous cover	-0.41 [-0.94, 0.12]	-0.51 [-1.08, 0.07]		
Shrub cover		0.24 [-0.23, 0.72]		
Cheatgrass cover			0.31 * [0.03, 0.59]	-0.21 [-0.49, 0.07]
Time since last fire	0.72 * [0.02, 1.41]			
Times burned		0.50 [-0.05, 1.05]	-0.06 [-0.36, 0.24]	0.14 [-0.13, 0.41]
Number of rock outcrops		0.52 *** [0.22, 0.81]		
Distance to rock outcrops			-0.30 * [-0.58, -0.01]	-0.29 [-0.58, 0.01]
N	48	48	48	48

	Lizard Richness		Snake Richness	
	Local	Landscape	Local	Landscape
AIC	109.18	107.31	161.40	137.16
BIC	116.67	116.66	168.88	144.65
Pseudo R2 (McFadden)	0.106017	0.1402835	-0.126175	0.0517596
Pseudo R2 (Pearson)	0.3145895	0.3752575	0.1404649	0.2499971
*** p < 0.001; ** p < 0.01; * p < 0.05.				

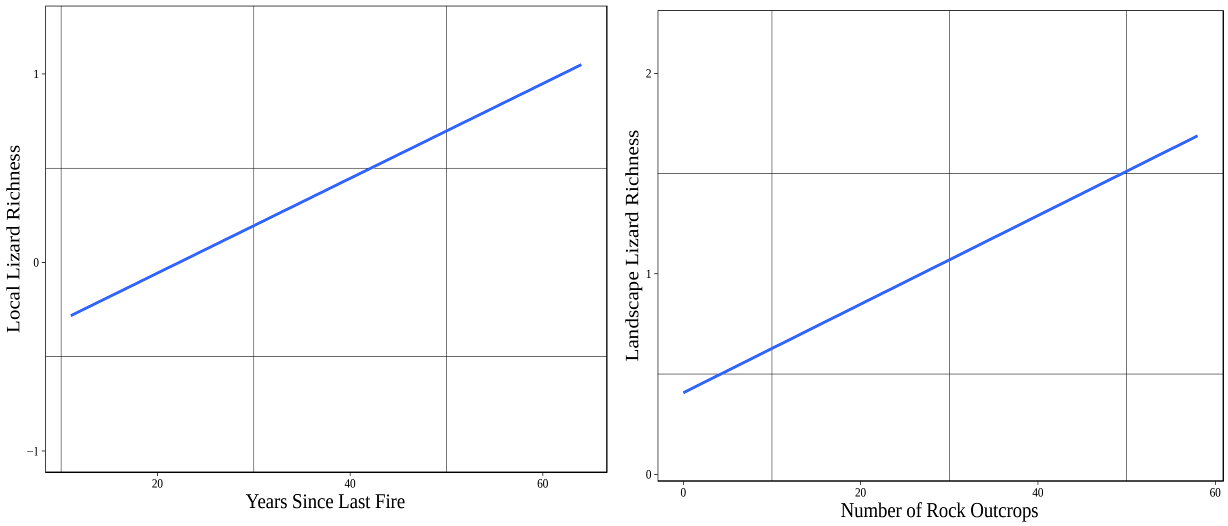


Figure 1. 2 Reptile richness via trapping at the Morley Nelson Snake River Birds of Prey National Conservation Area (NCA) in southwest Idaho in 2018. At the local level (area around a trapping array) we determined lizard richness established at locations that burned over 30 years ago Locations that never burned (65+ years) increased the likelihood of trapping two lizard species. The influence rock outcrops had a direct effect lizard richness at a landscape level (average dispersal range of lizards around the trapping array). We determined the number of rock outcrops increased the likelihood of more than one lizard species trapped.

Occupancy

We assessed the effect of cheatgrass-fire cycle had on occupancy for species with 20 or more observations. The species analyzed from both datasets are documented in chronological order (i.e., 2018 trap data followed by 2019 VES data). We reported and discussed the effect of our predictor variables on occupancy probability; refer to the appendix for the complete list of coefficients (Table 1. 4).

Gophersnake

We detected gophersnakes at 42 of 48 trapping locations and estimated a high probability of occupancy ($\psi = 0.99$, Table 1. 4). We determined the number of times burned had a negative effect; the probability of gophersnake occupancy declined to 0.02 at repeatedly burned locations (**Figure 1.** 3a). We found that cheatgrass cover had a greater negative effect than native herbaceous on occupancy probability as percent cover increased (Table 1. 4). We determined occupancy probability declined more than half, at locations with 60% cheatgrass cover ($\psi = 0.46$, **Figure 1.** 3b). Alternatively, gophersnake occupancy probability declined to 0.89 at 60% native herbaceous cover.

Table 1. 4 We assessed occupancy probability, for highly detected reptiles (20+), to infer the effect of the cheatgrass-fire cycle. We determined detected species that were either caught (2018 trapping survey) or observed (2019 visual encounter surveys) at predetermined survey locations within the Morley Nelson Snake River Birds of Prey National Conservation Area. The occupancy parameter estimates [a_psi: occupancy probability, beta_psi[2]: times burned, beta_psi[3]: cheatgrass cover, beta_psi[4]: native herbaceous cover, beta_psi[5]: shrub cover) , credible interval, and summary statistics are listed by species then by survey year.

	Parameter	mean	se_mean	sd	2.5%	97.5%	n_eff	Rhat
Gophersnake 2018	a_psi	6.64	0.01	0.86	5.16	8.52	8297	1
	beta_psi[2]	-5.19	0.01	0.84	-7.04	-3.73	8721	1
	beta_psi[3]	-0.11	0	0.03	-0.19	-0.06	9871	1
	beta_psi[4]	-0.04	0	0.01	-0.05	-0.02	17437	1
	beta_psi[5]	3.82	0.01	0.96	2.31	6	9812	1
Gophersnake 2019	a_psi	0.27	0	0.48	-0.57	1.3	12412	1
	beta_psi[2]	-0.35	0	0.46	-1.26	0.57	16043	1
	beta_psi[3]	0.66	0	0.49	-0.28	1.66	13276	1
	beta_psi[4]	-0.05	0	0.53	-1.09	1.02	12357	1
	beta_psi[5]	-0.03	0	0.46	-0.94	0.88	13327	1
Great Basin rattlesnake 2018	a_psi	-0.08	0	0.11	-0.29	0.13	5292	1
	beta_psi[2]	-0.68	0	0.13	-0.94	-0.42	6653	1
	beta_psi[3]	0.01	0	0	0	0.01	8745	1

	Parameter	mean	se_mean	sd	2.5%	97.5%	n_eff	Rhat
	beta_psi[4]	0.01	0	0	0.01	0.02	8112	1
	beta_psi[5]	0	0	0	-0.01	0	5806	1
Great Basin rattlesnake 2019	a_psi	-0.67	0	0.3	-1.26	-0.09	6037	1
	beta_psi[2]	-0.35	0	0.32	-1.01	0.25	5637	1
	beta_psi[3]	0.31	0.01	0.39	-0.45	1.1	4893	1
	beta_psi[4]	-0.07	0.01	0.39	-0.85	0.68	4297	1
	beta_psi[5]	-0.57	0.01	0.38	-1.31	0.16	4783	1
Striped whipsnake 2018	a_psi	-0.76	0	0.1	-0.97	-0.57	3068	1
	beta_psi[2]	-0.99	0	0.16	-1.3	-0.69	3925	1
	beta_psi[3]	0.01	0	0	0	0.02	4467	1
	beta_psi[5]	0.02	0	0	0.01	0.03	3246	1
Striped whipsnake 2019	a_psi	-0.79	0.01	0.61	-1.82	0.58	2438	1
	beta_psi[2]	-0.07	0.01	0.45	-0.95	0.83	5540	1
	beta_psi[3]	-0.07	0.01	0.56	-1.09	1.1	3514	1
	beta_psi[4]	-0.48	0.01	0.57	-1.57	0.65	4281	1
	beta_psi[5]	-0.52	0.01	0.52	-1.61	0.45	4740	1

	Parameter	mean	se_mean	sd	2.5%	97.5%	n_eff	Rhat
Tiger whiptail lizard 2018	a_psi	1.94	0	0.13	1.68	2.23	3091	1
	beta_psi[2]	-1.21	0	0.21	-1.62	-0.79	4341	1
	beta_psi[3]	3	0.02	1.17	1.02	5.57	3248	1
	beta_psi[4]	-0.11	0	0.01	-0.12	-0.1	3410	1
Tiger whiptail lizard 2019	a_psi	-1.3	0.01	0.47	-2.16	-0.29	3650	1
	beta_psi[2]	-0.3	0.01	0.47	-1.25	0.6	5492	1
	beta_psi[3]	-0.91	0.01	0.47	-1.85	0	2973	1
	beta_psi[4]	-1.33	0.01	0.62	-2.57	-0.21	3689	1
	beta_psi[5]	0.06	0.01	0.46	-0.85	0.98	3486	1
Sagebrush lizard 2019	a_psi	-0.07	0.01	0.73	-1.4	1.42	3267	1
	beta_psi[2]	0.31	0.01	0.73	-1.01	1.87	5100	1
	beta_psi[3]	0.13	0.01	0.69	-1.29	1.46	5656	1
	beta_psi[4]	0.3	0.01	0.64	-0.91	1.64	5801	1
	beta_psi[5]	0.97	0.01	0.53	-0.02	2.08	7186	1
Western fence lizard 2019	a_psi	-2.27	0.01	0.56	-3.31	-1.11	4449	1
	beta_psi[2]	-0.54	0.01	0.53	-1.66	0.42	7224	1

	Parameter	mean	se_mean	sd	2.5%	97.5%	n_eff	Rhat
	beta_psi[3]	0.73	0.01	0.53	-0.25	1.79	6579	1
	beta_psi[4]	-0.47	0.01	0.68	-1.91	0.76	6790	1
	beta_psi[5]	-0.15	0.01	0.51	-1.15	0.88	6709	1
Common side-blotched lizard 2019	a_psi	0.41	0	0.38	-0.26	1.23	6018	1
	beta_psi[2]	0.14	0.01	0.4	-0.57	1.01	6386	1
	beta_psi[3]	0.57	0.01	0.44	-0.27	1.48	6283	1
	beta_psi[4]	-0.41	0.01	0.42	-1.26	0.39	6486	1
	beta_psi[5]	0.14	0.01	0.41	-0.64	0.96	6386	1

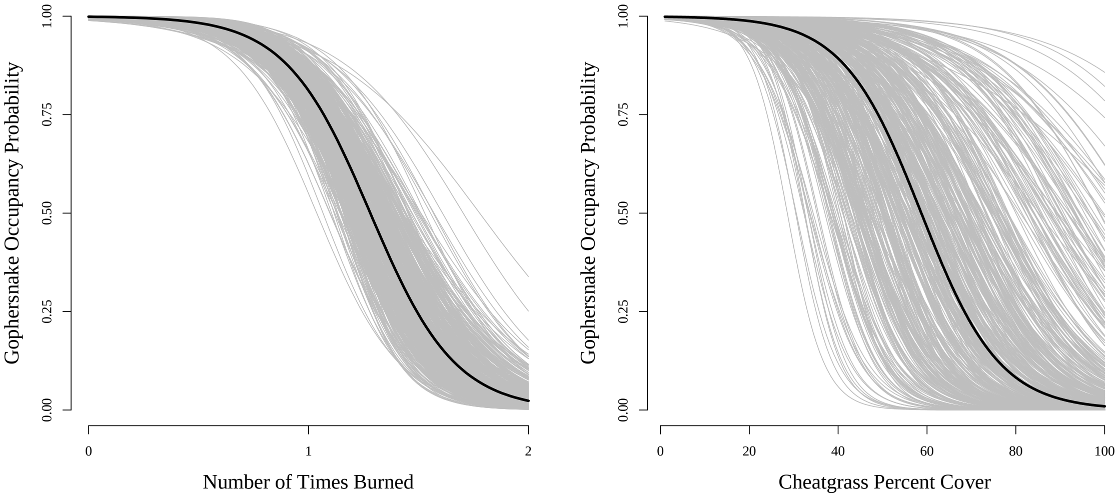


Figure 1. 3 The occupancy probability of Great Basin rattlesnake, striped whipsnake, and gophersnake from the 2018 trapping effort at the NCA. Occupancy probability (ψ) on the y-axis against number of times burned on the x-axis. The blue line was the estimate, and the gray lines are a subset of the posterior draws to visualize uncertainty. We determined the number of times burned and cheatgrass cover negatively affected gophersnakes. The effect of cheatgrass cover on gophersnake occupancy varied more than the consistent effect of repeated wildfires.

We analyzed occupancy probability from the VES dataset and assessed the mean probability of gophersnake occupancy was 0.57 at the survey areas (Table 1. 4). Our model estimated occupancy probability decreased at survey areas that burned, and sites with higher native herbaceous or shrub cover (ψ = 0.56). However, we found the probability of occupancy increased at survey areas with higher cheatgrass cover. We determined a decreased occupancy probability and increase of variance. Our estimates showed the mean probability of gophersnake occupancy declined at burned areas (ψ = 0.48, 95% CRI -1.26 – 0.57), the probability of occupancy varied more at burned locations than unburned. Out of the three habitat covariates, we found cheatgrass had the strongest effect on occupancy probability (ψ = 0.72 95% CRI -0.28 – 1.66) and the only positive effect. Native herbaceous slightly decreased occupancy probability (ψ = 0.55, 95% CRI -1.09 – 1.02). In contrast we saw increased variance of gophersnake occupancy at survey areas with native herbaceous.

Great Basin rattlesnake

We detected Great Basin rattlesnake at 19 of 48 trapping locations. The occupancy probability without covariates was 0.48 (Table 1. 4), the credible intervals slightly exceed zero which gave us confidence in the estimate. Times burned had a negative effect, lowering the occupancy probability to 0.32 after one burn (Table 1. 4). The cover predictor variables had negligible or no effect on occupancy probability, although the distance to rock outcrops was not included in these models because of convergence issues. The model estimated that increasing air temperature at the time of sampling had a small positive effect on detection.

The mean estimate for rattlesnake occupancy probability was 0.34 (95% CRI -1.26 -0.09). We determined the occupancy probability decreased at burned areas (ψ = 0.27 95% CRI -1.01 – 0.25). We determined the probability of occupancy declined to 0.08 at areas that burned five or more times. We found the probability of rattlesnake occupancy increased at survey areas with cheatgrass (ψ = 0.41 95% CRI -0.45 – 1.10). However, we noticed cheatgrass cover widened the variability of rattlesnake occupancy. Although native herbaceous lowered occupancy probability slightly, we noticed the variability of rattlesnake occupancy increased (0.32 95% CRI -0.85 – 0.68). Unexpectedly we found that shrub cover negatively affected rattlesnake occupancy probability (ψ = 0.23 95% CRI -1.31 – 0.16).

Striped whipsnake

We detected striped whipsnakes at 15 of the 48 trapping locations. The model estimated detection probability to be 0.04 (95% CRI -3.38 – -2.70) and the occupancy probability to be 0.32 (95% CRI -0.97 – - 0.57). Similarly, to the other snake species, the number of times a location burned had a negative effect on occupancy probability (ψ = 0.15, 95% CRI -1.3 – -0.69). The probability of occupancy declined to 0.06 after a location had burned twice (**Figure 1.** 3). For the model to converge, we removed native herbaceous as a predictor variable. The other habitat covariates all had a negligible effect size on occupancy probability. None of the predictor variables had reliable credible intervals for us to infer an effect on detection.

Our model estimated whipsnake had the lowest occupancy of all the three snakes with sufficient sample size (ψ = 0.31 95% CRI -1.82 – 0.58). The number of times an area burned, and certain habitat types reduced occupancy probability. We found that times burned and cheatgrass cover lowered occupancy probability by a similar value. Although times burned and cheatgrass lowered occupancy probability (ψ = 0.30), we determined cheatgrass increased the right-skewed variability of whipsnake occupancy (95% CRI -1.09 – 1.10). We assessed native herbaceous, and shrub cover effected occupancy probability similarly; both lowered the occupancy probability and increased the variance (ψ = 0.22 95% CRI -1.57 – 0.65, ψ = 0.21 95% CRI -1.61 – 0.45).

Tiger whiptail

The tiger whiptail was the most frequently detected lizard; we trapped them at 23 of 48 locations. The model estimated the detection probability was 0.07 (95% CRI -2.72 – -2.32) and the occupancy probability was 0.87 (95% CRI 1.68 – 2.23). The occupancy probability declined to 0.67 after the location burned once (95% CRI -1.62 – -0.79). We removed shrub cover from the model to achieve convergence. Cheatgrass cover had a strong positive effect on occupancy probability (ψ = 0.99, 95% CRI 1.02 – 5.57). Unexpectedly, we found that native herbaceous cover had a minor negative effect on occupancy.

Whiptail occupancy probability was 0.22 when no variables were considered. The number of times burned as well as cheatgrass and native herbaceous cover negatively affected whiptail occupancy probability. Shrub cover was the only covariate that had a positive influence on whiptail occupancy probability. The number of times burned slightly decreased occupancy and narrowed variance, which increased our confidence that repeated fires lower occupancy probability. The results showed cheatgrass and native herbaceous had a greater effect on whiptail occupancy than the other covariates. Areas that had low percentage of cheat grass or native herbaceous dropped the probability of whiptail occupancy close to zero. Although native herbaceous had the largest effect on occupancy, it also had the greatest variability for whiptail occupancy. We determined areas with cheatgrass had lowered probability with narrowed variance, meaning a high probability that whiptail lizard occupancy was lower at areas with cheatgrass cover. Although our model showed that increasing shrub cover increased whiptail occupancy, the mean estimate for probability did not increase dramatically. Instead, shrub cover increased our confidence in whiptail occupancy compared to null occupancy.

Common side-blotched lizard

The occupancy probability of side-blotched lizards (ψ = 0.60 95% CRI -0.26 – 1.23) increased at areas with cheatgrass, native herbaceous, or shrub cover and in areas burned previously. We found times burned (ψ = 0.63 95% CRI -0.57 – 1.01) and shrub cover (ψ = 0.63 95% CRI -0.64 – 0.96) positively affected the mean occupancy probability to similar degree. Our model determined cheatgrass cover had a greater positive effect on side-blotched occupancy but also increased the occupancy probability variance (ψ = 0.73 95% CRI -0.27 – 1.48). Native herbaceous had the strongest effect, we determined occupancy probability reduced to 0.50 and wider variability of occupancy probability (95% CRI -1.26 – 0.39).

Sagebrush lizard

Sagebrush lizard occupancy probability increased for all covariates (ψ = 0.48 95% CRI -1.40 – 1.42), but the level of increase varied by covariate. We discovered that times burned and native herbaceous increased occupancy probability to 0.56. However, occupancy variance at burned areas grew, which shifted the probability of occupancy to be uniform (95% CRI -1.01 – 1.87). We found native herbaceous (95% CRI -0.91- -1.64) and cheatgrass (ψ = 0.52 95% CRI -1.29 – 1.46) had a similar, positive effect on occupancy probability. Shrub cover increased probability of occupancy with positively skewed variability, we observed greater frequency of higher values for occupancy probability (ψ = 0.71 95% CRI -0.02 – 2.08).

Western fence lizard

The model estimated 0.09 for occupancy probability (95% CRI -3.31 - -1.11) of the western fence lizard at the NCA. We determined times burned (ψ = 0.06, 95% CRI -1.66 – 0.42), native herbaceous (psi = 0.06, 95% CRI -1.91 – 0.76), and shrub (ψ = 0.08, 95% CRI -1.15 – 0.88) cover barely influenced occupancy probability. Cheatgrass positively influenced western fence lizard occupancy probability (ψ = 0.18, 95% CRI -

0.25 – 1.79). None of our covariates improved the variability found in western fence lizard occupancy probability.

Abundance

To stay consistent, the species analyzed are reported at the local scale followed by landscape scale results.

Gophersnakes

The model showed that the number of times burned had a significant effect on abundance of gophersnakes at the local level ($p = 0.01$, Table 1. 5, Figure 1.4). At the landscape level, we found shrub cover positively affected gophersnake abundance ($p = 0.02$, Figure 1.4), with gophersnake abundance increasing by 0.44 for each additional percentage of shrub cover. Gophersnake abundance increased to 5 individuals at trap locations with 20% shrub cover.

Great Basin rattlesnakes

Of the several predictor variables we examined, none were a significant predictor for rattlesnake abundance at the local level. The likelihood of rattlesnake abundance decreased at a landscape level at locations with a higher percent cover of bare ground ($p = 0.04$, Table 1. 5). Our results suggested rattlesnake abundance decreased by half at locations with >40% bare ground.

Striped whipsnake

Distance to the nearest rock outcrop affected striped whipsnake abundance at both local ($p = 0.04$) and landscape ($p = 0.04$, Table 1. 5)levels. No other predictor variables fit the data at either scale, refer to Table 1.5 for details.

Tiger whiptail

At the local level, whiptail abundance was negatively affected by the distance to the nearest rock outcrop ($p = 0.0004$,Table 1. 5). We determined the likelihood of abundance declined below 1 when the nearest rock outcrop was ≥300 m. Although we anticipated cheatgrass would lower the likelihood of whiptail abundance, we found that native herbaceous significantly lowered abundance at these locations ($p = 0.001$). Whiptail abundance dropped below 1 at locations with 20% or more native herbaceous cover (Figure 1. 4). We found that shrub ($p = 0.04$) and bare ground ($p = 0.01$) cover had positive effect on abundance at a landscape level. A 20% increase of shrub cover increased the likelihood of whiptail abundance (Figure 1.4). Increasing distance to the nearest rock outcrop ($p = 0.0002$) lowered whiptail abundance. Specifically, abundance began to decrease below 1 once the nearest rock outcrop was greater than 400 m.

Table 1. 5 Abundance of four species was modeled at the local (area around a trapping array) and at the landscape level (area around the trapping array with distance equal the species dispersal range). The estimates and confidence interval (in brackets) are the top models selected through AICc.

	Gophersnake		**Great Basin rattlesnake**	
	Local	Landscape	Local	Landscape
(Intercept)	0.67*** [0.36, 0.99]	0.75 *** [0.46, 1.05]	-0.74 * [-1.34, -0.15]	-0.79 ** [-1.33, -0.25]
Times Burned	-0.60 ** [-1.02, -0.17]	0.22 [-0.17, 0.61]	-0.14 [-0.89, 0.61]	-0.17 [-0.92, 0.57]
Cheatgrass Cover	0.32 [-0.06, 0.70]	0.14 [-0.31, 0.59]	0.14 [-0.78, 1.06]	
Shrub Cover		0.45 * [0.07, 0.82]		
Bare ground Cover			-0.27 [-1.05, 0.50]	-0.72 * [-1.33, -0.11]
Distance to Rock Outcrops			0.03 [-0.53, 0.59]	0.11 [-0.41, 0.63]
Number of Rock Outcrops				0.38 [-0.22, 0.97]
N	48	48	48	48

AIC	206.49	211.56	109.74	104.76
BIC	213.98	220.92	120.97	115.98
Pseudo R2 (McFadden)	0.03	0.01	0.01	0.07
Pseudo R2 (Pearson)	0.21	0.21	0.03	0.22
	Striped whipsnake		**Tiger whiptail**	
	Local	Landscape	Local	Landscape
(Intercept)	-2.39 ** [-4.17, -0.61]	-2.50 ** [-4.17, -0.83]	-0.33 [-0.81, 0.16]	-0.34 [-0.81, 0.14]
Times Burned				
Cheatgrass Cover			-0.42 [-0.95, 0.12]	
Shrub Cover	-0.09 [-0.67, 0.49]	0.56 [-0.08, 1.19]		0.42 * [0.02, 0.82]
Bare ground Cover				0.69 ** [0.18, 1.21]
Distance to Rock Outcrops	-2.99 * [-5.79, -0.18]	-2.81 * [-5.42, -0.21]	-1.09 *** [-1.69, -0.49]	-1.11 *** [-1.69, -0.53]
Native Herbaceous Cover			-0.95 *** [-1.51, -0.40]	
N	48	48	48	48

AIC	87.10	84.65	147.63	147.47
BIC	94.58	92.14	156.99	156.83
Pseudo R2 (McFadden)	0.16	0.20	0.25	0.25
Pseudo R2 (Pearson)	0.24	0.31	0.38	0.35
*** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$.				

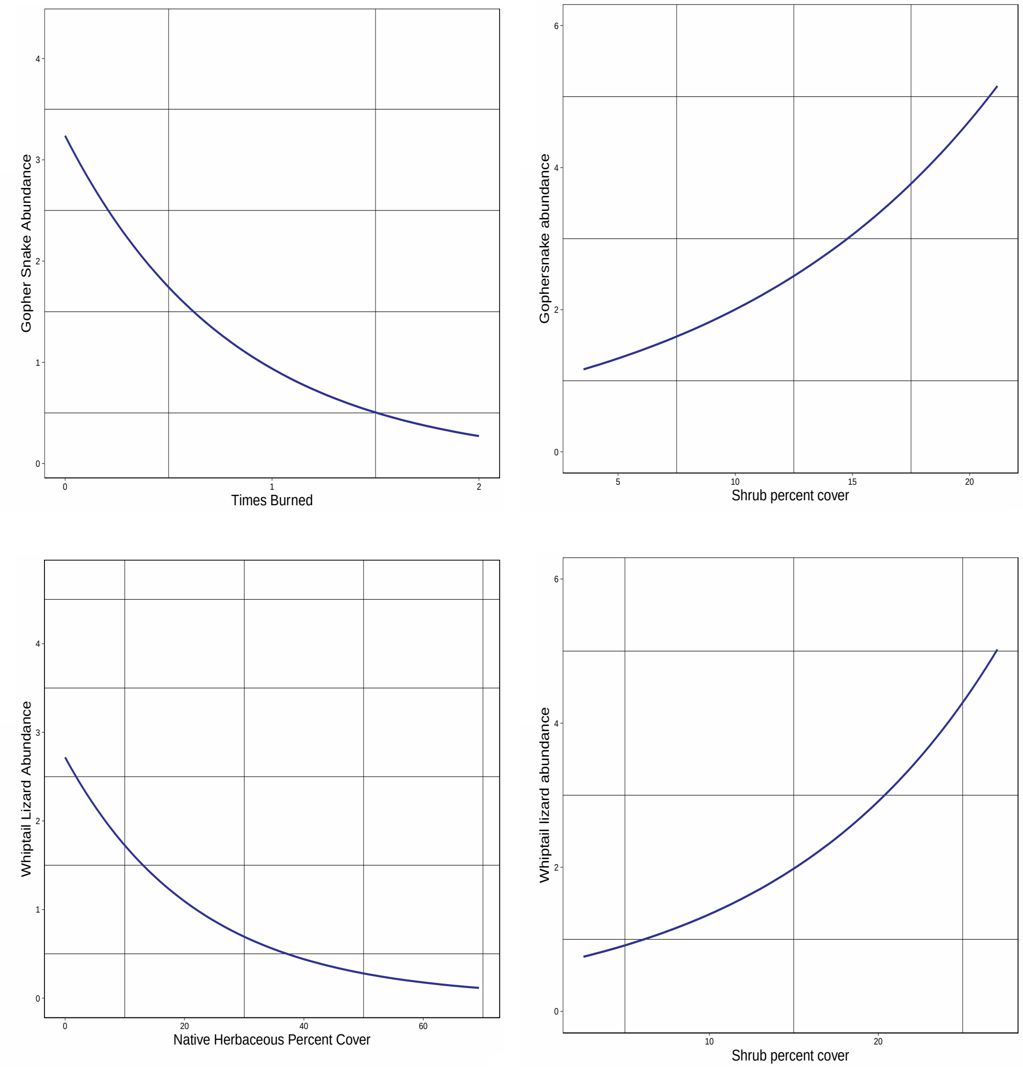


Figure 1. 4 Landscape level abundance (sum trapped at a location) of three snake species and one lizard at the Morley Nelson Snake River Birds of Prey National Conservation Area (NCA) in southwest Idaho in 2018. The top row shows local gophersnake abundance lowered at burned location. At the landscape level abundance increased at shrubland locations. We determined native herbaceous (local level) decreased whiptail abundance, while shrub cover (landscape level) increased whiptails (second row) abundance. We determined whiptail abundance is influenced by open corridors and shrub protection at both landscape levels.

Discussion

We sought to assess how the cheatgrass-fire cycle affects sagebrush steppe reptile communities, specifically focused on the assemblage of species and their distribution (i.e., occupancy) and relative abundances. Assessing the effects of the cheatgrass-fire cycle is complicated by interactions of variables and changes in the magnitude, frequency, and type of disturbance. In our case, both cheatgrass and wildfire are types of disturbances. Cheatgrass is an invasive species from Eurasia that proliferated across the Intermountain West over 100 years ago (Mack, 1981, Knapp, 1996). Cheatgrass can directly affect reptiles by inhibiting their movements, increasing exposure to predators, and reducing prey availability (Hall et al., 2009, Hall 2021, Rieder et al., 2010). Historically, wildfire was infrequent in sagebrush steppe, with a fire return interval of about 100 years or more (Baker 2006, Mensing et al., 2006). Fire is now 2 – 4 times more frequent where cheatgrass is dominant (Balch et al., 2013), occurring about every nine years on average in the northern Great Basin (Pilliod et al., 2021). Wildfires affect reptiles by reducing habitat heterogeneity and altering trophic interactions (Cossel, 2003, Jenkins & Peterson, 2008, Rochester et al., 2010).

Our data suggest that, at a local level, the cheatgrass-fire cycle has reduced lizard richness but not snake richness. The relatively small home range size of lizards may make them particularly vulnerable to frequent wildfire. We know that wildfire dramatically alters cover, the thermal environment, and the prey base in sagebrush ecosystems (Sharp-Bowman et al., 2017, Anthony et al., 2020). This lower richness in relation to burn frequency reflected our occupancy analyses at the species level for tiger whiptail. Contrary to expectations, whiptail occupancy was more likely in areas with higher cheatgrass cover but our abundance analyses revealed a negative relationship between whiptail abundance and cheatgrass cover. We suspect this may be an artifact of their active foraging behavior where at least one individual would get caught passing through marginal habitat.

Although overall snake richness was unrelated to wildfire or cheatgrass, we found that our 3 most common snakes – gophersnakes, rattlesnakes, and striped whipsnakes – were less likely to occupy areas that had burned more than once. Many reptiles are long-lived and slow to maturation, it is possible many snakes collected during this study experienced a fire or were born soon after a wildfire (Beaupre and Douglas 2009). Thus, a possible inference is that rattlesnake occupancy is shifting from burned areas to ones with higher shrub cover as they seek retreat sites and prey since fire can reduce both protection from predators and prey availability (Groves & Steenhof, 1988, Friend, 1993, Hall, 2012). Rattlesnake populations affected by wildfire can experience lower body conditions, limited movement patterns, and reduced reproductive characteristics (Jenkins & Peterson, 2008, Jenkins et al., 2009, Lomas et al., 2019). The cheatgrass-fire cycle can perpetuate these effects resulting in habitat fragmentation and genetically isolated populations (Clark et al., 2010, Pilliod et al., 2020). Of the reptiles we analyzed, gophersnakes appeared to be impacted the most by wildfire. Consequently, wildfire has the potential to also lower gophersnake abundance at the landscape level. As a result, gophersnake populations avoid burned areas for preferable ones which, in fragmented landscapes, can lead to smaller home range sizes (Rodriguez-Robles, 2003, Kapfer et al., 2010, Edkins et al., 2018).

Many reptiles found at the NCA are associated with a particular habitat/cover type or a suite of habitat types (**Table 1.** 1). Though we found reptile occupancy was mostly affected by wildfire, habitat heavily influences abundance. For example, rock outcrops are significant to overall snake richness as well as whipsnake and whiptail abundance at both spatial scales. The high vagility of whipsnakes and their use of shrubs while foraging could suggest a higher sensitivity to habitat loss (Hirth et al., 1969, Rochester et al., 2010, Mitrovich et al., 2018). Whipsnakes are the most arboreal species at the NCA, possibly utilizing shrub cover to gain a predatory advantage (Hirth et al., 1969, Mitrovich et al., 2018). This unique reliance on shrub cover could increase the negative effect of wildfire on abundance at a landscape level as shrublands are replaced by non-native grasslands. Therefore, we believe maintaining habitat heterogeneity that includes native shrublands will be vital for whipsnake populations (Cossel, 2003, Rochester et al., 2010). The strong relationship whiptail has with shrubs and open understory (Greenberg et al., 1993, Cossel, 2003) was also clear in our abundance results, suggesting that whiptails require microhabitats provided by heterogeneous open shrublands at a landscape level (Greenberg et al., 1993, Rochester et al., 2010, Germano et al., 2011).

We recognize the potential biases of reptile trapping data using drift fences, especially for highly vagile compared with sedentary species, like sit-and-wait predators or some lizards with home ranges linked to a specific feature (e.g., rock outcrop). The active survey method of VES included surveyor bias, which we integrated into the model as a varying intercept. Therefore, using VES, we expected and did analyze more reptile species, three more lizard species. We had similar observation of tiger whiptail and sagebrush lizard using both survey approaches. However, we had too low a capture rate for sagebrush lizards so our inclusion of VES allowed for more lizard species to be analyzed. Common side-blotched lizard – the most numerous species during our VES surveys – and western fence lizard were rarely (or never) trapped, but the detection of few lizard species strongly depends on habitat and surveyors search recognition. We observed many western fence lizards along the talus slopes, canyon rim or substantial rock outcrops. The strong association to locations across the NCA was shown to have low occupancy, however, we may not be capable of surveying the area occupied by western fence.

Our findings suggest that the cheatgrass-fire cycle negatively impacts lizards and snakes, but some species may be more affected than others. Unfortunately, few comparisons are available for a few taxa (but see Holbrook et al., 2016), which is worrisome given the occurring ecological transformations. Thus, a call for more research is warranted for further investigation on reptiles, and other taxa. We also highly suggest further research on fine-tuning of habitat restoration approaches. The cheatgrass-fire cycle is pervasive, difficult to manage, and has the potential to get worse. Considering how other non-native plants contribute to perpetuating the fire cycle, we believe other non-native plants can also affect whiptail abundance and potentially other lizard abundance. However, we lack an understanding of the impact of non-native plants proliferating in southwest Idaho, namely bur buttercup (*Ceratocephala testiculata*) and tall tumble mustard. This absence of information presents an opportunity for future research. The climate change projection for the western U.S. forecasts a shorter freeze season, variable frequency of wet winters, and a longer, drier fire season that would further feed the cheatgrass-fire positive feedback loop (Abatzoglou & Kolden, 2011).

Based on our results and current post-fire treatment methods, we encourage land managers to select treatment with returning wildlife in mind. For example, homogenous seedings of crested wheatgrass or Forage Kochia as fuel break lowers the diversity of reptiles and other taxa (Doherty et al., 2015). A mosaic of habitat diversity and structure, including invasive, can support reptile communities better than drill seeded monoculture (Bruton et al., 2015, Davies et al., 2021). Creating and maintaining a habitat mosaic could be challenging to achieve. Restoration “islands” of restored native vegetation and buffer strips have the potential to improve reptile occupancy by providing microhabitat (Schlesinger et al., 2020).

CHAPTER TWO: EVALUATION OF THE GREAT BASIN RATTLESNAKE (*CROTALUS OREGANUS LUTOSUS*) POPULATION GENETICS AND HUMAN INFLUENCE ON CRYPTIC GENETIC DIFFERENTIATION

Introduction

The western rattlesnake (*Crotalus oreganus*) species complex has been a taxonomically challenging to unravel and historically a contentious topic (Ashton and Queiroz, 2001, Davis et al., 2016, Pook et al., 2000). A possible reason is from the repeated allopatric divergence leading to cryptic species, that can only be identified through nuclear DNA sequencing (Goldenberg, 2013, Schield et al., 2018, Schield et al., 2019a). Due to the western rattlesnake capability for successful hybridization and repeated allopatric speciation, we decided to use nuclear DNA to investigate the population genetics of the Great Basin rattlesnake (*Crotalus oreganus lutosus*).

C.o. lutosus is an important species to the Great Basin sagebrush steppe ecosystem (Diller & Johnson, 1988, Marzluff et al., 1997), found throughout southern Idaho in sagebrush steppe habitat, rock outcrops, or talus slopes (Diller & Wallace, 1996, Cossel, 2003). Unfortunately, *C.o. lutosus* faces with an onslaught of external stressors, from habitat disturbances (e.g., cheatgrass-fire cycle, roads, urbanization) to direct persecution from the public out of fear or intrigue (Jochimsen et al., 2014, Katzner et al., 2020). Stressors such as these have led to diminished prey resources, interrupted dispersal, reduced body size, and lower fecundity in *C.o. lutosus* (Claunch 2016, Jenkins & Peterson 2008, Lomas et al., 2019). The loss of connectivity between den complexes have resulted in genetic isolation, genetic diversity can slowly decline or sped up from human disturbance (Clark et al., 2010, Schmidt et al., 2020).

Given that *C.o. lutosus* are long-lived species, 16-20 years, and have a slow generational, genetic variation might be difficult to assess. The females reach maturity around 4-5 years of age and reproducing 2-4 offspring, at most, biannually (Diller & Wallace 1984, Jenkins et al. 2009). Despite these slower processes, Parson et al. (2019) assessed gene flow of *C.o. lutosus* among den complexes in southeastern Idaho and found that multiple individuals dispersed from the most prolific den to rest of the dens within the study area. The high fecundity rate and dispersal of individuals helped Parson et al. to observe gene flow with 6 microsatellites. The advances of DNA sequencing have made restriction associated-site DNA sequencing (RAD-seq) a ‘simple’, cost-effective way to achieve deep coverage to call thousands of single-nucleotide polymorphisms (SNPs; Davey & Blaxter, n.d., Zimmerman et al., 2020). Through RAD-seq we can determine phylogenetics and phylogeography of non-model species, with enough depth to determine cryptic genetic differentiation within populations (Adams et al., 2019, Schield et al., 2018, Schield et al., 2019a, Schield et al., 2019b, Schmidt et al., 2020)

Of the known den complexes in our study area, all have experienced multiple habitat disturbances (e.g., cheatgrass-fire cycle, roads, agriculture). Although the majority of the NCA den complexes are faced with these disturbances, we noted a den complex (hereafter referred as “NCA_B”) that appear geographically isolated from the other known dens within and adjacent to the NCA. The NCA_B has burned 6 times in the last 65 years (Welty & Jeffries, 2020), with cheatgrass (*Bromus tectorum*, invasive annual) as the predominate habitat cover in the surrounding landscape (Enterkine, 2019). In addition to agriculture fields and major highways surrounding. We hypothesized the ecological speciation of *C.o. lutosus* was occurring at the NCA_B, and the recent human disturbances facilitated the genetic differentiation observed within 8 to 10 generations of rattlesnakes.

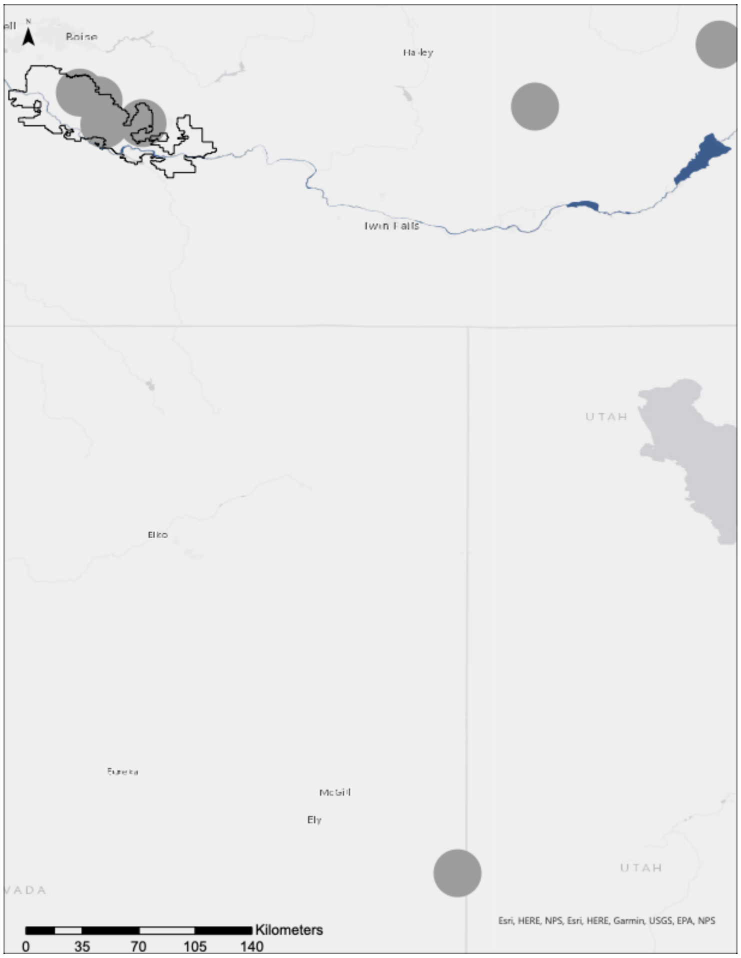
Methods

Study Area

The range of C. o. lutosus encompasses large parts of the Great Basin and into southern Idaho at its northern edge. The Morley Nelson Snake River Birds of Prey National Conservation Area (NCA, Figure 2.1) in southwestern Idaho was established in 1993 to provide conservation, protection and enhancement of raptor populations and habitats. At the NCA, raptors typically prey on rodents, lagomorphs, lizards, and snakes that inhabit shrublands and grasslands (Steenhof & Kochert, 1988, Marzluff et al., 1997). Historically the NCA was extensive sagebrush steppe, but now it is a mosaic of native vegetation and exotic annuals. The area has been fragmented by roads, fences, and frequent wildfire scars (Whisenant, 1990, Knick & Rotenberry, 1997). The NCA is 195,746 hectares of public land with 55,846 hectares of it used by the Idaho Army National Guard for military training since 1953 (USDI, 2008). The NCA supports research, military training, livestock grazing, and recreational activities (USDI, 2008).

The steep basalt slopes of the Snake River canyon are a major topographic feature of the NCA, bisecting the southern portion. Basalt buttes are scattered throughout the southern portion and shrublands predominantly shadscale (Atriplex confertifolia), winterfat (Krascheninnikovia lanata), and greasewood (Sarcobatus vermiculatus). The topography flattens further north, and shrubs transition to mainly Wyoming big sagebrush

(Artemisia tridentata wyomingensis) and green rabbitbrush (Chrysothamnus viscidiflorus). C.o. lutosus den in talus slopes along the canyon wall or the base of buttes as well as in basalt outcrops and collapsed lava tubes (Diller & Wallace 1984, Diller & Wallace 1996, Huey et al., 1989).



Esri, HERE, NPS, Esri, HERE, Garmin, USGS, EPA, NPS

Figure 2. 1 We compiled C.o. lutosus (Great Basin rattlesnake) tissue and blood samples from three geographically distant locations within C.o. lutosus range. We collected tissue samples from southwestern Idaho during the summers of 2018 and 2019, at the NCA (Morley Nelson Snake River Birds of Prey National Conservation area). We received tissue and blood samples from Craters of the Moon and Idaho National Laboratory, southeastern Idaho and the Great Basin National Park, Nevada.

Sample Collection

We collected tissue samples (ventral scale clips or blood) for genetic analysis from living specimens obtained during live-trapping, visual encounter surveying, and incidental encounters. All animals were handled according to approved protocols under permit Boise State University IACUC permit AC17-024 and released at their point of capture. The live-trapping effort took place throughout the military training area and adjacent areas north of the Snake River, at 48 historical reptile trap locations in the summer of 2018. The visual encounter surveying areas were more dispersed throughout the NCA, a total of 74 areas surveyed for reptiles (refer to chapter1 for further details on the survey methods). All the samples used were collected above the Snake River, samples were intentionally collected from known dens (i.e., NCA_B).

We included samples from geographically distanced populations within *C.o. lutosus* range, to increase our understanding of the population's phylogeography. The Great Basin National Park (GBNP) contributed blood and tissue samples, all stored in ethanol at -30°C (Table 2.1). We received blood samples collected in southeast Idaho (hereafter, SEID) by graduate students at the Idaho State University. These samples came from Craters of the Moon National Park and ~60 miles northeast at the Idaho National Laboratory; all were stored in ethanol at -70°C (Figure 2.1). To protect *C.o. lutosus* and den sites, we are not reporting the coordinates for any samples or hibernaculum.

RAD-Seq

We performed DNA extractions were performed on 265 samples, using E.Z.N.A. Tissue DNA Extraction Systems from Omega Bio-tek. We followed the manufacturer's protocol for tissue and blood DNA extraction. We sent the extractions to Collaborative

Ecological Genetics Lab, University of Illinois to perform ddRAD-Seq. Samples (n = 143) with too low of DNA concentration were removed from the pipeline. The samples with > 13 ug (n = 122) were then digested by Pstl and Mspl restriction enzymes. Our RAD library was built from 53 unique barcodes and 7 Illumina indexes. The pair-end libraries were normalized and multiplexed before being sequenced on an Illumina NovaSeq6000 ran at the, University of Illinois. We included the used RAD-Seq protocol as a supplementary document.

We trimmed low quality reads and adapters, then demultiplexed the raw data, preformed with the program ‘cutadapt’ on a high processing computer (BORAH, Research Computing Department, Boise State University). Afterward we checked for base pair content quality and remaining contamination with FASTQC. We decided to assemble a subset of the samples to gain a snapshot of our dataset and test our pipeline. Our subset comprised of 24 samples from the SEID (n = 4), GBNP (n = 4), NCA (n = 8), and NCA_B (n = 8) regions (Table 2.1). Our focus was on *C.o. lutosus* genetic structure and diversity at the NCA; thus, we included more samples for the predicted subpopulations. We selected the samples with the highest read count were selected for each region.

Table 2. 1 The samples selected for the subset, based on highest number of reads for the four regions. The NCA samples we collected at the Morley Nelson Snake River Birds of Prey National Conservation area from 2018-2020. NCA_B samples are only from the geographically isolated den complex at the NCA. We received samples from the Great Basin National Park (GBNP) and southeastern Idaho (SEID).

Sample ID	Number of Reads (150 nt long)	gDNA Extract Concentration (ng/ul)	gDNA Digestion Volume ul (250 ng)
GBNP_1	18131698	17.5	6.93
GBNP_2	44594399	21.6	6.09
GBNP_3	22763261	6.56	19.35
GBNP_4	31872667	5.87	19.5
NCA_1	17495282	7.67	19.5
NCA_2	16044782	10.3	19.5
NCA_3	14297086	37.5	18.49
NCA_4	11606857	42.7	14.26
NCA_5	12241325	6.36	15.9
NCA_6	15067985	45.5	19.5
NCA_7	15780867	12.9	19.5
NCA_8	16890356	51	19.5
NCA_B1	14133941	28.4	9.15
NCA_B2	11206701	15	19.5
NCA_B3	16149558	12.1	19.5
NCA_B4	14189695	12.6	19.2
NCA_B5	11461263	11.4	19.5
NCA_B6	12799994	5.36	8.72
NCA_B7	9375043	11.8	19.5
NCA_B8	12436771	13	19.5
SEID_1	6529530	13.5	19.5
SEID_2	31996105	29.8	5.71
SEID_3	9989566	12.8	12.04
SEID_4	10301142	15.7	19.5

We mapped our reads with a reference genome and called for SNPs using ipyrad (Eaton & Overcast, 2020). We set the assembly parameters to ensure Illumina adapters and low-quality bases are removed. Due to time constrains we used a reference genome for the assembly (*Crotalus viridis viridis* (prairie rattlesnake), GenBank accession no.

PDHV00000000.2, Schield et al., 2019b). Mapping against a reference genome could bias toward high polymorphic nucleotides found in the reference genome, thus reducing the total amount of SNPs discovered. However, we deemed this was less of a concern due to the close relationship (i.e., a sister clade) and the high introgression of the western rattlesnake species complex (Adams et al., 2019, Schield et al., 2019a).

To examine *C.o. lutosus* genetics in the NCA and test our hypothesis about the potential for subpopulation formation in a geographically isolated area of the NCA. We inferred the phylogeography and population genetics of the focal species using a coupled approach based on Maximum Likelihood (ML) phylogenetic inference and principal component analysis (PCA) based on the cleaned SNP data. The ML phylogenetic tree was inferred using RAxML (Stamatakis, 2014) implemented on the CIPRES portal (Miller et al., 2015) and using SEID as the most external output and GTRCAT model with 1000 bootstraps. The PCA was inferred in ipyrad as follows: we called SNPs that are shared across 75% of our samples and required 50% coverage from the assigned populations (i.e., NCA, NCA_B, SEID, GBNP).

Results

Of our 24 samples we called 444,268 SNPs from 397 million pair-end reads. We filtered the SNPs that are shared across less than 75% of the samples, we also ensured 50% coverage from the assigned populations (i.e., NCA, NCA_B, SEID, GBNP). We subsampled 32,321SNPs, 25 times, of the 1222,730 SNPs filtered for the PCA. Our results determined 4 clusters (**Figure 2.** 2) that corresponded to the two hypothesized subpopulations found within the NCA, the GBNP populations and the eastern Idaho population. The samples clustered into three groups horizontally, with the NCA subpopulations are more closely related to the GBNP population than the eastern Idaho populations. The NCA and NCA_ B samples are genetically similar to each other when compared to the two geographically distant groups. However, the PCA assigned the NCA and NCA_B into their own clusters, shown on the vertical axis (**Figure 2.** 2). Although we had no overlapping of samples in the genetic clusters, we noticed a few NCA_ B individuals closer to the NCA cluster, and vice versa. The SNPs we sampled explained 6.0% of genetic variance between the NCA subpopulations, and 10.6% genetic variance explained between regions.

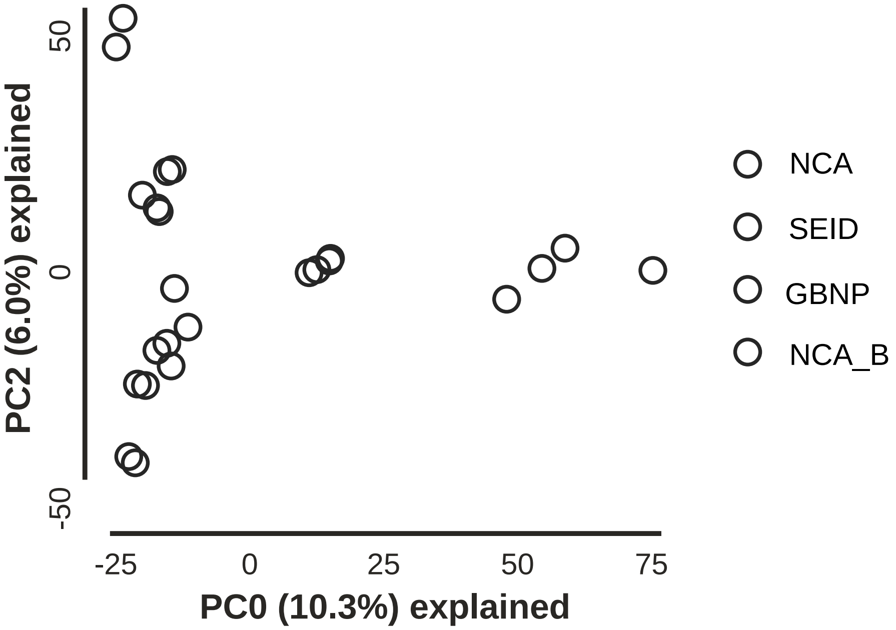


Figure 2. 2 PC analysis of 24 C.o. lutosus samples, color coordinated to the collection location. We found four clusters, corresponding to the two geographically distant populations (southeastern Idaho = SEID and Great Basin National Park = GBNP) and the NCA subpopulations (geographically isolated den complex = NCA_B and the rest of the NCA samples = NCA) with no overlap of individuals.

The phylogeny of our samples found four supported clades, which are nodes with a bootstrap value > 80 (**Figure 2.** 3). The SEID samples diverged first, which was expected since we set it as the outgroup, followed by the GBNP samples. We chose to set SEID as the outgroup after we inferred the PCA results. We found supported nodes that assigned separate NCA_B and NCA clades. We also found individuals from the NCA subpopulations with supported nodes and unsupported nodes.

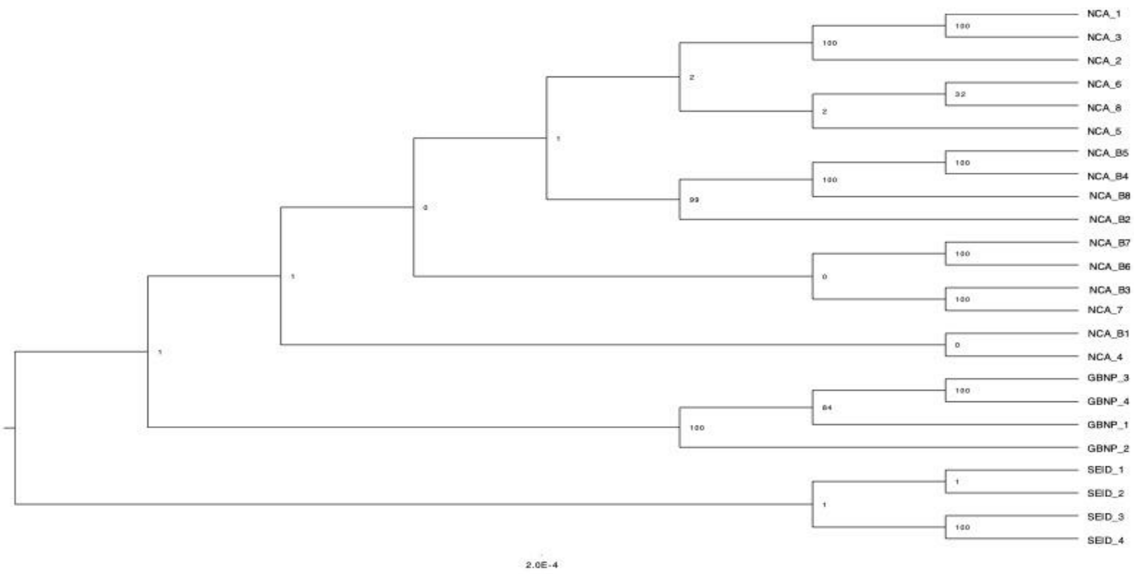


Figure 2. 3 The maximum likelihood phylogenetic relationship of C.o. lutosus sampled. We determined nodes with a bootstrap value greater that 80 was supported. Four clades were supported by bootstrap values, these four clades consist of two geographically distant populations (GBNP and SEID) and NCA subpopulations (NCA_B and rest of NCA). The two NCA samples are not completely separated, the subpopulations are still mixed.

Discussion

We conducted a novel analysis to examine the genetic structure of *C.o. lutosus* at the NCA in southwestern Idaho. We called 444,268 SNPs from 24 samples, collected from the NCA and two geographically distanced populations within *C.o. lutosus* range. To analyze the phylogeography and population genetics within the NCA and between geographically distant locations we performed a ML phylogenetic inference and PCA. Our main findings were finding support for our hypothesis of two genetically structured subpopulations within the NCA, for the divergence to occur recent.

Through our PCA we determined genetic differentiation of *C.o. lutosus* across our sampled populations (**Figure 2.** 3). The four genetic clusters showed a closer relationship between the southwestern Idaho (NCA and NCA_B samples) and GBNP, than the SEID samples. From a biogeological viewpoint, the two Idaho populations might be assumed to be more genetically similar as both these populations are in the Snake River Plain without major geological barriers. Meanwhile, the southwestern Idaho population and GBNP are separated by the many basins and ranges of the Great Basin Desert. The genetic relationship between these two populations suggests these populations diverged after the last glacial maximum as *C. oreganus* range expanded north. Despite the geographical barriers between these two populations, our PCA indicates GBNP population as an ancestral lineage. The phylogenetic analysis supports the genetic relationship seen between the three populations sampled (Figure 2. 3).

Our PCA showed evidence for two genetically differentiated subpopulations within the NCA. The genetic variance shown between the site B and rest of the NCA diverges in a different direction than from ancestral lineages (**Figure 2.** 3). The close distance of the NCA subpopulations samples clustered closely with no samples overlapping suggests a more recent divergence. Indeed, examination of ML phylogeography indicated a more recent divergence occurring within the NCA population. The two supported clades corresponded to the genetic structure visualized in the PCA. The mixture of NCA and site B samples lead us to predict a recent divergence, compared to the GBNP divergence.

The two genetic divergences shown through our genetic structure (PCA) and ML phylogenetic inference suggested two occurrences of genetic divergence. The first from the ancestral lineage (GBNP), the second within the NCA. The subpopulations are genetically structured, with a couple of individuals still closely related. We inferred these results as a recent, continuing divergence within a population. Based on the genetic differentiation seen within the NCA and knowledge of the western rattlesnake species complex reoccurrence of allopatric divergence (Adams et al., 2019, Goldenberg, 2013).

The genetic structure and phylogeography we determined at the NCA aligned with ecological speciation pattern of the *C. oreganus* spp. However, the lack of geological barriers and proximity of hibernaculum would allow for admixture between subpopulations. Human disturbances can lower connectivity, thus increase of genetic differentiation and structure (Clark et al., 2010, Vandergast et al., 2016). Human disturbances (e.g., roads and agriculture) further fragments the altered mosaic of the sagebrush steppe from the cheatgrass-fire cycle. As mentioned before there is a large human presence at the NCA increasing over in the past 50 plus years, as the population in southwestern Idaho has grown rapidly (Katzner et al., 2020, Pauli et al., 2019). Genetic differentiation between the NCA_B and rest of the NCA cannot be explained solely by human disturbances, especially with the slow annual recruitment and introgression. We hypothesized two genetically different subpopulations at the NCA and predicted human presence as an influential factor. We tested *C.o. lutosus* genetic structure and phylogeography; however, further dissection of the components driving the genetic differentiation of *C.o. lutosus* at the NCA is needed. Our research gave looked at the effects of habitat disturbances (i.e., cheatgrass-fire cycle and human presence) on reptiles at the NCA through multiple scopes. We examined the cheatgrass-fire cycle on reptiles, at a landscape and local scale, and determined that the effects are species dependent. The diversity of reptile of ecology present at the NCA, leans toward winners and losers after disturbances. We then examined deeper into the genetics of one reptile species, the C.o. lutosus. To determine an initial inquiry of genetic structure and phylogeny of two subpopulations on the NCA. Further investigation will help evaluate future research, conservation, and management needs.

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APPENDIX

Drift Fence

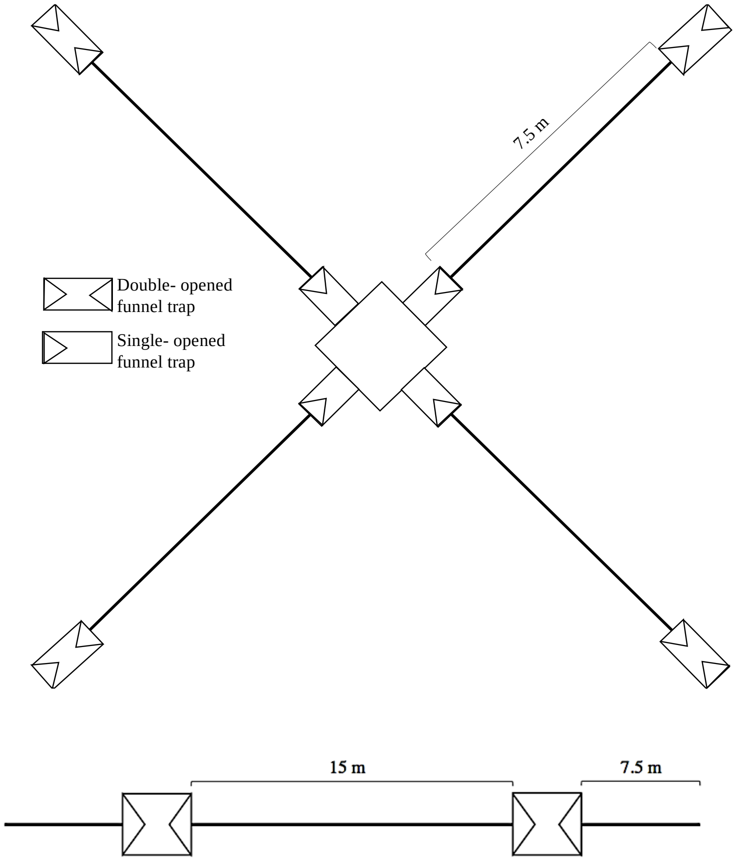

Figure A. 1 Historical reptile trapping array configurations used in 2018 on the OCTC and NW NCA within the NCA in southwestern Idaho. The cross-shaped trapping array (top) is what we used on the OCTC whereas the linear trapping array (bottom) is what we used in the NW NCA.

Table A. 1 The trapping arrays were gradually opened through May and beginning of June in 2018. All trapping arrays closed on the same date (6/30/2018). The 'N#' arrays were closed on weekends while the rest stayed open every day. We calculated trap nights for each array by the number of nights the traps were opened.

Trapping Array	Date Opened	Date Closed	Trap nights
NS2, FG2, NS3, FG1, NG1	5/7/18	6/30/18	54
SG1, FG3, FS2, FG4, FS4, FS1, SG4	5/9/18	6/30/18	52
FS3, NS1, NG3	5/10/18	6/30/18	51
SD3, ND4, ND2, SG2	5/11/18	6/30/18	50
SD4	5/15/18	6/30/18	46
NG2, SS3, SD1, ND1	5/16/18	6/30/18	45
SS1, SS2, ND3, FD1	5/17/18	6/30/18	44
FD3, SD2, FD2, FD4	5/20/18	6/30/18	41
NG4, SS4	5/21/18	6/30/18	40
SG3	5/22/18	6/30/18	39
NS4	5/23/18	6/30/18	38
N2, N5, N6, N7, N8	5/30/18	6/30/18	23
N3, N9, N10, N11, N12, N13	5/31/18	6/30/18	22
N4	6/4/18	6/30/18	20
Total			1977

Model Selection

Table A. 2 Lizard richness of local coefficients with confidence intervals. Top model selected through AICc. We evaluated goodness-of-fit for the top model by pseudo R^2 value. We observed goodness-of- fit for the other models, to determine important predictor variables.

	Model 1	Model 2	Model 3	Model 4
(Intercept)	-0.88 ***	-0.84 ***	-0.74 ***	-0.87 ***
	[-1.33, -0.42]	[-1.32, -0.36]	[-1.15, -0.32]	[-1.34, -0.40]
Bare ground cover	0.29	0.53 **		
	[-0.10, 0.68]	[0.14, 0.91]		
Native Herbaceous Cover	-0.41		-0.80 **	-0.75 **
	[-0.94, 0.12]		[-1.35, -0.24]	[-1.30, -0.20]
Time since last fire	0.72 *			
	[0.02, 1.41]			
Cheatgrass cover		0.31	-0.17	
		[-0.30, 0.93]	[-0.77, 0.42]	
Times burned		-0.84 *		-0.58
		[-1.55, -0.13]		[-1.29, 0.14]
Distance to rock outcrop		-0.16		
		[-0.53, 0.20]		
Shrub cover			0.41 *	0.36
			[0.05, 0.77]	[-0.00, 0.73]
			-0.07	-0.09

	Model 1	Model 2	Model 3	Model 4
Number of rock outcrops			[-0.34, 0.20]	[-0.37, 0.18]
N	48	48	48	48
AIC	109.18	111.35	112.45	109.30
BIC	116.67	120.71	121.81	118.65
Pseudo R2 (McFadden)	-0.15	-0.12	-0.13	-0.15
Pseudo R2 (Pearson)	0.18	0.145	0.13	0.07
*** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$.				

Table A. 3 Lizard richness at landscape level coefficients with confidence intervals. Top model selected through AICc. We evaluated goodness-of-fit for the top model by pseudo R^2 value. We observed goodness-of- fit for the other models, to determine important predictor variables.

	Model 1	Model 2	Model 3	Model 4
(Intercept)	-0.69 ***	-0.50 **	-0.70 ***	-0.59 **
	[-1.07, -0.32]	[-0.85, -0.14]	[-1.09, -0.31]	[-0.99, -0.20]
Bare ground cover	0.09	0.27		
	[-0.32, 0.51]	[-0.30, 0.83]		
Shrub cover	0.17		0.14	0.24
	[-0.25, 0.59]		[-0.33, 0.62]	[-0.23, 0.72]
Native Herbaceous cover	-0.33		-0.60 *	-0.51
	[-0.92, 0.26]		[-1.19, -0.02]	[-1.08, 0.07]
Time since last fire	0.19			
	[-0.16, 0.53]			
Cheatgrass cover		-0.26	0.17	
		[-1.14, 0.62]	[-0.40, 0.75]	
Times burned		0.61		0.50
		[-0.06, 1.28]		[-0.05, 1.05]
Distance to rock outcrops		-0.27		
		[-0.64, 0.11]		
Number of rock outcrop			0.52 ***	0.52 ***
			[0.22, 0.83]	[0.22, 0.81]
N	48	48	48	48

	Model 1	Model 2	Model 3	Model 4
AIC	119.56	119.74	109.40	107.31
BIC	128.92	129.10	118.76	116.66
Pseudo R2 (McFadden)	0.0320068	0.0303763	0.1217705	0.14
Pseudo R2 (Pearson)	0.1739686	0.1417084	0.3766509	0.38
*** p < 0.001; ** p < 0.01; * p < 0.05.				

Table A. 4 Snake richness of local coefficients with confidence intervals. Top model selected through AICc. We evaluated goodness-of-fit for the top model by pseudo R^2 value. We observed goodness-of- fit for the other models, to determine important predictor variables.

	Model 1	Model 2	Model 3	Model 4	Model 5
(Intercept)	0.02	0.09	0.07	0.13	0.08
	[-0.23, 0.26]	[-0.15, 0.34]	[-0.18, 0.31]	[-0.10, 0.36]	[-0.17, 0.32]
Shrub cover	0.08	0.16	0.13	0.22	
	[-0.17, 0.34]	[-0.09, 0.42]	[-0.12, 0.39]	[-0.03, 0.47]	
Time since las fire	0.03				
	[-0.29, 0.35]				
Distance to rock outcrop	-0.30 *	-0.27	-0.28		-0.30 *
	[-0.59, -0.01]	[-0.55, 0.01]	[-0.57, 0.01]		[-0.58, -0.01]
Bare ground cover		-0.02			
		[-0.40, 0.36]			
Cheatgrass cover		0.33		0.38 *	0.31 *
		[-0.10, 0.76]		[0.09, 0.68]	[0.03, 0.59]
Native herbaceous cover		-0.05		-0.03	
		[-0.41, 0.31]		[-0.32, 0.25]	
Times burned			0.02		-0.06
			[-0.29, 0.33]		[-0.36, 0.24]
N	48	48	48	48	48
AIC	164.86	163.91	164.45	164.00	161.40
BIC	172.34	175.14	173.80	171.49	168.88
Pseudo R2 (McFadden)	-0.1515587	-0.1152716	-0.1338609	-0.15	-0.126175
Pseudo R2 (Pearson)	0.17503	0.1452959	0.1289426	0.07	0.1404649
*** p < 0.001; ** p < 0.01; * p < 0.05.					

Table A. 5 Snake richness of landscape coefficients with confidence intervals. Top model selected through AICc. We evaluated goodness-of-fit for the top model by pseudo R^2 value. We observed goodness-of- fit for the other models, to determine important predictor variables.

	Model 1	Model 2	Model 3	Model 4	Model 5
(Intercept)	0.03	0.18	0.14	0.39 **	0.37 **
	[-0.20, 0.27]	[-0.06, 0.42]	[-0.11, 0.38]	[0.16, 0.63]	[0.12, 0.61]
Shrub Cover	-0.16	0.18	-0.11	-0.15	
	[-0.41, 0.08]	[-0.19, 0.55]	[-0.39, 0.16]	[-0.43, 0.14]	
Time since last fire	-0.10				
	[-0.46, 0.25]				
Distance to rock outcrops	-0.34 *	-0.41 **	-0.41 **		-0.29
	[-0.63, -0.05]	[-0.70, -0.12]	[-0.71, -0.11]		[-0.58, 0.01]
Bare ground cover		0.77 *			
		[0.10, 1.45]			
Cheatgrass cover		1.31 **	0.45 **	-0.24	-0.21
		[0.50, 2.12]	[0.14, 0.75]	[-0.57, 0.08]	[-0.49, 0.07]
Native herbaceous cover		0.34		0.07	
		[-0.07, 0.74]		[-0.17, 0.31]	
Times burned			-0.04		0.14
			[-0.34, 0.27]		[-0.13, 0.41]
N	48	48	48	48	48
AIC	163.02	154.17	158.49	140.47	137.16
BIC	170.51	165.39	167.84	147.96	144.65
Pseudo R2 (McFadden)	-0.14	-0.04	-0.09	0.03	0.05
Pseudo R2 (Pearson)	0.17	0.19	0.14	0.13	0.25
*** p < 0.001; ** p < 0.01; * p < 0.05.					

Table A. 6 Gophersnake abundance at local scale coefficients with confidence intervals. Top model selected through AICc. We evaluated goodness-of-fit for the top model by pseudo R^2 value. We observed goodness-of- fit for the other models, to determine important predictor variables.

	Model 1	Model 2	Model 3	Model 4	Model 5
(Intercept)	0.67 ***	0.69 ***	0.73 ***	0.75 ***	0.67 ***
	[0.36, 0.98]	[0.38, 1.01]	[0.44, 1.03]	[0.45, 1.04]	[0.36, 0.99]
Time since last fire	0.45 *				
	[0.02, 0.88]				
Cheatgrass cover	0.26	0.36		0.08	0.32
	[-0.12,0.63]	[-0.02, 0.74]		[-0.29, 0.45]	[-0.06, 0.70]
Native herbaceous cover	-0.23		-0.30	-0.27	
	[-0.58, 0.11]		[-0.65, 0.05]	[-0.61, 0.08]	
Shrub cover	0.24	0.23	0.29		
	[-0.07, 0.55]	[-0.08, 0.54]	[-0.01, 0.60]		
Times burned		-0.52 *			-0.60 **
		[-0.96, -0.08]			[-1.02, -0.17]
Distance to rock outcrop			-0.14	-0.15	
			[-0.45, 0.16]	[-0.44, 0.14]	
N	48	48	48	48	48
AIC	207.49	206.31	210.06	213.69	206.49
BIC	218.72	215.67	219.42	223.04	213.98
Pseudo R2 (McFadden)	0.04	0.04	0.02	0.00	0.03
Pseudo R2 (Pearson)	0.20	0.16	0.15	0.21	0.20
*** p < 0.001; ** p < 0.01; * p < 0.05.					

Table A. 7 Gophersnake abundance at landscape scale coefficients with confidence intervals. Top model selected through AICc. We evaluated goodness-of-fit for the top model by pseudo R^2 value. We observed goodness-of- fit for the other models, to determine important predictor variables.

	Model 1	Model 2	Model 3	Model 4	Model 5
(Intercept)	0.74 ***	0.75 ***	0.70 ***	0.74 ***	0.80 ***
	[0.45, 1.03]	[0.46, 1.05]	[0.41, 1.00]	[0.44, 1.04]	[0.49, 1.11]
Time since last fire	-0.39 *				
	[-0.72, -0.05]				
Cheatgrass cover	0.03	0.14		-0.05	-0.12
	[-0.47, 0.52]	[-0.31, 0.59]		[-0.45, 0.34]	[-0.55, 0.31]
Native herbaceous cover	-0.25		-0.18	-0.30	
	[-0.68, 0.19]		[-0.57, 0.20]	[-0.65, 0.05]	
Shrub cover	0.35	0.45 *	0.26		
	[-0.09, 0.79]	[0.07, 0.82]	[-0.11, 0.64]		
Distance to rock outcrops	-0.21		-0.15	-0.18	
	[-0.50, 0.09]		[-0.45, 0.14]	[-0.49, 0.13]	
Times burned		0.22			0.20
		[-0.17, 0.61]			[-0.23, 0.62]
N	48	48	48	48	48
AIC	210.30	211.56	212.11	213.94	214.32
BIC	223.40	220.92	221.46	223.30	221.81
Pseudo R2 (McFadden)	0.042	0.01	0.01	0.002	0.01
Pseudo R2 (Pearson)	0.23	0.21	0.22	0.19	0.14
*** p < 0.001; ** p < 0.01; * p < 0.05.					

Table A. 8 Great Basin rattlesnake abundance at local scale coefficients with confidence intervals. Top model selected through AICc. We evaluated goodness-of-fit for the top model by pseudo R^2 value. We observed goodness-of- fit for the other models, to determine important predictor variables.

	Model 1	Model 2	Model 3	Model 4	Model 5	Model 6
(Intercept)	-0.73 *	-0.74 *	-2.33 *	-0.73 *	-0.77 *	-0.75 *
	[-1.32, 0.13]	[-1.34, -0.15]	[-4.12, 0.54]	[-1.32, -0.14]	[-1.37, -0.17]	[-1.35, -0.16]
Cheatgrass cover	0.07	0.14		0.32		
	[-0.80, 0.94]	[-0.78, 1.06]		[-0.41, 1.05]		
Bare ground cover	-0.31	-0.27	-0.13			-0.36
	[-1.07, 0.46]	[-1.05, 0.50]	[-0.71, 0.45]			[-1.00, 0.27]
Shrub cover	-0.05		-0.07		-0.15	
	[-0.69, 0.59]		[-0.65, 0.51]		[-0.80, 0.51]	
Distance to rock outcrops	0.03	0.03	-2.89 *	0.03	0.00	0.03
	[-0.55, 0.60]	[-0.53, 0.59]	[-5.70, -0.07]	[-0.53, 0.59]	[-0.58, 0.58]	[-0.53, 0.59]
Times burned		-0.14		-0.19		-0.11
		[-0.89, 0.61]		[-0.91, 0.54]		[-0.81, 0.60]
Time since last fire					0.12	
					[-0.62, 0.85]	
N	48	48	48	48	48	48
AIC	109.86	109.74	88.91	108.09	108.72	107.83
BIC	121.08	120.97	98.27	117.44	118.07	117.18
Pseudo R2 (McFadden)	0.00	0.01	0.16	0.00	0.00	0.01
Pseudo R2 (Pearson)	0.03	0.03	0.19	0.03	0.04	0.03

*** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$.

Table A. 9 Great Basin rattlesnake abundance at landscape scale coefficients with confidence intervals. Top model selected through AICc. We evaluated goodness-of-fit for the top model by pseudo R^2 value. We observed goodness-of- fit for the other models, to determine important predictor variables.

	Model 1	Model 2	Model 3	Model 4	Model 5	Model 6
(Intercept)	-0.83 **	-0.84 **	-0.82 **	-0.71 *	-0.73 *	-0.83 **
	[-1.38, -0.28]	[-1.40, 0.28]	[-1.36, 0.27]	[-1.29, -0.12]	[-1.30, -0.17]	[-1.39, -0.27]
Time since last fire	-0.05				-0.46	
	[-0.75, 0.64]				[-1.11, 0.20]	
Cheatgrass cover	-0.25	-0.24		0.32		
	[-1.20, 0.69]	[-1.23, 0.74]		[-0.48, 1.11]		
Bare ground cover	-0.72	-0.77	-0.63 *			-0.67 *
	[-1.53, 0.09]	[-1.54, 0.01]	[-1.22, 0.05]			[-1.31, -0.04]
Shrub cover	-0.01	-0.03	0.07	-0.05	-0.01	
	[-0.72, 0.70]	[-0.73, 0.68]	[-0.56, 0.71]	[-0.80, 0.71]	[-0.68, 0.66]	
Distance to rock outcrops	0.14	0.14	0.11	0.03	0.08	0.12
	[-0.42, 0.70]	[-0.42, 0.71]	[-0.41, 0.63]	[-0.56, 0.62]	[-0.47, 0.62]	[-0.41, 0.65]
Times burned		-0.03				-0.14
		[-0.87, 0.80]				[-0.93, 0.65]
N	48	48	48	48	48	48
AIC	108.16	108.17	104.43	107.92	106.55	104.40
BIC	121.26	121.27	113.79	117.28	115.90	113.75
Pseudo R2 (McFadden)	0.05	0.05	0.04	0.00	0.019	0.04
Pseudo R2 (Pearson)	0.32	0.29	0.21	0.02	0.10	0.20
*** p < 0.001; ** p < 0.01; * p < 0.05.						

Table A. 10 Striped whiptail abundance models at the local scale with calculated coefficients with confidence intervals. Top model selected through AICc. We evaluated goodness-of-fit for the top model by pseudo R^2 value. We observed goodness-of- fit for the other models, to determine important predictor variables.

	Model 1	Model 2	Model 3	Model 4	Model 5	Model 6
(Intercept)	-2.34 *	-2.35 *	-2.33 *	-0.84 **	-2.39 **	-0.90 **
	[-4.15, 0.53]	[-4.17, 0.54]	[-4.12, 0.54]	[-1.46, -0.23]	[-4.17, -0.61]	[-1.53, -0.28]
Time since last fire	-0.04					
	[-0.74, 0.65]					
Bare ground cover	-0.13		-0.13			
	[-0.71, 0.45]		[-0.71, 0.45]			
Shrub cover	-0.06	-0.03	-0.07	0.02	-0.09	
	[-0.65, 0.54]	[-0.64, 0.58]	[-0.65, 0.51]	[-0.65, 0.69]	[-0.67, 0.49]	
Distance to rock outcrops	-2.92 *	-2.98 *	-2.89 *		-2.99 *	
	[-5.81, -0.02]	[-5.86, -0.09]	[-5.70, -0.07]		[-5.79, -0.18]	
Times Burned		0.10		0.14		
		[-0.59, 0.79]		[-0.58, 0.86]		
Cheatgrass cover		0.10				0.27
		[-0.58, 0.78]				[-0.42, 0.96]
Native herbaceous cover						-0.53
						[-1.36, 0.29]
N	48	48	48	48	48	48
AIC	90.89	90.84	88.91	100.27	87.10	97.97
BIC	102.12	102.06	98.27	107.75	94.58	105.46
Pseudo R2 (McFadden)	0.16	0.16	0.16	0.00	0.16	0.02
Pseudo R2 (Pearson)	0.19	0.20	0.19	0.01	0.20	0.02

*** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$.

Table A. 11 Striped whiptail abundance models at the landscape scale with calculated coefficients with confidence intervals. Top model selected through AICc. We evaluated goodness-of-fit for the top model by pseudo R^2 value. We observed goodness-of- fit for the other models, to determine important predictor variables.

	Model 1	Model 2	Model 3	Model 4	Model 5	Model 6
(Intercept)	-3.10 **	-2.39 **	-2.51 **	-2.34 **	-2.50 **	-1.02 **
	[-5.27, 0.93]	[-4.06, 0.72]	[-4.22, -0.80]	[-3.96, -0.71]	[-4.17, -0.83]	[-1.69, -0.35]
Time since last fire	0.76					
	[-0.19, 1.71]					
Bare ground cover	-0.55		-0.03			
	[-1.60, 0.49]		[-0.72, 0.66]			
Shrub cover	0.53	0.81 *	0.56	0.79 *	0.56	
	[-0.10, 1.15]	[0.09, 1.53]	[-0.08, 1.20]	[0.09, 1.49]	[-0.08, 1.19]	
Distance to rock outcrops	-3.45 *	-2.80 *	-2.84 *	-2.67 *	-2.81 *	
	[-6.73, -0.18]	[-5.47, -0.13]	[-5.57, 0.12]	[-5.18, -0.16]	[-5.42, -0.21]	
Times burned		0.35		0.48		
		[-0.57, 1.27]		[-0.12, 1.07]		
Cheatgrass cover		0.23				-0.07
		[-1.13, 1.59]				[-0.83, 0.68]
Native herbaceous cover						-0.76
						[-1.74, 0.21]
N	48	48	48	48	48	48
AIC	86.26	86.40	86.65	84.51	84.65	98.01
BIC	97.49	97.63	96.01	93.86	92.14	105.50
Pseudo R2 (McFadden)	0.24	0.22	0.20	0.22	0.20	0.02
Pseudo R2 (Pearson)	0.35	0.24	0.31	0.24	0.31	0.05
*** p < 0.001; ** p < 0.01; * p < 0.05.						

Table A. 12 Tiger whiptail abundance models at the local scale with calculated coefficients with confidence intervals. Top model selected through AICc. We evaluated goodness-of-fit for the top model by pseudo R^2 value. We observed goodness-of- fit for the other models, to determine important predictor variables.

	Model 1	Model 2	Model 3	Model 4	Model 5	Model 6
(Intercept)	-0.20	-0.18	-0.13	-0.33	-0.13	-0.35
	[-0.67, 0.28]	[-0.69, 0.32]	[-0.64, 0.38]	[-0.81, 0.16]	[-0.62, 0.35]	[-0.84, 0.14]
Time since last fire	0.46					
	[-0.12, 1.04]					
Bare ground cover	0.38		0.06		0.39	-0.18
	[-0.03, 0.79]		[-0.43, 0.54]		[-0.04, 0.82]	[-0.79, 0.43]
Shrub cover	0.06				0.16	
	[-0.36, 0.48]				[-0.25, 0.58]	
Distance to rock outcrops	-0.99 **	-0.98 **		-1.09 ***	-1.11 **	-1.07 ***
	[-1.61, -0.37]	[-1.57, -0.38]		[-1.69, -0.49]	[-1.79, -0.43]	[-1.65, -0.49]
Times burned		-0.49	-0.78 *			
		[-1.10, 0.11]	[-1.48, -0.08]			
Cheatgrass cover		-0.29		-0.42		-0.56
		[-0.91, 0.34]		[-0.95, 0.12]		[-1.31, 0.19]
Native herbaceous cover			-0.88 **	-0.95 ***		-1.09 **
			[-1.53, -0.22]	[-1.51, -0.40]		[-1.83, -0.35]
N	48	48	48	48	48	48
AIC	155.19	155.29	157.88	147.63	155.56	149.27
BIC	166.41	164.64	167.23	156.99	164.91	160.49
Pseudo R2 (McFadden)	0.20	0.18	0.16	0.25	0.18	0.26
Pseudo R2 (Pearson)	0.28	0.19	0.17	0.38	0.24	0.41

*** p < 0.001; ** p < 0.01; * p < 0.05.

Table A. 13 Tiger whiptail abundance models at the landscape scale with calculated coefficients with confidence intervals. Top model selected through AICc. We evaluated goodness-of-fit for the top model by pseudo R^2 value. We observed goodness-of- fit for the other models, to determine important predictor variables.

	Model 1	Model 2	Model 3	Model 4	Model 5
(Intercept)	-0.36	-0.25	-0.17	0.08	-0.34
	[-0.84, 0.12]	[-0.73, 0.23]	[-0.71, 0.37]	[-0.39, 0.55]	[-0.81, 0.14]
Time since last fire	0.23				
	[-0.42, 0.88]				
Bare ground cover	0.67 **		0.84		0.69 **
	[0.16, 1.17]		[-0.21, 1.90]		[0.18, 1.21]
Shrub cover	0.35	0.38		0.26	0.42 *
	[-0.10, 0.81]	[-0.07, 0.82]		[-0.27, 0.78]	[0.02, 0.82]
Distance to rock outcrops	-1.04 ***	-1.04 ***			-1.11 ***
	[-1.61, -0.47]	[-1.62, -0.47]			[-1.69, -0.53]
Times burned		-0.24	-0.76 *		
		[-0.88, 0.39]	[-1.50, -0.01]		
Cheatgrass cover		-0.36	0.16	-0.63	
		[-0.88, 0.16]	[-0.88, 1.21]	[-1.27, 0.01]	
Native herbaceous cover			-0.01	-0.42	
			[-0.74, 0.72]	[-1.02, 0.18]	
N	48	48	48	48	48
AIC	148.94	153.04	162.29	163.82	147.47
BIC	160.17	164.27	173.51	173.17	156.83
Pseudo R2 (McFadden)	0.26	0.22	0.14	0.11	0.25
Pseudo R2 (Pearson)	0.36	0.33	0.18	0.12	0.35
*** p < 0.001; ** p < 0.01; * p < 0.05.					