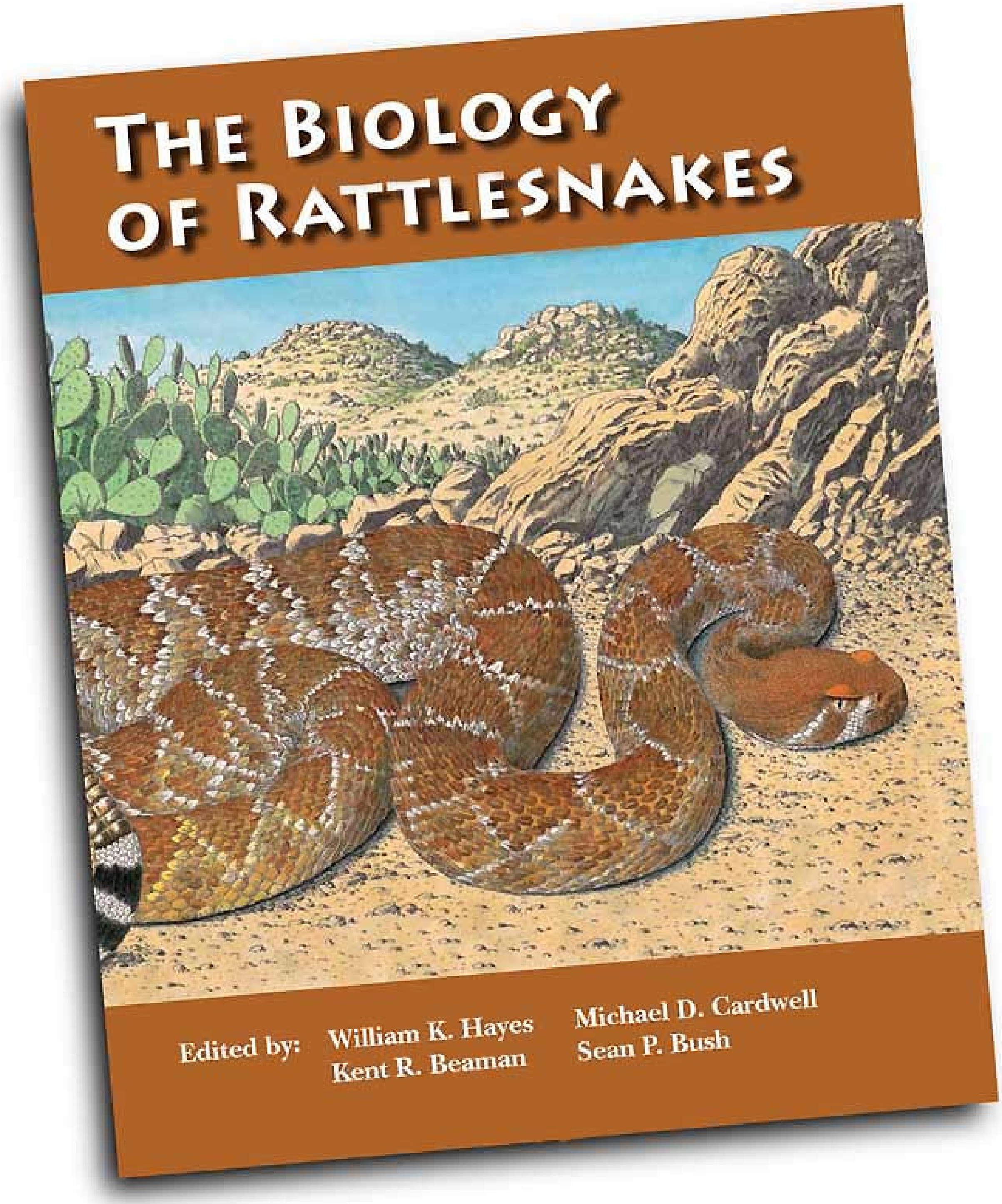
THE BIOLOGY OF RATTLESNAKES
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A Trophic-Based Approach to the Conservation Biology of Rattlesnakes: Linking Landscape Disturbance to Rattlesnake Populations

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Abstract.—Rattlesnakes are a group of North American snakes that are especially threatened by human activities. In the northern Intermountain West, rattlesnakes are threatened by widespread landscape disturbance that is converting native sagebrush steppe ecosystems to ecosystems dominated by invasive plants. We developed an approach to studying the effects of landscape scale disturbance on rattlesnakes based on trophic relationships. We studied Great Basin Rattlesnakes (*Crotalus oreganus lutosus*) in a sagebrush steppe ecosystem that is in various stages of being converted to grasslands. Specifically, we studied how substrate, vegetation, and prey vary among areas with different levels of disturbance. We also studied how variation in substrate and vegetation influence prey availability and how prey availability influences weight gain in snakes. We found that disturbed areas were characterized by less biological crust, more bare soil, less shrub cover, more grass cover, lower shrub heights, and prey communities that had lower species richness, abundance, and biomass. In addition, disturbed areas had lower proportions of larger prey items. Telemetered rattlesnakes using disturbed areas gained less weight than snakes using undisturbed areas. We found that habitat characteristics typical of undisturbed sites best predicted high prey biomass and that as prey biomass increased so did snake weight gain. Our results support the idea that landscape disturbance is influencing rattlesnake populations by altering trophic interactions. This approach should be considered when studying the conservation biology of rattlesnakes because it has important implications for understanding how human activities affect snake populations.

Introduction

Human activities are threatening global biodiversity (Cincotta et al., 2000). One group of vertebrates that is especially threatened by human activities is reptiles (Gibbons et al., 2000). For example, the collection of turtles for food and the pet trade have caused declines in turtle populations around the world (Bjorndal et al., 1993). Similarly, the persecution of crocodilians as threats to humans and for the use of their skin has resulted in their global decline (Platt and Van Tri, 2000). Snakes have also experienced widespread global declines due to human activities (Gibbons et al., 2000). In North America, rattlesnakes comprise one group of snakes that has experienced pronounced declines due to human activities such as habitat loss and direct persecution (Brown, 1993).

Rattlesnakes in sagebrush steppe ecosystems (one of the most endangered ecosystems in the world; Noss et al., 1995) of western North American are threatened by widespread landscape conversion. The combination of livestock overgrazing and invasive plants has altered natural fire regimes, resulting in widespread landscape conversion from shrublands to grasslands (Whisenant, 1990). Landscape conversion in sagebrush steppe is having well-documented effects on a variety of wildlife taxa (Wisdom et al. 2000; Vander Haegen et al., 2001). However, few studies have examined the effects on reptiles (Reynolds, 1978; Beck and Peterson, 1995; Cossel, 2003).

To address this problem, we developed a conceptual framework that uses trophic ecology to study the conservation biology of rattlesnakes. Specifically, we hypothesized that widespread landscape conversion in the sagebrush steppe ecosystem is influencing rattlesnakes through a series of trophic interactions (Fig. 1). Our conceptual framework focuses on three trophic levels: primary producers (i.e., vegetation), primary consumers (i.e., small mammals), and secondary consumers (i.e., rattlesnakes). Using this framework, we predicted that disturbance will have a significant impact on vegetation. Second, we predicted that variation in vegetation characteristics will influence small mammal communities. Third, we predicted that changes in small mammal communities will influence weight gain in rattlesnakes, which may ultimately have population-level consequences by affecting reproductive output.

A number of studies have examined either the influence of disturbance on small mammals (e.g., Van Horne et al., 1997; Wijesinghe and Brook, 2005; Scott et al., 2006) or the influence of snake size on reproductive output (e.g., Seigel and Ford, 1987). However, few have linked these types of studies to examine how disturbance-induced changes in prey availability influence snakes. The two examples that linked disturbance to snake reproductive ecology through prey resources come from studies on Arafura Filesnakes (*Acrochodus arafurae*) and Water Pythons (*Liasis fuscus*) in Australia. Madsen and Shine (2000) found that variation

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in precipitation, duration of flooding, abundance of snake prey (catfish), Arafura Filesnake body size, and Filesnake recruitment were correlated, indicating that disturbance influenced snake populations through trophic pathways. Similarly, Madsen et al. (2006) found that variation in the length of the monsoon season influenced prey abundance (rats), which was correlated with female body condition, survival, and the proportion of female Water Pythons pregnant. Thus, examples of similar approaches exist in snake ecology, but the overall approach has not been formally described in terms of its importance and applicability to rattlesnake conservation biology. Although this approach may not be appropriate for of all rattlesnake species, it is important to consider with respect to the conservation biology of rattlesnakes.

In this study, we used a trophic-based approach to examine the influence of disturbance on Great Basin Rattlesnake (*Crotalus oreganus lutosus*) populations in the sagebrush steppe ecosystem of southeast Idaho. We studied vegetation and small mammals in areas randomly distributed among landscape disturbance categories and in areas used by rattlesnakes to determine if a trophic link exists between landscape disturbance and rattlesnake populations. Our specific objectives included: 1) quantify how disturbance influences substrate, vegetation, and prey availability; 2) quantify how substrate and vegetation characteristics influence prey availability; 3) quantify how prey availability influences rattlesnake weight gain; and 4) discuss the importance of trophic approaches to rattlesnake conservation biology.

Materials and Methods

Study area.—The Idaho National Laboratory (INL) is located in the Upper Snake River Plain of southeast Idaho and is administered by the United States Department of Energy (DOE). It includes 2,305 km^2 of predominately sagebrush steppe habitat. The landscape has received minimal disturbance as compared to adjacent Bureau of Land Management (BLM) and private lands. Human development and access is limited on the INL with only peripheral areas (~40%) receiving light grazing. Conversely, extensive agriculture and heavy grazing occurs on adjacent BLM and private lands.

Topography in the study area is generally flat with dispersed volcanic features, including buttes, cinder cones, lava flows, and collapsed lava tubes. Climate is characteristic of cold deserts, with high daily fluctuations in temperature and low levels of precipitation (Anderson et al., 1996). Similarly, there are dramatic seasonal fluctuations in temperature, with hot summers and cold winters. The average annual temperature is 5.6°C and annual precipitation is approximately 220 mm. Precipitation peaks are in the months of April, May, and June.

We studied Great Basin Rattlesnakes from the Rattlesnake Cave hibernaculum (Fig. 2). Snake populations at Rattlesnake Cave have been monitored by the Herpetology Laboratory at Idaho State University for 11 yr. The area surrounding Rattlesnake Cave that is accessible to rattlesnakes as summer habitat (5 km radius, as determined by previous radiotelemetry studies) was also considered part of the study area. The study area is located in the southeastern portion of the INL; 7% of the area is undisturbed (not grazed or burned for ≥55 years), 41% has recently burned (within the last 55 yr), 51% is lightly grazed by domestic livestock, and 1% is grazed and burned (although no grazed and burned sites were sampled in this study). In addition, most of the burned areas and the understories of some unburned areas are dominated by non-native plants (e.g., Cheatgrass, *Bromus tectorum*, and Crested Wheatgrass, *Agropyron cristatum*).

Study design and sampling methods.—We measured a suite of substrate and vegetation characteristics in 50 randomly-distributed plots. We determined the locations of random plots using the Animal Movements extension (Hooge and Einchenlaub, 1997) in ArcView GIS 3.2 (ESRI Inc., Redlands, California, USA). Specifically, we generated random points within a 5 km radius buffer around Rattlesnake Cave to sample the areas available to snakes during the summer active period. We used hand-held GPS units (Geoexplorer, Trimble Navigation Limited, Sunnyvale, California, USA) to navigate to each habitat plot. At each plot, we measured the following characteristics: biological crust cover, bare soil cover, litter cover (i.e., downed plant material), rock cover, shrub cover, grass cover, forb cover, and average shrub height. We also recorded the dominant shrub species (i.e., the shrub species that dominated the shrub canopy layer).

Each habitat plot was 20 × 20 m and centered on the random point (Fig. 3). Plots were oriented so that the four sides faced the four cardinal directions. We measured habitat cover values (e.g., bare soil, biological crust, litter, rock, shrub, grass, and forb) using the line intercept method along two perpendicular 20-m transects that crossed at the center of the plot. Specifically, we counted the number of

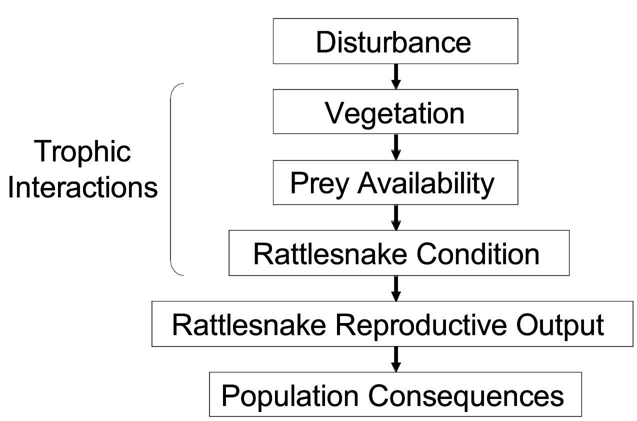

Figure 1. Diagram outlining the approach we used to study the conservation biology of Great Basin Rattlesnakes (*Crotalus oreganus lutosus*). Specifically, it outlines how landscape disturbance can trigger a series of trophic interactions that ultimately influence rattlesnakes. This diagram does not contain all ecological interactions; it includes only those that were the focus of this study.

centimeters of each cover type that intersected the transects. Each cover type was measured independently. For example, a given centimeter could intercept the foliage of a shrub and also intercept bare soil beneath the shrub foliage. To measure shrub height, we divided the plot into four quadrants delineated by the perpendicular transects. Within each quadrant, we visually assessed the average canopy height and measured a representative shrub height. To assure that visual assessments of average canopy height were precise, we conducted blind tests where all field workers took measurements separately and results were compared. In general, the measurements were precise among field workers but to further assure precision, at least two field workers conducted each visual assessment.

After taking habitat measurements, we also conducted small mammal trapping at each random habitat plot. We trapped small mammals by placing 16 Sherman live traps (H. B. Sherman Traps, Tallahassee, Florida) within each plot. We set one trap every 2 m along both line transects, beginning at the 2 m mark (Fig. 3). Traps were baited with a peanut butter, oat, bird seed, and bacon mixture. The bait combination was selected to target a variety of small mammal species with varying diets. We trapped each plot for two nights and checked them between 0500-1000 h each morning to prevent heat-induced mortality. Each small mammal we captured was identified to species, weighed, and marked with a hair clip on the lower back. From small mammal trapping data, we calculated the species richness, abundance, and total biomass of small mammals per plot.

In the spring of 2003, we initiated radiotelemetry studies on 11 Great Basin Rattlesnakes from the Rattlesnake Cave hibernaculum. All transmitters were implanted into adult male and nonpregnant female snakes (>60 cm SVL) to target sexually mature snakes that were predicted to spend the majority of their time feeding. Pregnant females were not used in this study because they reduce movements and foraging activity in favor of optimal thermal environments for gestation (Cobb, 1994). Transmitters were surgically implanted into the body cavity of snakes following procedures outlined in Reinert and Cundall (1982). We located snakes every 24-48 h using a hand-held radio receiver (Model R-1000, Communications Specialist Inc., Orange, California, USA) and a Yagi antenna (Wildlife Materials International Inc., Murphysburo, Illinois, USA). To visually locate snakes before disturbing them, we used binoculars to scan for individuals and made only careful movements as we approached. Using this approach, we were often able to observe snakes with no apparent influence on behavior. Once a snake was located, we noted any behaviors (e.g., coiled in foraging posture or in rodent burrow), marked the location with labeled flagging, and recorded a location using a GPS receiver. We post processed (i.e., differentially corrected) the GPS locations to improve location accuracy. Once per month during the summer activity period, we attempted to capture each snake. Snakes were then measured and weighed at the location of capture and released after 2-5 min of handling.

In conjunction with random habitat plots described previously, we also conducted habitat and small mammal sampling at snake locations. Snake plots were sampled following the exact procedures outlined previously. We sampled plots at snake locations approximately 1-3 d after the snake had left the location to minimize disturbance to the snake and maximize the safety of the individuals recording the habitat data. In cases when the snake stayed in the same location for 7 d, we measured habitat characteristics at a time when the snake was not active on the surface (e.g., at the warmest time of the day).

Data analysis.—We used a combination of geospatial techniques and statistics to quantify how habitat characteristics (i.e., substrate, vegetation, prey availability) varied by disturbance category. First, we used ArcMap to intersect a disturbance category layer (undisturbed, grazed, burned, and grazed and burned) with a point file of habitat sampling locations. We defined undisturbed areas as those that had not been grazed or burned in ≥55 yr, grazed areas as those that

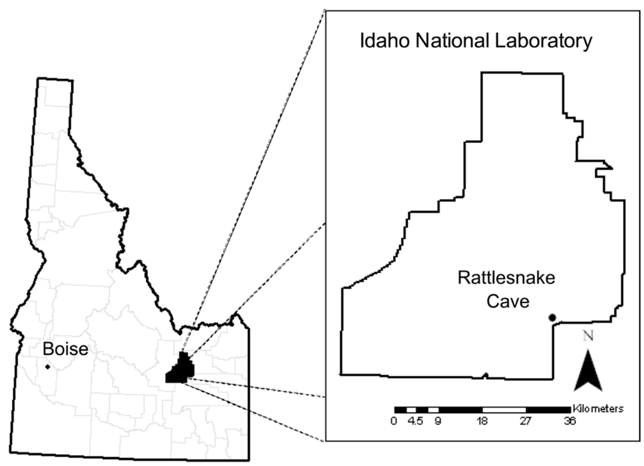

Figure 2. Study area map highlighting the location of the Idaho National Laboratory and the Rattlesnake Cave hibernaculum.

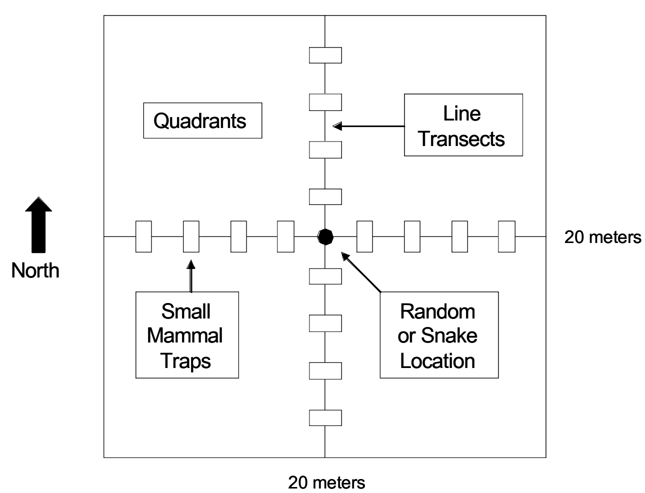

Figure 3. Diagram illustrating how we sampled habitat and small mammal plots.

Table 1. Mean (± 1 SE) cover (from line-intercept transects) of seven habitat types and mean shrub heights (± 1 SE) by disturbance category (undisturbed, grazed, and burned). Superscripts indicate results from ANOVAs; values with matching letters are not significantly different among disturbance categories.

Habitat Characteristics	Undisturbed	Grazed	Burned
Cryptogamic crust cover (cm)	524 ± 36.39[a]	505.67 ± 104.54[a]	93.42 ± 15.85[b]
Rock cover (cm)	434.36 ± 58.76[a]	211.33 ± 118.46[b]	325.94 ± 55.77[b]
Bare soil cover (cm)	1100.140 ± 55.12[a]	1599.75 ± 191.25[a,b]	1548.48 ± 70.14[b]
Litter cover (cm)	472.86 ± 38.23[a]	239.92 ± 56.79[b]	391.36 ± 30.09[b]
Shrub cover (cm)	713.24 ± 39.23[a]	720.92 ± 104.09[a]	405.69 ± 38.87[b]
Grass cover (cm)	446.36 ± 28.48[a]	431.08 ± 50.96[a]	652.37 ± 51.96[b]
Forb cover (cm)	99.74 ± 10.33	66.42 ± 15.87	76.57 ± 10.25
Shrub height (cm)	47.74 ± 3.12[a]	32.46 ± 3.18[b]	20.99 ± 1.64[c]

had been grazed for >55 yr, burned areas as those that had been burned within 55 yr, and grazed and burned areas as those that had been burned and grazed within 55 yr. We then characterized each sampling location by disturbance category and calculated descriptive statistics for each habitat variable by disturbance category. We used a series of one-way analyses of variance (ANOVAs) and Tukey post hoc tests to determine if habitat characteristics differed significantly by disturbance category. In addition, we characterized overall prey community composition as the proportion of each small mammal species captured relative to the total number of small mammals captured by disturbance category.

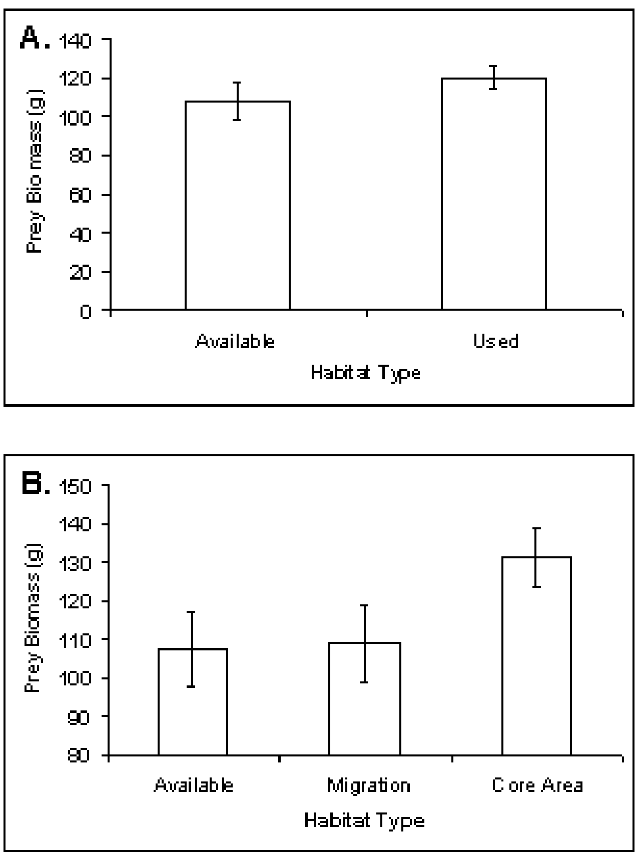

Figure 4. (**A**) Prey biomass in grams at sites available to snakes and sites used by snakes. (**B**) Prey biomass at sites available to snakes, used by snakes for migration, and used by snakes in core activity areas. Error bars represent ± 1 SE.

To determine the habitat characteristics that best predicted small mammal biomass, we used multiple linear regression. Small mammal biomass was used as the dependant variable and habitat characteristics were used as the independent variables. We used Akaike's Information Criterion (AIC) to select the model that explained the most variation in small mammal biomass using the least amount of independent variables. We examined variables for normality and made transformations as necessary.

To determine if snakes preferred certain disturbance categories, we compared the proportion of snake relocations in each disturbance category to the availability of each category within a 5 km buffer surrounding the hibernaculum. We then compared how weight gain in snakes varied among disturbance categories, using a two-sample *t*-test (snakes primarily used two disturbance categories). All radiotracked snakes were relocated at least 60% of the time in only one disturbance category. Thus, for *t*-tests we categorized each snake by the disturbance category it was relocated in most often. Each snake was then considered a sampling unit for the *t*-test.

We used linear regression to quantify how well small mammal biomass predicted weight gain in rattlesnakes. Before running the analysis, we refined our estimate of prey availability based on known movement and foraging patterns in Great Basin Rattlesnakes and other closely related rattlesnakes. Great Basin Rattlesnakes and Prairie Rattlesnakes (*Crotalus viridis*; a species closely related to Great Basin Rattlesnakes) typically leave hibernacula and move along a straight bearing until they reach an area of high prey availability (Duvall et al., 1985; Cobb, 1994). To account for this, we defined areas where snakes spent the majority of the active season and termed them core areas. To define core areas, we used the Animal Movement Extension in ArcView GIS to develop utility distributions of snake movements (i.e., estimated home ranges). We used fixed

Table 2. Mean (± 1 SE) small mammal species richness, abundance, and biomass by disturbance category (undisturbed, grazed, and burned). Superscripts indicate results from ANOVAs; values with matching letters are not significantly different among disturbance categories.

Small Mammal Characteristics	Undisturbed	Grazed	Burned
Species richness (# species/plot)	1.92 ± 0.04[a]	1.75 ± 0.18[a,b]	1.48 ± 0.08[b]
Abundance (# individuals/plot)	7.21 ± 0.32[a]	5.25 ± 1.03[a,b]	4.52 ± 0.34[b]
Biomass (grams/plot)	144.17 ± 6.66[a]	91.33 ± 18.00[b]	78.79 ± 6.80[b]

Table 3. Small mammal community composition (i.e., number and proportion of each species) by disturbance category.

Small Mammal Taxa	Undisturbed	Grazed	Burned
Deer Mice (*Peromyscus maniculatus*)	114 (0.75)	52 (0.83)	70 (0.77)
Least Chipmunks (*Tamias minimus*)	37 (0.24)	10 (0.15)	13 (0.14)
Harvest Mice (*Reithrodontomys megalotis*)	1 (0.01)	1 (0.02)	5 (0.06)
Pocket Mice (*Perognathus parvus*)	0	0	2 (0.02)
Grasshopper Mice (*Onchomys leucogaster*)	0	0	1 (0.01)

kernels and estimated 50% use areas. Hereafter, we refer to snake locations within 50% use areas as core areas and all other snake points as migration areas.

For each snake, we calculated the average prey biomass of all plots within their core area (i.e., plots that were contained within the 50% isopleth of the kernel home range estimate). For the regression, we used the average prey biomass in a snake's core area as an independent variable and the amount of weight gained by a snake over the course of the active season as the dependent variable. We only included snakes in analyses if they were captured and weighed at both the beginning and the end of the active season. In many cases, it was not possible to capture snakes at the end of the active season because they often spent long periods of time underground. Due to difficulties capturing snakes before they entered hibernacula, we used data from 2003 and 2004 at Rattlesnake Cave to determine how well small mammal biomass predicts snake weight gain (adding four additional snakes for a total sample size of nine).

Analyses were conducted using Minitab software (Minitab, Inc., State College, Pennsylvania, USA).

Results

We found that disturbance (i.e., grazing and fire) influenced substrate and vegetation characteristics (Table 1). Specifically, cryptogamic crust cover, rock cover, shrub cover, litter cover, and shrub height were high in undisturbed sites. Grass cover was highest in burned sites. Grazed sites had similar cryptogamic crust cover, bare soil cover, and shrub cover to undisturbed sites and similar rock cover, bare soil cover, and litter cover to burned sites. Shrub heights were intermediate in grazed areas. The dominant shrub species was green rabbit brush in burned areas, whereas the dominate shrub was big sagebrush in undisturbed and grazed areas.

Disturbance similarly influenced small mammal communities (Table 2). Small mammal species richness, abundance, and biomass were highest in undisturbed sites, intermediate in grazed sites, and lowest in burned sites. The majority of small mammals captured were Deer Mice and Least Chipmunks, although the composition of small mammals varied based on disturbance category (Table 3). In both grazed and burned areas, we captured a lower proportion of Least Chipmunks (i.e., large prey items). In all areas, we captured primarily Deer Mice, whereas in burned areas we also captured other species, such as Pocket Mice.

Results from linear regression models showed that substrate and vegetation characteristics influenced prey availability. The model that explained the most variation in small mammal biomass had a 3.79 lower AIC value than the next closest model. Small mammal biomass was higher in areas with higher cryptogamic crust cover, lower grass cover, and taller shrubs (Table 4). High crust cover, low grass cover, and tall shrubs were characteristics of areas with lower levels of disturbance (Table 1).

Overall, rattlesnakes used a higher proportion of undisturbed and burned areas and a lower proportion of grazed areas relative to availability (Table 5). However, most individual snakes used primarily one disturbance category and the category used varied among snakes (Table 5). Snakes that used primarily undisturbed habitats gained significantly more weight than snakes that used burned areas (undisturbed weight gain = 51 ± 6.11 g; burned weight gain = 29 ± 3.17; df = 7, $t = 3.59$, $P = 0.009$). Within these broad disturbance categories, our small mammal trapping results show that Great Basin Rattlesnakes are selecting core activity areas with high prey availability. Specifically, we found that, when comparing all used sites to random sites, there was slightly higher prey biomass in used sites (Fig. 4a). However, when comparing core area sites, migration sites,

Table 4. Results of multiple linear regression using Akaike's information criterion to determine the habitat characteristics that best predict the biomass of snake prey (small mammals). Overall, these variables explained 25% of the variation in small mammal biomass.

Factor	df	Coefficient	*t*-value	*P*
Intercept	1	1.701	6.78	<0.0001
Cryptogamic crust cover (cm)	1	0.114	3.67	0.0003
Grass cover (cm)	1	-0.204	-2.28	0.0236
Shrub height (cm)	1	0.355	4.63	<0.0001

and random sites, we found that prey biomass in migration areas was approximately equal to biomass in available areas but that prey biomass in core areas was much greater (Fig. 4b). We also found that snakes with high small mammal biomass in their core activity area gained more weight (Fig. 5). Specifically, as the average prey biomass within a snake's core activity area increased by 1 g, the snake gained 0.22 g of weight.

Discussion

We found that landscape disturbance influences rattlesnakes through a series of trophic interactions. First, we found that disturbance category has a significant influence on substrate and vegetation characteristics (Table 1). These results were similar to a number of studies in sagebrush steppe that found habitat characteristics such as biological crust cover and sagebrush cover to be lower and grass cover to be higher in burned areas (e.g., Belnap et al., 2001). Second, our results showed that 25% of the variation in small mammal biomass was explained by substrate and vegetation characteristics that correlate with disturbance categories (e.g., crust cover, grass cover, and shrub height). Although our model explained a significant portion of the variation in small mammal biomass, there were a number of other factors that could have been responsible for the unexplained variation in biomass, such as precipitation and predation (Kalcounis-Ruepell et al., 2002; Huitu et al., 2004; Korpimaki et al., 2005). Similar to other studies, we found that small mammal populations were negatively affected by disturbances such as grazing and fire (Olson et al., 2003; Seigel-Thines et al., 2004). Third, our results showed that snakes selected both undisturbed and burned areas, but snakes selecting undisturbed areas gained significantly more weight. In addition, a large proportion of the variation in snake weight gain (55%) was explained by small mammal biomass in their core activity areas (Fig. 5). The remaining unexplained variation in weight gain was likely due to individual variation in factors such as foraging efficiency. Negative impacts on weight gain, such as those found in this study, can result in reproductive characteristics that could ultimately have population-level consequences, such as longer times to sexual maturity, longer pregnancy intervals, and fewer and/or smaller offspring (Holt et al., 2003). Future studies should examine trophic relationships over longer time periods to determine the long-term impacts of disturbance on snake populations.

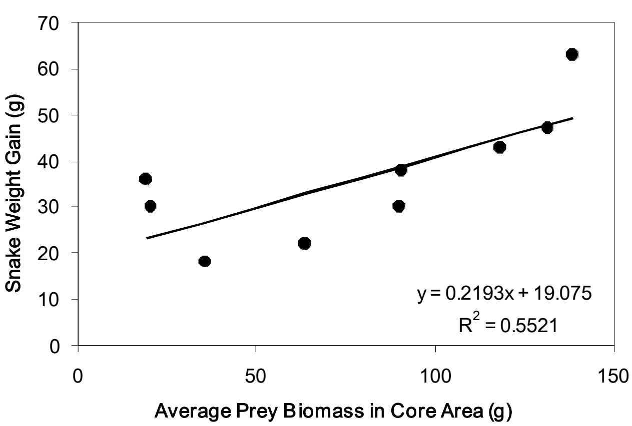

Figure 5. Seasonal weight gain by individual Great Basin Rattlesnakes (*C. oreganus lutosus*) as a function of average prey biomass in core areas of their home range.

Our results were similar to studies on other snake species that showed an indirect trophic effect of disturbance on snake populations. For example, Madsen and Shine (2000) found that characteristics of monsoons influence file snakes by altering flooding and prey resources. Our results indicated similar trophic effects, but examined the influence of human-caused disturbances (i.e., grazing and altered fire regimes) on rattlesnakes. One important characteristic that file snakes and many rattlesnake species have in common is that they are capital breeders. Specifically, both are characterized by having low reproductive output due to late ages to maturity, long pregnancy intervals, and low fecundity (Madsen and Shine, 2001; Diller and Wallace, 2002). One characteristic that is seen throughout snakes is plasticity in these types of reproductive characteristics (Seigel and Ford, 1991; Taylor and Denardo, 2005). We think that the combination of reproductive plasticity and a capital breeding strategy makes some snake species especially sensitive to human-caused disturbance. If a disturbance lowers adult survival, it could take a capital breeding snake species many years to replace those lost individuals due to low reproductive output. Similarly, if disturbance lowers the prey base, it could further extend times to maturity and pregnancy intervals and lower fecundity in these snakes.

This study used two techniques that are novel to the study of snake ecology and conservation. First, to our

Table 5. Number and proportion of relocations by disturbance category for individual snakes and all snakes totaled, as well as the proportion of the surrounding landscape (i.e., 5 km buffer surrounding the hibernaculum) in each disturbance category.

Snake	Undisturbed	Grazed	Burned	Grazed and Burned
RCAV-A	63 (0.93)	5 (0.07)	0	0
RCAV-Be	0	0	17 (1)	0
RCAV-Bu	63 (1)	0	0	0
RCAV-C	0	0	46 (1)	0
RCAV-De	25 (0.35)	0	47 (0.65)	0
RCAV-Di	9 (0.17)	43 (0.83)	0	0
RCAV-E	0	0	82 (1)	0
RCAV-Je	37 (0.64)	21 (0.36)	0	0
RCAV-Jo	48 (1)	0	0	0
RCAV-L	0	0	76 (1)	0
RCAV-P	0	0	51 (1)	0
Total	245 (0.39)	69 (0.11)	319 (0.50)	0 (0)
Available	0.22	0.37	0.40	0.01

knowledge, this is the first study that conducted intensive small mammal trapping at snake locations and random locations to indicate prey availability. In an innovative study, King and Duvall (1990) conducted small mammal trapping at snake locations and showed that snakes ceased linear movements when prey were present. Their study used two traps per snake location to identify initial prey occurrence along snake movement routes. Our study used 16 traps for two nights in snake locations and in random areas to examine prey availability. We think that there are many additional aspects in snake ecology that can be studied using intensive small mammal sampling, including, but not limited to, habitat preference/selection, foraging ecology, and conservation biology. Second, this is the first study to use utility distributions to define snake core use areas as a way to approximate the areas snakes are using for foraging. Our results showed that, by defining snake core activity areas with utility distributions, we were able to detect a relationship between prey resources and snake weight gain. In cases where rattlesnakes show obvious differences in movements in response to resources such as prey distribution, similar approaches may be useful. However, it is important to note that snakes from the same populations can have drastically different movement patterns (see Jørgensen and Gates, this volume), and thus one model of snake movement may not be appropriate even in a single population. To account for individual variation in movements, future studies that use utility distributions should consider additional approaches to delineating core activity areas based on individual snake movements. In this study, we selected a set isopleth value (50%) to standardize core area delineation across snakes, but an individual-based system for classifying core activity areas could also provide a good representation of prey available to snakes.

Our results emphasize the importance of considering prey resources and associated trophic interactions when studying the conservation biology of rattlesnakes. By considering prey resources, we gained a better understanding of how human impacts on landscapes can affect rattlesnakes. It is important to consider this approach when studying the conservation biology of other rattlesnake species because landscape-scale disturbances, such as grazing, fire, residential development, agriculture, and forestry, are occurring throughout the ranges of *Crotalus* and *Sistrurus* (Ernst, 1992). These disturbances are likely having indirect effects on many rattlesnake species by altering the availability of prey. We also recognize that other factors, such as microclimate, competition, and predation, can have significant impacts on snake populations (Grothe, 1992; Beaupre, 1995, 1996; Himes, 2003). Thus, we recommend considering the approach used in this paper as one possible approach to studying snake conservation biology.

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