A two-level problem: habitat selection in relation to prey abundance in an ambush predator, the speckled rattlesnake (*Crotalus mitchellii*)

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Summary

Understanding how food distribution influences habitat choice is a central goal of behavioural ecology. Because animals select habitats at different scales, and because the selection criteria used may be scale-dependent, studies examining the significance of food in relation to habitat selection should ideally incorporate more than one spatial scale. We relied on spatial ecology data and prey abundance estimates to examine whether prey (rodent) abundance is a consistent predictor of habitat selection at two different spatial scales in an ambush predator, the speckled rattlesnake (*Crotalus mitchellii*), during the mating and post-mating seasons. At the macrohabitat level, selection and avoidance of particular macrohabitats by *C. mitchellii* positively correlated with rodent abundance during the post-mating season. Because most snake foraging activity occurs during the post-mating season, this finding suggests that *C. mitchellii* selects macrohabitats that increase prey encounter rates. In contrast, rodent abundance was relatively low at the microhabitats selected by the snakes. Therefore, the higher prey abundance in *C. mitchellii*'s preferred macrohabitat did not translate into increased access to prey at the snake microhabitats, indicating that prey distribution may not be a constant predictor of predator habitat choice across spatial scales. Indirect evidence suggests that lower prey abundance at the snake microhabitats was the result of changes in rodent behaviour (e.g., avoiding or reducing activity at snake locations) to decrease predation risk. Our study underscores the dynamics of predator–prey interactions in nature, and emphasizes the challenges that ambush predators may face when foraging for risk-sensitive prey.

Keywords: model averaging, Mojave Desert, optimal foraging, predator–prey relationship, Reptilia, spatial ecology, wood rat nest.

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1. Introduction

Habitat selection is one of the most important factors affecting organismal fitness (Bearhop et al., 2004; Norris et al., 2004; Gunnarsson et al., 2005), because an individual's survival and reproduction are fundamentally linked to critical resources (e.g., refuges, mating partners, nesting sites) that vary in space and time (MacArthur & Pianka, 1966; Schoener, 1983; Fryxell et al., 2005). Food is one of these key resources. Therefore, understanding how food distribution influences habitat choice is a central goal of behavioural ecology (Charnov, 1976; Fortin et al., 2003).

Optimal foraging theory predicts that predators should select habitats where net energy gain per unit time is increased (Charnov, 1976; Stephens & Krebs, 1986; Bergman et al., 2001). One way animals can forage optimally is by selecting habitats where prey encounter rate is maximized (Comins & Hassell, 1979; Pyke, 1984; Ropert-Coudert et al., 2006). Numerous empirical investigations show that various taxa select habitats where food is more abundant at a single focal spatial scale (macro- or microhabitat level; e.g., Heithaus et al., 2002; Reichwaldt, 2008; Wang et al., 2010). However, habitat selection often is intrinsically hierarchical and occurs at multiple spatial scales (Johnson, 1980; Levin, 1992; Horne et al., 2008). For instance, individuals first choose a home range at the landscape level (macrohabitat selection), and then select specific patches or sites within their home range (microhabitat selection). Because the selection criteria used by animals when choosing a habitat may be scale-dependent (Martínez et al., 2003; Ciarniello et al., 2007; Mayor et al., 2007), studies examining the relationship between food and habitat choice should ideally incorporate more than one biologically-relevant spatial scale. This approach allows researchers to more thoroughly test the significance of food on the decision-making process of habitat selection. For example, the consistent preference for habitats with high food abundance across spatial scales would suggest that food is a key predictor of habitat choice, whereas relatively low food availability at some of the studied spatial scales would indicate that factors other than food (e.g., refuges) are significant determinants of habitat selection. Herein we use the terms abundance and availability interchangeably.

The multi-scale approach to study the relationship between an animal's distribution and the abundance of trophic resources has largely been applied to herbivore–plant systems (Ward & Saltz, 1994; Mysterud et al., 1999;

Fortin et al., 2003; Massé & Côté, 2009), possibly reflecting the relative ease with which food (vegetation) abundance can be quantified. These investigations demonstrate that patterns of habitat selection in relation to food may or may not be congruent across scales. For example, in herbivores, food abundance is the primary predictor of habitat selection at multiple spatial scales in dorcas gazelles (*Gazella dorcas*; Ward & Saltz, 1994), feral domestic sheep (*Ovis aries*; Mysterud et al., 1999), and white-tailed deer (*Odocoileus virginianus*; Massé & Côté, 2009), but not in roe deer (*Capreolus capreolus*; Mysterud et al., 1999) or American bison (*Bison bison*; Fortin et al., 2003). In contrast, whether predators exhibit congruence of habitat selection in regards to prey abundance across spatial scales is largely unknown. The scarcity of such studies is probably related to the fact that habitat choice studies on predators are typically conducted at a single macrohabitat scale, because quantifying prey abundance at a fine (microhabitat) scale is challenging. This is so because researchers would first need to determine the exact microhabitats where the predator forages, and quantify prey abundance at those precise foraging locations with little disturbance. Further, prey can adjust its behaviour in response to the presence of a potential predator (Sih, 1984; Lima & Dill, 1990). This behavioural adjustment is more likely to occur at fine habitat scales, when both species are in relatively close proximity, and prey can more easily detect the presence of a predator. The possibility of behavioural adjustment of the prey is an important consideration, because the predator could attempt to maximize prey encounter rate by selecting microhabitats where prey is more abundant, but prey could leave these sites or reduce activity when a predator is present to decrease predation risk. In these cases, quantifying the abundance of prey at the predator's microhabitats would likely indicate that the predator does not select microhabitats that maximize prey encounter rate, because the prey's avoidance behaviour would decrease the probability of being caught by the predator, or detected during surveys.

Herein we tested the hypothesis that habitat choice positively correlates with prey distribution at two biologically-relevant spatial scales in a venomous vertebrate predator, the speckled rattlesnake (*Crotalus mitchellii*). Our study system exhibits two characteristics that make it amenable to conduct this type of investigation. First, rattlesnakes are mobile ambush predators that rely on the presence of prey chemical cues to select foraging sites (Duvall et al., 1990; Roth et al., 1999; Theodoratus & Chiszar, 2000; Clark,

2004), where they can remain for periods ranging from several hours to several days (Reinert et al., 1984; Greene, 1997; Clark, 2006). This 'sit-and-wait' foraging strategy allowed us to identify the precise microhabitats that the snakes selected. Second, rattlesnakes can be carefully approached in nature with little disturbance, which facilitated quantifying prey abundance in a small perimeter around the locations selected by snakes. We radiotracked male and female *C. mitchellii* to quantify macro- and microhabitat selection in this ambush predator, and estimated prey (rodent) abundance to correlate snake habitat selection with prey distribution at two spatial scales. A higher abundance of rodent prey at the macro- and microhabitats selected by *C. mitchellii*, compared to random sites, would indicate that this rattlesnake exhibits habitat selection behaviour that maximizes the rate at which it encounters prey. Alternatively, a lack of high prey abundance at one or both of the habitat levels would suggest that snakes rely on environmental cues other than prey availability to select habitats at these spatial scales, and/or that prey may alter its behaviour to decrease predation risk. Because habitat choice can vary temporally (Orians & Wittenberger, 1991), we examined these alternative predictions in an explicit seasonal context (mating vs. post-mating season). Finally, we also quantified the significance of refuge availability (i.e., wood rat nests, rock refuges) on *C. mitchellii*'s habitat selection process.

2. Materials and methods

2.1. Study site and species

The study site is a ca. 5 km^2 area located in the Eldorado Mountains, Clark County, southern Nevada (35°44′N, 114°49′W), in the eastern Mojave Desert of southwestern North America. This region is characterized by an extremely arid climate (2006–2009 average annual rainfall (range): 8.3 cm (5.2–12.5 cm)), with high temperatures in summer (2006–2009 average daily temperatures: 27.1°C (14.5–36.5°C)) and relatively cool temperatures in winter (7.1°C (−7.5–23.7°C); environmental data from Station ID4814, Clark County Regional Flood Control District, Nevada). The area consists of sparsely vegetated rocky desert at an elevation of ca. 1100 m. Dominant plants include yucca trees (*Yucca* sp.), Brigham tea shrubs (*Ephedra*
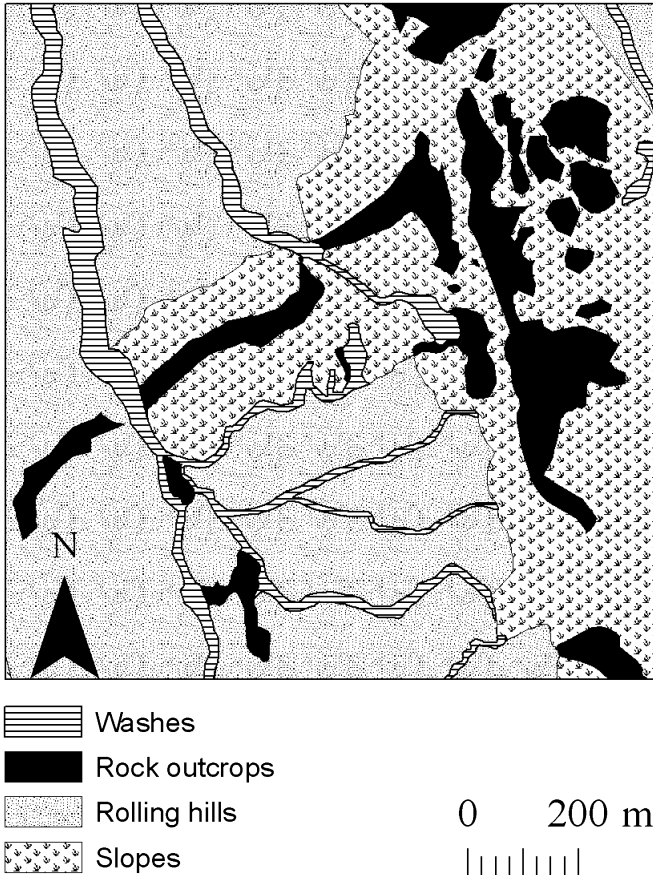
Figure 1. Macrohabitat GIS data layer of the study site, located in Eldorado Mountains, Clark County, southern Nevada (35°44′N, 114°49′W), in the eastern Mojave Desert, USA.

sp.), buckwheats (*Eriogonum* sp.), catclaw acacias (*Acacia greggii*), creosote bushes (*Larrea tridentata*), and various annual herbaceous plants.

Four macrohabitat types are found on the study site: rolling hills, washes, slopes and rock outcrops (Figure 1). The rolling hills consist of sparsely vegetated and gently sloping ridges. Yucca trees (*Yucca* sp.) are common in this habitat, and wood rat (*Neotoma lepida*) nests are sometimes found at the base of the yuccas. The substrate of this habitat mostly consists of gravel; rocks that could provide refuge to snakes are rare. The rolling hills are dissected by a few washes that are typically dry most of the year (but flowing water sometimes occurs in the winter), and vegetation is relatively

more common than in the rolling hills. Slopes consist of steep and long versants, and are characterized by a relatively high shrub cover, compared to the other macrohabitat types. The slopes lead to rock outcrops, which typically occur at the highest elevation on the site. Rocks and boulders of various sizes dominate this habitat type, and rock refuges (e.g., crevices, cavities under rocks) are readily available.

Crotalus mitchellii is a medium-sized rattlesnake (maximum reported total body length: 137 cm; Ernst & Ernst, 2003) that typically thrives in the rocky habitats of the Mojave Desert, where it mostly feeds on rodents (Glaudas & Rodríguez-Robles, unpubl. data). The snake is usually active from April to October (Glaudas & Rodríguez-Robles, 2011). During the summer, the activity patterns of *C. mitchellii* are constrained by environmental temperatures, because midday temperatures approach the critical thermal maximum (ca. 39–42°C) of many reptiles, including desert-dwelling species (Brattstrom, 1965). Consequently, *C. mitchellii* becomes nocturnal in the summer (Glaudas, unpubl. data). The low autumn and winter temperatures also prevent this snake from being active during these times of the year, and *C. mitchellii* hibernates, typically in crevices, from mid-October to late March. The movement patterns of *C. mitchellii* vary seasonally. Adult snakes of both sexes display increased activity during the mating season (late April to early June), compared to the post-mating season (early June to mid-October; Glaudas & Rodríguez-Robles, 2011). Therefore, we conducted analyses of habitat selection for the entire active season (mid-April to mid-October), as well as for the mating (late April to early June) and post-mating seasons (early June to mid-October) separately to investigate whether patterns of habitat choice vary seasonally.

2.2.   *Radiotelemetry*

From April, 2006 to October, 2008, we radiotracked 25 *C. mitchellii* (18 males, 7 non-gravid females). Snakes were opportunistically caught during visits to the field site. We surgically implanted temperature-sensitive radiotransmitters (model SI-2T, 9 g, Holohil, Carp, ON, Canada; or model WST2, 5 g, Wildlife Track, Caldwell, ID, USA) in the body cavity of the snakes following established procedures (Reinert & Cundall, 1982; Reinert, 1992). At the time of transmitter implantation, males measured (mean ± SD) 85.3 ± 6.9 cm snout-to-vent length (SVL) and weighed 558.6 ± 144.3 g,

whereas females measured 74.6 ± 2.8 cm SVL and weighed 373.9 ± 53.3 g. The transmitter's mass was less than 3% of the snake's body mass in all cases. We released the snakes at their exact capture location 1–3 days following surgery. We used a radio receiver (model WTI-1000, Wildlife Track) and a directional antenna (model F151-3FB, Wildlife Track) to relocate snakes every 2–3 days during the active season, and once per week during the hibernation period. Each time a snake moved, we recorded its geographic coordinates using a sub-meter accuracy GPS unit (model GS20, Leica Geosystems, Torrance, CA, USA), as well as the macrohabitat type where the snake was found. Periods of radiotracking ranged from 15–1073 days per individual (mean $\pm$ SD $= 407 \pm 265$ days). In total, our study resulted in 5582 relocations and 1098 movements by snakes.

2.3. Macrohabitat selection

Using a geographic-information system (ArcMap 9.2; ESRI, Redlands, CA, USA), we generated a detailed macrohabitat data layer using a 1 m resolution aerial photography of the study area. The data layer included the four macrohabitat types found in the study area: rolling hills, washes, slopes, and rock outcrops (Figure 1). We checked the accuracy of the map by comparing the macrohabitat type predicted by the map at particular locations to the actual macrohabitat in the field. The map was 84.8% (417/492 points) accurate.

We radiotracked some snakes during multiple active seasons. Because the home range of these snakes overlapped between years (e.g., site fidelity between years; mean $\pm$ SD: $52 \pm 8.6\%$, $N = 6$), we randomly picked one year for each snake, so that each individual snake was only included once in the analyses. As a result, we included 13 males and 7 females in the macrohabitat analysis.

We used the kernel density estimator (KDE) to estimate home range size, because this technique includes a utilization distribution function that allows prediction of the probability of finding an animal in a given area within its home range (Millspaugh & Marzluff, 2001). We used the methodology recommended to generate KDEs for reptile and amphibian species (Row & Blouin-Demers, 2006). We first generated Minimum Convex Polygons (MCP) that included all of an individual's known locations within the boundary of the smallest polygon possible. We then created 95% KDEs for each individual by manually adjusting h, the smoothing parameter, until the MCP

and the KDE were of similar size. We calculated 50% KDEs by plotting the 50% contour line within the 95% KDEs (95% KDEs provide an estimate of the overall size of a home range, whereas 50% KDEs identify the core area used by snakes within the overall home range). This technique provides an objective method for selecting h, and generates biologically-relevant KDEs for amphibians and reptiles (Row & Blouin-Demers, 2006). All home ranges were created in the Home Range Tools (Rodgers et al., 2007) for ArcGIS.

Using the macrohabitat layer (Figure 1), we determined the proportion of each macrohabitat type within the home range of each snake. To estimate the availability of the different macrohabitats at the study site, we generated 10 random home ranges of similar size for each actual snake home range. For example, if a snake had a home range of 10 ha, we created 10 random home ranges of 10 ha. For simplicity, we generated circular home ranges to circumvent the problem associated with home range orientation. We determined the location of the random home ranges by generating random points within the macrohabitat data layer that included all of the snake locations. We used the randomly generated point locations as the center of the circular home ranges, calculated the proportions of each habitat type in the randomly generated home ranges, and compared these proportions to those in the actual snake home ranges.

2.4. *Microhabitat selection*

To examine microhabitat selection in *C. mitchellii*, we quantified rodent abundance and refuge availability (see below) at a subset of snake locations where snakes were found coiled on the surface or in a refuge (a behaviour that indicated that the snake had selected a site), and at random locations. We generated the random locations using the snake locations as a point of reference. From each snake location, we walked a random distance (30–100 m) in a random direction (east, north, south, west). Each snake location for which we recorded microhabitat characteristics was paired to a random location within the same macrohabitat type. For individual snakes, we quantified microhabitat characteristics at snake locations at a minimum of 3-week intervals, to ensure that these locations were relatively independent from one another.

2.4.1. Prey abundance

We quantified rodent abundance at 86 snake and 86 random locations throughout the active season using oat-baited Sherman live-traps (Bock et al., 2002; Reed & Douglas, 2002). Sherman traps allow researchers to capture small mammals without injuring them. We placed 8 rodent traps equidistant from each other in a 2 m radius circle around 86 snake and 86 random locations, for a total of 1376 trap nights. We opened the traps in the early evening (1800–2100 h), when rodents typically started to become active and when snakes were more likely to be observed on the surface. We checked and closed the traps early the following morning (0400–0700 h) to prevent rodent mortality (which was 0%). At the snake locations, we found the snakes at the same sites in the morning 83.7% (72/86) of the time. Estimates of prey abundance (rodent trap success) were not affected by the presence (mean $\pm$ SE 0.05 ± 0.02) or absence (0.05 ± 0.01; $F_{1,84} = 0.002$, $p = 0.96$) of the snakes the following morning, and consequently we combined all the snake locations to estimate prey availability at the snake-selected sites. After identifying the trapped rodents to species level, we released them unharmed at their place of capture. To eliminate the effect of environmental conditions (e.g., temperature, cloud cover, lunar cycle) on rodent activity, we trapped at paired snake and random locations on the same night. The number of rodents caught at a location provided an estimate of prey abundance at that site.

2.4.2. Refuge availability

We recorded refuge availability at most of the snake (72/86, 83.7%) and random (72/86) locations where we trapped rodents. We did not quantify refuge availability at all locations where we trapped rodents because some of the flags we used to mark the trapping areas disappeared and, thus, we were sometimes unable to relocate the exact trapping location. At our study site, *C. mitchellii* almost exclusively uses wood rat nests, cavities under rocks, and crevices as retreat sites (Glaudas, pers. obs.). Therefore, we quantified refuge availability at the snake and random locations by recording absence/presence of a wood rat nest within a 2 m radius area around the snake and random locations. Further, we measured the distance of the location to the closest potential rock refuge (i.e., a rock or crevice that a snake could use as a refuge) within a 10 m radius. When a rock refuge was not available in the 10 m radius area, we scored this variable as '10 m +'.

2.5. *Wood rat nests and rodent abundance*

Studies have shown that faeces counts are robust estimators of species density in a variety of taxa, including ungulates (Neff, 1968), macropods (Johnson & Jarman, 1987), elephants (Barnes, 2001), lagomorphs (Krebs et al., 2001; Murray et al., 2002), and rodents (Karels et al., 2004). Therefore, we assessed whether rodent abundance varied between locations with and without a wood rat nest by counting the number of rodent faecal pellets at these sites in December 2011. We quantified rodent faeces at 20 locations with a wood rat nest by counting the faecal pellets contained in three, 20 cm² quadrants located at the entrance of the nest, and at 1 m north and 1 m south of the nest's entrance. Using the same methodology, we also quantified rodent abundance at 20 random locations without a wood rat nest. We selected the random locations by using the wood rat nest locations as a point of reference, and walking a random distance (10–100 m) in a random direction (east, north, south, west) from each nest. To control for potential differences in rodent abundance across macrohabitat types, we paired each location with a wood rat nest to a random location without a wood rat nest in the same macrohabitat (paired locations: rolling hills: 6; slopes: 6; rock outcrops: 8).

2.6. *Statistical analyses, model selection, and model averaging*

We used logistic regressions to model macro- and microhabitat selection in *C. mitchellii* (see below for details). Logistic regressions have become increasingly popular to analyze availability-use data in habitat selection studies (Keating & Cherry, 2004), because this technique allows researchers to model the probability of occurrence of an event based on the factors included in the analysis. The predictive power of logistic regressions is demonstrated by the odds ratio, which estimates how a change in one unit of an independent variable affects the probability of occurrence of an event (in our case the occurrence of a snake at a particular location). The change in one unit of an independent variable increases or decreases the probability of occurrence of an event if the estimate is positive or negative, respectively (Glas et al., 2003). For example, a variable with an odds ratio of $+3$ indicates that the probability of snake occurrence at a particular site is multiplied by 3.

 We used an information theoretic approach to select a set of best-fit models (Burnham & Anderson, 2002) for the macro- and microhabitat selection

data. We first generated all the possible candidate models given the number of parameters, and tested the fit of each model using the second-order Akaike's information criterion (AIC_C; hereafter referred to as AIC). The AIC provides a measure of the relative goodness of fit of a statistical model among a set of competing models (Akaike, 1974).

We ranked all the candidate models according to their AIC values, with the model with the lowest AIC being the best model, AIC_{min}. We then calculated Δ_i and the Akaike weights, ω_i, for all models. Δ_i is the difference between the AIC value of a model i relative to the best fit model, AIC_{min}, and provides a 'strength' estimate of model i compared to AIC_{min}. The Akaike weight is the proportional likelihood of model i over the sum of likelihood of all models, and can be interpreted as the probability that model i is the best-fit model, given the data and set of candidate models (Johnson & Omland, 2004). For instance, an Akaike weight of 0.90 for a model indicates that this model has a 90% chance of being the best model among the set of candidate models. Because none of the candidate models overwhelmingly supported our macro- and microhabitat data (i.e., the Akaike weights of the best model in all analyses were $\leqslant 0.79$), we used model averaging, a technique that reduces model selection bias and accounts for model selection uncertainty, to obtain robust estimates of the model (Johnson & Omland, 2004). Model averaging calculates weighted average estimates (and the associated variances) for the parameters that are included in a set of candidate models and, therefore, allows to make inferences based on a set of plausible candidate models (Wasserman, 2000). The candidate models included in model averaging were selected by adding the Akaike weights of successively ranked models (from best to worst) until the added models cumulated to $\geqslant 0.95$. This value represented our minimum confidence set of models, which is analogous to a 95% confidence interval around a mean (Johnson & Omland, 2004). That is, when the Akaike weights of the candidate models add up to 95%, there is a 95% probability that the best approximation model to the true model is contained within the candidate models. We interpreted the significance and magnitude of the model-averaged estimates in two ways. First, we considered an effect significant when the 95% confidence interval of the estimate did not include 0 (Burnham & Anderson, 2002). Second, when two predictor variables were significant in the same analysis, we calculated the importance weight, which quantified the relative importance (magnitude) of significant

individual parameters, by adding the Akaike weights for each model that included the parameter of interest. We provide below the detailed descriptions of the statistical analyses used to examine macro- and microhabitat selection in *C. mitchellii*.

2.6.1. Macrohabitat selection

The predictor variables (the proportions of macrohabitat types) were highly correlated, i.e., they were multicollinear. This was problematic for our statistical analysis, because multicollinearity produces unstable models (Wang & Jain, 2003). We conducted preliminary analyses of *C. mitchellii*'s macrohabitat selection to examine the significance of each predictor variable on macrohabitat choice. The results indicated that two macrohabitats (washes and slopes) were not preferred nor avoided by the snakes. Consequently, these two macrohabitat types were candidates for removal from the macrohabitat model. Because the multicollinearity among predictor variables only disappeared when we removed the slopes habitat from the analysis, we excluded this habitat type from the macrohabitat model.

We entered 'snake vs. random home ranges' as the dependent variable, and the proportion of habitat types (rock outcrops, rolling hills, washes) and sex as candidate predictor variables for the macrohabitat selection analyses. We generated all possible macrohabitat models using these four predictor variables, which resulted in a total of 15 candidate models (4 with 1 parameter, 6 with 2 parameters, 4 with 3 parameters, and 1 with 4 parameters). We conducted logistic regressions (Proc Logistic procedure in SAS; SAS Institute, Cary, NC, USA) and obtained the AIC value for each candidate model. We used parametric (ANOVA) and non-parametric tests (Fisher's exact test, Wilcoxon signed ranks test) to examine variation in prey abundance and refuge availability among macrohabitat types and/or microhabitat features. We used our larger rodent trapping data set (the 86 random locations) to examine variation in rodent abundance across macrohabitats.

2.6.2. Microhabitat selection

We analyzed the rodent abundance and refuge availability data together using case-controlled logistic regressions (Proc Phreg procedure in SAS). These analyses included the 72 snake and 72 random locations for which we had data for both rodent abundance and refuge availability. The case-controlled

approach allows comparisons of the availability-use data within a specified controlled variable. We used the paired snake and random locations as the case control in the analyses. This statistical design allowed us to control for macrohabitat type (because the paired locations were in the same macrohabitat) and for temporal variation in rodent activity (because we trapped rodents at paired locations on the same night). For these analyses we entered 'snake vs. random location' as the dependent variable, and 'number of rodents caught', 'distance to rock refuge' and 'absence/presence of a wood rat nest' as candidate predictor variables. We generated all possible microhabitat models using these four predictor variables, which resulted in a total of 7 candidate models (3 with 1 parameter, 3 with 2 parameters, and 1 with 3 parameters). We conducted logistic regressions and obtained the AIC value for each candidate model. The paired statistical design used did not allow us to include sex as a factor in the microhabitat analyses, because each random location was paired to an individual snake of a given sex.

We conducted macro- and microhabitat selection analyses for the entire active season, and for the mating and post-mating seasons separately. We conducted all analyses using the statistical program SAS (version 9.2; SAS Institute). Values given are means $\pm$ 1 SE (unless otherwise indicated), and all reported p values are two-tailed. Significance level for all tests was determined at $\alpha = 0.05$.

3. Results

3.1. Macrohabitat selection

3.1.1. Entire active season

We examined whether *C. mitchellii* selected macrohabitats during the active season. For the overall home range of snakes (95% KDEs), 8 of 15 candidate models were included in model averaging (confidence set = 98%; Table 1). The averaged model revealed that *C. mitchellii* did not select macrohabitats in its overall home range (Table 2). We used the 50% KDEs to investigate habitat selection in the snake's core activity areas. Seven of 15 models were averaged (confidence set = 95%; Table 1), and the resulting model indicated that *C. mitchellii* positively selected rock outcrops (Table 2).

Table 1. AIC$_C$-ranked models of logistic regressions included in model averaging for inferring patterns of macrohabitat selection by *Crotalus mitchellii* (13 males, 7 females) in Eldorado Mountains of southern Nevada, USA.

Model	AIC$_C$	Δ_i	ω_i
Entire active season (200 random home ranges, 20 snake home ranges)			
95% KDEs			
Rock outcrops	114.9	0	0.28
Rock outcrops + rolling hills	115.2	0.3	0.24
Rock outcrops + washes	116.6	1.7	0.12
Rock outcrops + sex	116.8	1.9	0.11
Rock outcrops + rolling hills + washes	117.1	2.2	0.09
Rock outcrops + rolling hills + sex	117.7	2.8	0.07
Rock outcrops + washes + sex	118.5	3.6	0.05
Rock outcrops + rolling hills + washes + sex	119	4.1	0.04
50% KDEs			
Rock outcrops + rolling hills	115.5	0	0.37
Rock outcrops	117.3	1.8	0.15
Rock outcrops + rolling hills + washes	117.5	2	0.14
Rock outcrops + rolling hills + sex	117.5	2	0.14
Rock outcrops + washes	119.2	3.7	0.06
Rock outcrops + sex	119.3	3.8	0.05
Rock outcrops + rolling hills + washes + sex	119.5	4	0.04
Mating season (190 random home ranges, 19 snake home ranges)			
95% KDEs			
Rolling hills	113.8	0	0.3
Rolling hills + sex	114.8	1	0.19
Rock outcrops + rolling hills	115.5	1.7	0.13
Rolling hills + washes	115.6	1.8	0.12
Rock outcrops + rolling hills + sex	116.4	2.6	0.09
Rolling hills + washes + sex	116.6	2.8	0.08
Rock outcrops + rolling hills + washes	117.4	3.6	0.05
50% KDEs			
Rock outcrops + rolling hills	112.9	0	0.24
Rolling hills	113	0.1	0.22
Rolling hills + washes	114	1.1	0.13
Rock outcrops + rolling hills + washes	114.4	1.5	0.11
Rock outcrops + rolling hills + sex	114.7	1.8	0.09
Rolling hills + sex	114.8	1.9	0.08
Rolling hills + washes + sex	115.8	2.9	0.06
Rock outcrops + rolling hills + washes + sex	116.2	3.3	0.04

Table 1. (Continued.)

Model	AIC$_C$	Δ_i	ω_i
Post-mating season (200 random home ranges, 20 snake home ranges)			
95% KDEs			
Rock outcrops	124.4	0	0.31
Rock outcrops + rolling hills	125.6	1.2	0.17
Rock outcrops + washes	126.3	1.9	0.12
Rock outcrops + sex	126.3	1.9	0.12
Rock outcrops + rolling hills + sex	127.6	3.2	0.06
Rock outcrops + rolling hills + washes	127.6	3.2	0.06
Rolling hills	128	3.6	0.05
Rock outcrops + washes + sex	128.3	3.9	0.04
Rolling hills + washes	129.2	4.8	0.03
50% KDEs			
Rock outcrops + rolling hills	117.5	0	0.34
Rock outcrops + rolling hills + washes	119.2	1.7	0.15
Rock outcrops + rolling hills + sex	119.2	1.7	0.15
Rock outcrops	120	2.5	0.1
Rock outcrops + rolling hills + washes + sex	120.8	3.3	0.07
Rock outcrops + washes	121	3.5	0.06
Rolling hills	121.8	4.3	0.04
Rock outcrops + sex	121.6	4.1	0.04

Candidate models were generated separately for the 95% and 50% kernel density estimators (KDEs) for the entire active season (mid-April to mid-October), the mating season (late April to early June), and the post-mating season (early June to mid-October), and are listed in decreasing order of probability. The variable(s) included in each model and the resulting AIC$_C$ values, AIC$_C$ differences (Δ_i) and Akaike weights (ω_i) are indicated.

3.1.2. *Mating season*

We investigated whether *C. mitchellii* preferred or avoided certain macrohabitats during the mating season. For the 95% KDEs (confidence set = 96%), the averaged model included 7 of 15 candidate models (Table 1), and we did not detect any evidence of macrohabitat selection. Model averaging for the 50% KDEs included 8 of 15 candidate models (confidence set = 98%; Table 1), and the resulting model indicated that *C. mitchellii* avoided the rolling hills habitat (Table 2).

3.1.3. *Post-mating season*

We assessed whether *C. mitchellii* selected macrohabitats during the post-mating season. The 95% KDEs model, which included 9 of 15 candidate

Table 2. Average model estimates of macrohabitat selection by *Crotalus mitchellii* (13 males, 7 females) in Eldorado Mountains of southern Nevada, USA.

Macrohabitat (availability/use)	Estimate ± SE (95% CI)	Odds ratio (95% CI)
Entire active season		
95% KDEs		
(Intercept)	−2.93 ± 0.66 (−4.23–(−1.64))	
Rolling hills (61.5/27.2)	−0.013 ± 0.01 (−0.03–0.006)	0.98 (0.96–1)
Washes (7/5.7)	0.01 ± 0.02 (−0.29–0.5)	1.01 (0.74–1.05)
Rock outcrops (6.4/22.7)	0.067 ± 0.02 (−0.349–0.11)	1.07 (0.70–1.11)
Sex	0.09 ± 0.27 (−0.43–0.62)	1.09 (0.64–1.85)
50% KDEs		
(Intercept)	−2.44 ± 0.57 (−3.55–(−1.33))	
Rolling hills (58.2/19.7)	−0.016 ± 0.03 (−0.07–0.07)	0.98 (0.93–1.08)
Washes (7.9/5.2)	0.001 ± 0.016 (−0.03–0.03)	1 (0.97–1.03)
Rock outcrops* (8.3/36.1)	0.03 ± 0.01 (0.009–0.05)	1.03 (1.01–1.05)
Sex	−0.026 ± 0.27 (−0.55–0.5)	0.97 (0.57–1.65)
Mating season		
95% KDEs		
(Intercept)	−1.33 ± 0.36 (−2.05–(−0.63))	
Rolling hills* (54.3/16.9)	−0.03 ± 0.009 (−0.048–(−0.012))	0.97 (0.95–0.99)
Washes (8.4/6.4)	−0.005 ± 0.01 (−0.03–0.02)	0.99 (0.97–1.02)
Rock outcrops (11.3/29.4)	0.005 ± 0.009 (−0.012–0.023)	1 (0.99–1.02)
Sex	−0.28 ± 0.28 (−0.82–0.27)	0.75 (0.44–1.31)
50% KDEs		
(Intercept)	−1.54 ± 0.41 (−2.36–(−0.73))	
Rolling hills* (56.9/14.1)	−0.026 ± 0.009 (−0.04–(−0.009))	0.97 (0.96–0.99)
Washes (8.2/5.6)	−0.01 ± 0.01 (−0.04–0.016)	0.99 (0.96–1.02)
Rock outcrops (10.5/36.3)	0.01 ± 0.007 (−0.004–0.025)	1.01 (0.99–1.03)
Sex	−0.12 ± 0.27 (−0.66–0.42)	0.89 (0.52–1.52)

models (confidence set = 96%; Table 1), indicated that the proportion of rock outcrops habitat in the overall home range of snakes was higher than expected by chance (Table 2). The averaged model for the 50% KDEs included 8 of 15 candidate models (confidence set = 95%; Table 1), and revealed that snakes preferred rock outcrops and avoided rolling hills (Table 2). We compared the relative importance of these two predictor variables of habitat selection by dividing their importance weight (rock outcrops/rolling hills: 0.896/0.736 = 1.2). Preference for rock outcrops is a more plausible explanation for macrohabitat selection in *C. mitchellii* than avoidance of rolling hills.

Table 2. (Continued.)

Macrohabitat (availability/use)	Estimate ± SE (95% CI)	Odds ratio (95% CI)
Post-mating season		
95% KDEs		
(Intercept)	−2.71 ± 0.64 (−3.96–(−1.48))	
Rolling hills (57.2/30.1)	−0.01 ± 0.01 (−0.03–0.009)	0.99 (0.97–1.01)
Washes (9.1/5.5)	0.0007 ± 0.02 (−0.03–0.03)	1 (0.97–1.03)
Rock outcrops* (8.2/24.5)	0.04 ± 0.015 (0.013–0.072)	1.04 (1.01–1.07)
Sex	0.04 ± 0.26 (−0.46–0.54)	1.04 (0.63–0.72)
50% KDEs		
(Intercept)	−2.29 ± 0.58 (−3.42–(−1.16))	
Rolling hills* (59.8/19.7)	−0.016 ± 0.008 (−0.03–(−0.001))	0.98 (0.97–0.99)
Washes (7.9/7.8)	0.009 ± 0.01 (−0.013–0.03)	1 (0.99–1.03)
Rock outcrops* (7.9/35.7)	0.024 ± 0.009 (0.005–0.043)	1.02 (1.01–1.04)
Sex	−0.16 ± 0.27 (−0.69–0.38)	0.85 (0.5–1.46)

Average models were generated separately for the 95% and 50% kernel density estimators (KDEs) for the entire active season (mid-April to mid-October), the mating season (late April to early June), and the post-mating season (early June to mid-October). Average availability and use of macrohabitat types, unconditional standard errors (SE; and their 95% confidence intervals) and odds ratios (and their 95% confidence intervals) are shown. Asterisks denote significant effects of variables in a model.

3.2. *Differences in prey availability and structural characteristics among macrohabitats*

At the study site, we caught 90 rodents (trap success: $90/1376 = 6.5\%$) representing four species: canyon mouse (*Peromyscus crinitus*, $N = 68$), long-tailed pocket mouse (*Chaetodipus formosus*, $N = 18$), Merriam's kangaroo rat (*Dipodomys merriami*, $N = 3$) and desert wood rat (*Neotoma lepida*, $N = 1$). Examination of museum specimens revealed that mammals composed 65% (50/77) of the total number of prey items consumed by adult *C. mitchellii* (Glaudas & Rodríguez-Robles, unpubl. data). Our data set on *C. mitchellii*'s diet only includes five prey items for which we could determine approximate body mass, because the remaining prey were too digested to allow for accurate estimates of body mass. Consequently, we could not reliably estimate the proportion of mammal biomass in *C. mitchellii*'s diet. Mammalian prey are typically more significant in the diets of rattlesnakes when expressed in terms of biomass, rather than in total number of prey items (Fitch, 1949; Diller & Johnson, 1988; Wallace & Diller, 1990). There-

fore, mammals probably account for more than 65% of the total prey biomass of *C. mitchellii* at our study site.

We tested whether rodent abundance (rodent trap success) varied among macrohabitats (rolling hills, slopes, rock outcrops) at random locations during the post-mating season, when snakes actively selected and avoided certain macrohabitats in their core activity range, and when most foraging activity occurs (Glaudas & Rodríguez-Robles, 2011). The rarity of random locations in the washes macrohabitat precluded their inclusion in this analysis. We only used the random locations in this analysis, to eliminate the potential effect of the snake's presence on rodent behaviour. Because snakes preferred rock outcrops and avoided rolling hills in their core activity areas, we used a planned comparison ANOVA to test whether selection and avoidance of these habitats correlated with rodent abundance. Rodents were significantly more common in rock outcrops than in rolling hills ($F_{1,56} = 3.7$, $p = 0.05$; Figure 2A). This difference in prey availability between rock outcrops and rolling hills during the post-mating season was primarily caused by the preference of *Peromyscus crinitus* (i.e., the most common rodent on the study site, and the most frequent prey of *C. mitchellii*; Glaudas & Rodríguez-Robles, unpubl. data) for rock outcrops, because the capture frequency of *P.*
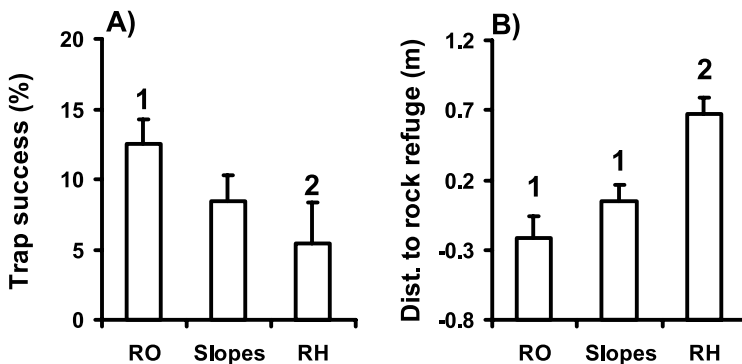

Figure 2. Microhabitat characteristics of the three major macrohabitat types (rolling hills, slopes, rock outcrops) found at random locations in Eldorado Mountains, southern Nevada, USA. (A) Rodent trap success (%); (B) distance to rock refuge (m; log-transformed data). Sample sizes are: rolling hills, $N = 14$; slopes, $N = 36$; rock outcrops, $N = 20$. Group means with the same number above the bars are not statistically different ($p \geqslant 0.05$). For A, we only show the significant difference between rock outcrops (habitat preferred by *C. mitchellii*) and rolling hills (habitat avoided by *C. mitchellii*) using a planned contrast ANOVA, because we specifically tested whether macrohabitat choice correlates with rodent abundance. RO, rock outcrops; RH, rolling hills.

crinitus was significantly higher in rock outcrops than in rolling hills (rock outcrops: 16/24 locations, 66.7%; rolling hills: 1/12, 8.3%; Fisher's exact test, $p = 0.001$).

We examined whether macrohabitat types (rolling hills, slopes, rock outcrops) differed in refuge availability, to determine whether macrohabitat selection in *C. mitchellii* is correlated with these structural features. We only used the random locations in this analysis, because including the snake locations could bias our estimate of refuge availability across macrohabitats if the snakes exhibited macrohabitat-specific preferences for refuge type. Further, we did not include data from the washes macrohabitat, because *C. mitchellii* rarely used this habitat, and consequently washes locations were under-represented in the data set. The analysis revealed that 'distance to rock refuge' varied significantly among macrohabitats (single-factor ANOVA; $F_{2,67} = 7.2$, $p = 0.001$; Figure 2B). Rock outcrops were characterized by a higher availability of rock refuges, compared to the rolling hills. We also tested whether availability of wood rat nests differed among macrohabitat types at random locations. Wood rat nests were similarly available across macrohabitats (proportion of locations with a wood rat nest: rolling hills: 0/14, 0%; slopes: 2/36, 5.6%; rock outcrops: 3/20, 15%; Fisher's exact test; rolling hills vs. rock outcrops: $p = 0.25$).

3.3. Microhabitat selection

3.3.1. Entire active season

We examined whether snake and random locations differed in prey abundance and refuge availability during *C. mitchellii*'s active season (mid-April to mid-October). Two of seven models qualified for model averaging (confidence set: 99%; Table 3). Rodent abundance did not differ between snake and random locations (Table 4). However, snake locations were characterized by the presence of a wood rat nest. The strong selection of wood rat nests by *C. mitchellii* is effectively illustrated by the contrasting number of nests found at snake (38/72, 52.8%) and random (5/72, 6.9%) locations. Wood rat nests were not readily available at the study site, yet snakes sought out these structures, which resulted in a strong positive relationship between the presence of snakes and wood rat nests. Further, snake locations were located closer to rock refuges than expected by chance (mean ± SE distance between snake locations and rock refuges: 1.1 ± 0.3 m; mean ± SE distance

Table 3. AIC$_C$-ranked models of case-controlled logistic regressions included in model averaging for inferring patterns of microhabitat selection by *Crotalus mitchellii* in Eldorado Mountains of southern Nevada, USA.

Model	AIC$_C$	Δ_i	ω_i
Entire active season (72 random locations, 72 snake locations)			
N Rod + WRN (present) + Dist Rock	49.6	0	0.71
WRN (present) + Dist Rock	51.4	1.8	0.28
Mating season (20 random locations, 20 snake locations)			
Dist Rock	13.8	0	0.72
N Rod + Dist Rock	15.7	1.9	0.27
Post-mating season (52 random locations, 52 snake locations)			
N Rod + WRN (present) + Dist Rock	36.2	0	0.79
N Rod + WRN (present)	40.1	3.9	0.11
WRN (present) + Dist Rock	40.5	4.4	0.09

Candidate models were generated separately for the entire active season (mid-April to mid-October), the mating season (late April to early June), and the post-mating season (early June to mid-October), and are listed in decreasing order of probability. The variable(s) included in each model and the resulting AIC$_C$ values, AIC$_C$ differences (Δ_i) and Akaike weights (ω_i) are indicated. N Rod = number of rodents caught; WRN (present) = presence of a wood rat nest; Dist Rock = distance to rock refuge (m).

between random locations and rock refuges: 2.8 ± 0.3 m). The importance weight of the two refuge availability predictor variables, 'absence/presence of a wood rat nest' and 'distance to rock refuge', were identical (1.0), which indicated that both factors are equally plausible explanations for patterns of snake microhabitat selection.

3.3.2. *Mating season*

We examined whether rodent abundance and refuge availability differed between snake and random locations during the mating season. We removed the variable 'absence/presence of a wood rat nest' from the mating season analysis, because the large standard error associated with this variable in all candidate models made these models questionable. Wood rat nests were rare at random locations (1/20, 5%) compared to snake locations (8/20, 40%), and the lack of variation in this predictor at random locations may have precluded the logistic models from detecting an effect of this variable. Accordingly, 'number of rodents caught' and 'distance to rock refuge' were the only two candidate predictor variables for this analysis. Two of three candidate

Table 4. Average model estimates of macrohabitat selection by *Crotalus mitchellii* in the Eldorado Mountains of southern Nevada, USA.

Variable	Estimate ± SE (95% CI)	Odds ratio (95% CI)
Entire active season		
Number of rodents caught	−0.69 ± 0.37 (−1.42–0.04)	0.5 (0.24–1.04)
Wood rat nest (present)*	3.37 ± 1.03 (1.35–5.39)	29.07 (3.86–219.2)
Distance to rock refuge* (m)	−0.68 ± 0.22 (−1.11–(−0.24))	0.5 (0.33–0.79)
Mating season		
Number of rodents caught	0.21 ± 0.83 (−1.42–1.84)	1.23 (0.24–6.29)
Distance to rock refuge* (m)	−1.97 ± 0.95 (−3.83–(−0.1))	0.14 (0.022–0.901)
Post-mating season		
Number of rodents caught*	−1.12 ± 0.5 (−2.1–(−0.15))	0.33 (0.12–0.87)
Wood rat nest (present)*	3.15 ± 1.02 (1.14–5.15)	23.24 (3.1–171.8)
Distance to rock refuge* (m)	−0.46 ± 0.23 (−0.92–(−0.006))	0.63 (0.397–0.993)

Average models were generated separately for the entire active season (mid-April to mid-October), the mating season (late April to early June), and the post-mating season (early June to mid-October). Unconditional standard errors (SE; and their 95% confidence intervals) and odds ratios (and their 95% confidence intervals) are shown. Note that there are no intercepts in case-controlled logistic regressions. Asterisks denote significant effects of variables in a model.

models were averaged (confidence set = 99%; Table 3). Rodent abundance did not vary between snake and random locations (Table 4). The model indicated that snake locations were closer to rock refuges (0.32 ± 0.16 m) than random locations were (1.97 ± 0.4 m). We conducted an independent chi-square analysis to investigate whether the occurrence of wood rat nests varied between snake and random locations. Wood rat nests were more common at snake than at random locations (Fisher's exact test: $p = 0.02$). At snake locations with a wood rat nest, snakes were located inside the nests in 3 of 8 (37.5%) occasions, and under a rock refuge or at the entrance of the nests (mean distance ± SD from nest entrance: 0.96 ± 0.42 m) in 5 of 8 (62.5%) instances.

3.3.3. Post-mating season

We examined whether snakes selected locations based on rodent abundance and refuge availability during the post-mating season (Table 3), when most of *C. mitchellii*'s foraging activity takes place (Glaudas & Rodríguez-Robles, 2011). The averaged model, which included 3 of 7 candidate models (con-

fidence set $= 99\%$; Table 3), indicated that snake locations were characterized by low abundance of rodents (Table 4). The average number of rodents caught was 0.32 ± 0.1 at snake locations, compared to 0.71 ± 0.1 at random locations. The odds ratio (0.33) showed that the probability of finding a snake at a given location decreased by a factor of 0.67 $(1 - 0.33)$ for each rodent captured. Further, snake locations were strongly characterized by the presence of a wood rat nest. Wood rat nests were less frequent at random locations (4/52, 7.7%) than at snake locations (30/52, 57.7%). The odds ratio indicated that the occurrence of a wood rat nest at a location increased the probability of a snake's presence by a factor of 23. Snakes were inside the nests in 18 of 30 (60%) instances, or located close to the entrance of the nests (mean distance $\pm$ SD from nest entrance: 0.9 ± 0.6 m) in 12 of 30 (40%) occasions.

Snakes also selected microhabitats closer to rock refuges than expected by chance (mean $\pm$ SE distance between snake locations and rock refuges: 1.4 ± 0.4 m; mean $\pm$ SE distance between random locations and rock refuges: 3.14 ± 0.4 m). We compared the magnitude of the two refuge availability predictor variables, 'absence/presence of a wood rat nest' and 'distance to rock refuge', on microhabitat selection by dividing their importance weights (0.99/0.88, respectively $=1.1$). The occurrence of a wood rat nest at a location was a more plausible explanation for microhabitat selection than distance to a rock refuge, a finding that suggests that *C. mitchellii* likely favors wood rat nests over rock refuges.

3.4. *Wood rat nests and rodent abundance*

Because snakes preferred locations with a wood rat nest, we investigated whether rodents were more abundant at microhabitats where these nests occurred. First, we used rodent fecal pellet counts as a proxy for rodent abundance, to examine the relationship between rodent availability and wood rat nest occurrence. Rodent fecal pellets were significantly more common at locations with a wood rat nest (26 ± 3 pellets), compared to sites without these nests (0.66 ± 0.3 pellets; Wilcoxon signed ranks test, $N = 40, z = 5.51$, $p < 0.0001$; Figure 3A). Second, we investigated the relationship between presence of a wood rat nest and rodent occurrence during the post-mating season, when snakes strongly selected wood rat nests and when rodents were less abundant at snake locations. To remove the potential effect of the
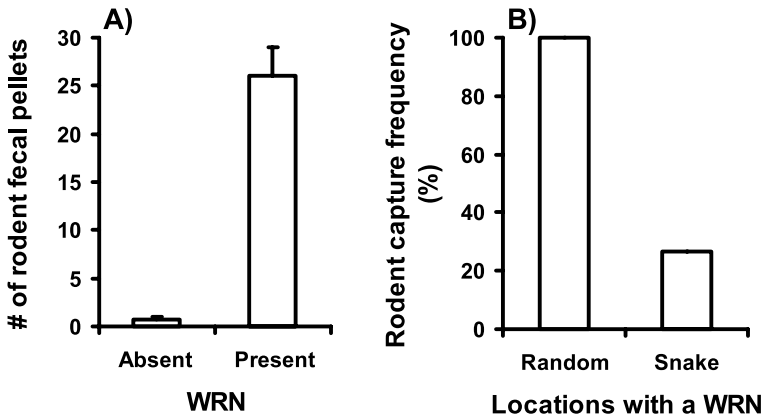
Figure 3. Estimates of rodent abundance at Eldorado Mountains, southern Nevada, USA. (A) At locations with ($N = 20$) and without ($N = 20$) a wood rat nest; (B) at random ($N = 4$) and snake-selected ($N = 30$) locations with a wood rat nest during the post-mating season. Both comparisons are statistically significant at $p \leqslant 0.05$. WRN, wood rat nest.

snake's presence on rodent's behaviour, we only used random locations for this analysis. Capture frequency of rodents at random locations was higher when a wood rat nest was present (4/4, 100%) than when a nest was absent (25/48, 52.1%), but this difference was not statistically significant (Fisher's exact test; $p = 0.12$). Finally, we examined whether the probability of catching a rodent when a wood rat nest was present differed between snake and random locations during the post-mating season. The analysis showed that capture frequency of rodents at wood rat nests was higher at random (4/4, 100%) than at snake locations (8/30, 26.7%; Fisher's exact test: $p = 0.01$; Figure 3B).

3.5. Temporal variation in prey availability

We investigated whether temporal (monthly) trends of rodent abundance differed between snake and random locations. We removed July from the analyses due to small ($N = 5$) sample size. There was no monthly variation in rodent abundance at snake locations (single-factor ANOVA; $F_{3,74} = 0.39$, $p = 0.75$; Figure 4). In contrast, rodent abundance varied monthly at random locations ($F_{3,74} = 3.41$, $p = 0.02$; Figure 4). This statistical difference was caused by the significantly higher abundance of rodents in June, compared to other months (least squares difference post hoc tests; June > May: $p = 0.005$; June > August: $p = 0.04$; June > September: $p = 0.01$). We
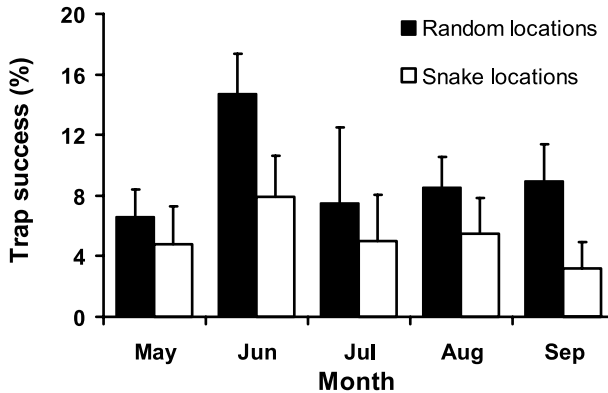
Figure 4. Temporal variation in rodent prey abundance at Eldorado Mountains, southern Nevada, USA. The number of traps that successfully caught a rodent at a given location was used to estimate average rodent abundance at snake-selected and random locations from May to September. Sample sizes (number of snake and random locations where rodents were trapped) are: May, $N = 19$; June, $N = 23$; July, $N = 5$; August, $N = 26$; September, $N = 13$.

also explored whether prey abundance temporally differed between snake and random locations. A factorial ANOVA with month (May, June, August, September) and location (snake vs. random) as factors confirmed that rodent availability was lower at snake locations than at random locations ($F_{1,156} = 4.12$, $p = 0.04$), and that this difference varied by month ($F_{3,156} = 2.87$, $p = 0.03$), with a peak in June (June > May, September; $p = 0.01$).

4. Discussion

The primary objective of our study was to examine whether prey distribution correlated with habitat selection behaviour at the landscape (macrohabitat) and local (microhabitat) levels in an ambush vertebrate predator, the speckled rattlesnake, *Crotalus mitchellii*. Our results demonstrate that the relationship between prey abundance and habitat selection in *C. michellii* varies according to the spatial scale considered and the time of the year (mating vs. post-mating seasons). Below we discuss patterns of macro- and microhabitat choice in *C. mitchellii* in relation to prey abundance in a seasonal context (mating vs. post-mating seasons), and also address the importance of refuges on habitat selection.

4.1. Macrohabitat selection

Our findings revealed that two macrohabitat types, rock outcrops and rolling hills, were significantly related to home range selection in *C. mitchellii*. We presented results for the 95% and 50% home ranges, but focus our discussion of habitat selection at the 50% scale, which is the most heavily used area within snakes' home ranges and, therefore, the best estimate of macrohabitat selection.

During the entire active season, *C. mitchellii* positively selected rock outcrops in its core home range (50% KDEs). In the mating season, snakes avoided rolling hills, whereas during the post-mating season the core activity areas of *C. mitchellii* were characterized by preference of rock outcrops and avoidance of rolling hills. This pattern of macrohabitat selection during the post-mating season correlated with the varying availability of prey between macrohabitats, because rodents were significantly more abundant in rock outcrops than in rolling hills at this time of the year. The finding that predators select macrohabitats with higher prey density has been reported for other vertebrate species (Madsen & Shine, 1996; Bost et al., 2009; Skomal et al., 2009), and is consistent with the hypothesis that *C. mitchellii* prefers the macrohabitat where prey encounter rate is likely maximized, at least during the non-mating season, when snakes are primarily engaged in foraging activities (Shine, 1980; King & Duvall, 1990; Bonnet & Naulleau, 1996; Madsen & Shine, 2000). Further, rock outcrops were also characterized by a similar availability of wood rat nests, but a significantly higher availability of rock refuges, compared to rolling hills. Consequently, the rock outcrops macrohabitat provided *C. mitchellii* with a relatively abundant supply of prey as well as refuges, which snakes may use to reduce predation risk and to thermoregulate (see below).

4.2. Microhabitat selection

We tested the hypothesis that *C. mitchellii* exhibits behaviour that maximizes its rate of prey encounter at the microhabitat (local) level by selecting sites where rodents are relatively abundant. Our findings showed that during the entire active season and the mating season, rodents were equally common at snake and random locations. In contrast, snake locations were characterized by low prey availability during the post-mating season. The factor(s) responsible for the difference in rodent availability at the snake and random locations between seasons is (are) unclear. The low rodent abundance at snake

locations during the post-mating season is surprising, because as previously stated, snakes allocate more time and effort to foraging during the post-mating season, when they are not engaged in sexual activities (O'Donnell et al., 2004; Glaudas & Rodríguez-Robles, 2011).

Three explanations can account for the scarcity of rodents at snake locations during the post-mating season. First, snakes actively selected areas where prey is less available. This presumed avoidance behaviour of prey-rich locations by *C. mitchellii* can theoretically be explained by a food for safety trade-off (Lima & Dill, 1990; Verdolin, 2006; Wirsing et al., 2007). Specifically, snakes may prefer areas with lower prey abundance, because locations where rodents are more available may also attract other predatory species, which could feed on *C. mitchellii*. This scenario is not supported by our data. *Crotalus mitchellii* strongly selected wood rat nests, which are structures made by rodents and that are commonly used by small mammal species that *C. mitchellii* feeds upon (Vestal, 1938; Stones & Hayward, 1968; this study). Consequently, the environmental structure (wood rat nest) preferred by *C. mitchellii* was not characterized by a low number of rodents, which refutes the idea that snakes actively selected microhabitats with lower prey abundance.

Second, *C. mitchellii* consumed most of the rodents at the snake locations, resulting in significantly fewer prey at these sites, compared to the random locations. This explanation requires snakes to consistently remove a portion of the rodent population at their selected locations, to cause a statistical difference in prey abundance between the snake and random locations. Even though there is little doubt that snakes were sometimes successful at preying on rodents, the systematic capture of these mammals by *C. mitchellii* seems improbable. This notion is supported by the typically low prey capture success of vipers (Pierce et al., 1992; Shine et al., 2002; Clark, 2006), the clade of snakes (Viperidae) to which rattlesnakes belong, and by the lack of body condition improvement of snakes at the study site (Glaudas, unpubl. data), which suggests that snakes did not feed often during this study. Further, we estimated that female *C. mitchellii* in this population reproduced infrequently (Glaudas & Rodríguez-Robles, 2011). The low reproductive frequency of females provides additional support for the idea that the lower abundance of rodents at snake-selected areas was not caused by *C. mitchellii* depleting food resources at their preferred sites, because one would expect females to reproduce more frequently if they fed relatively often (Taylor et al., 2005).

Third, rodents abandoned areas where snakes occurred or reduced their activity at snake locations, decreasing prey availability in those areas. Our data suggest that this is a likely scenario. First, wood rat nests, which are strongly selected by *C. mitchellii*, are commonly used by many rodent species (Vestal, 1938; Stones & Hayward, 1968; this study; see below). The odds of catching a rodent at a particular location when a wood rat nest was present were higher at random sites than at snake locations (Figure 3A). This finding indicates that sites with wood rat nests were more commonly used by rodents when snakes were absent, suggesting that rodents altered their behaviour in response to the presence of a snake, presumably to decrease their predation risk. Second, prey abundance was consistently low at snake locations, which contrasted with the observed temporal variation in rodent availability at random locations (Figure 4). This lack of temporal consistency in rodent availability between snake and random locations would be expected if rodents consistently adjusted their behaviour at sites where snakes were present. Finally, studies have demonstrated that mammals can display effective avoidance behaviour that reduces the likelihood of being predated by snakes (e.g., Randall et al., 1995; Swaisgood et al., 1999; Rundus et al., 2007). For example, the deer mouse (*Peromyscus maniculatus*), a close relative of the canyon mouse (*Peromyscus crinitus*, a modal prey species of *C. mitchellii,* and by far the most commonly captured species at the study site), avoided capture by Great Basin rattlesnakes (*Crotalus lutosus*) 75% of the time in a confined environment (Pierce et al., 1992).

A corollary of the previous discussion is that snakes could originally choose microhabitats with higher prey density, but that rodents leave or reduce activity when a predator is present. Our data indeed suggest that this was likely the case. Feces counts provide robust estimates of species density in numerous taxa (Barnes, 2001), and wood rat nests, a strongly selected environmental structure by *C. mitchellii*, were characterized by a large quantity of rodent fecal pellets, compared to locations without these nests (Figure 3B). In addition, the capture frequency of rodents at random locations was higher (although not statistically different) when a wood rat nest was present than when it was absent (100% (4/4) versus 52.1% (25/48), respectively; $p = 0.12$). If this lack of statistical significance is a consequence of the small sample size of random locations with a wood rat nest ($N = 4$), then rodents may indeed be more abundant at locations with wood rat nests,

which would indicate that *C. mitchellii* initially selected microhabitats that increase prey encounter rate.

Regardless of whether or not *C. mitchellii* initially selects microhabitats where prey encounter rate is maximized, the relatively low rodent abundance at *C. mitchellii*'s preferred microhabitats has potentially important consequences for this rattlesnake's energetics, because in ambush predators food intake is likely correlated with prey availability (Huey & Pianka, 1981; Reilly et al., 2007). Field and laboratory experiments that used prey chemical cues or manipulated the occurrence of prey (i.e., by placing caged rodents in the field) demonstrated that rattlesnakes presumably maximize feeding opportunities by selecting sites where prey is most abundant (Duvall et al., 1990; Roth et al., 1999; Theodoratus & Chiszar, 2000; Clark, 2004), and following emergence from hibernation, foraging prairie rattlesnakes (*Crotalus viridis*) stop their migratory routes when they reach areas where prey occurs (Duvall et al., 1985; King & Duvall, 1990). Still, we are not aware of any studies that compared prey abundance at random locations and at the actual sites selected by free-ranging rattlesnakes. Our findings show that prey abundance is low at snake locations, seemingly because rodents exhibit risk-sensitive behaviour that decreases their predation risk in the presence of a snake. As a result, *C. mitchellii*'s prey encounter rate is probably low, and these snakes may be food-limited, as is the case in diamond-backed rattlesnakes (*Crotalus atrox*), a close relative of *C. mitchellii* (Murphy et al., 2002). Wild female *C. atrox* that were supplementally-fed significantly increased their reproductive frequency (Taylor et al., 2005). The hypothesis that rodents avoided locations where *C. mitchellii* occurred, thereby decreasing the snake's prey encounter rate, provides a mechanism to explain why some rattlesnake populations are food-limited, and why females of most of these viviparous snakes, including *C. mitchellii*, reproduce infrequently.

Our primary objective was to examine habitat selection in *C. mitchellii* in relation to prey abundance, but the significance of refuge availability on the snake's microhabitat selection should not be overlooked. Our microhabitat analyses demonstrated that the two main types of refuges available to snakes at the study site, wood rat nests and rock refuges, are heavily used throughout the year. The selection of locations close to refuges by *C. mitchellii* is not surprising, for two reasons. The extremely hot daytime temperatures characteristic of the Mojave Desert from late spring to early fall would likely

be lethal for *C. mitchellii* if the snakes could not retire into a refuge to escape these temperatures. Daytime temperatures in the shade approach the critical thermal maximum (ca. 39–42°C) of many desert reptiles, including *C. mitchellii* (Brattstrom, 1965), and shade is not readily available on the surface at the study site. Therefore, by selecting locations close to refuges, *C. mitchellii* can escape potentially lethal temperatures. Second, predation-induced mortality is relatively high in *C. mitchellii* (average annual mortality rate: males 21.8%, females 8.4% (Glaudas & Rodríguez-Robles, 2011)), and locations close to refuges may help *C. mitchellii* minimize predation risk. In conclusion, wood rat nests probably provide *C. mitchellii* with a suitable thermal environment in the harsh (hot and dry) conditions characteristic of the Mojave Desert, and with a refuge from predators.

4.3.   Concluding remarks

Our study suggests that the relationship between habitat selection and prey abundance in an ambush predator is scale-dependent. At the macrohabitat level, rodent prey was significantly more common in the preferred habitat compared to the avoided sites, but the microhabitats selected by the snakes had lower rodent abundance than random locations. Therefore, the higher abundance of prey in *C. mitchellii*'s preferred macrohabitat did not translate into increased access to prey at the microhabitat level. The lack of congruence between patterns of macro- and microhabitat choice in relation to food abundance in this species was likely caused by the behavioural adjustment of rodents in response to the snake's presence at fine habitat scales. These findings underscore the dynamics of predator–prey interactions in nature, and highlight the challenges that ambush predators may face when foraging for risk-sensitive prey.

References

Akaike, H. (1974). A new look at the statistical model identification. — IEEE Trans. Automat. Control 19: 716-723.

Barnes, R.F.W. (2001). How reliable are dung counts for estimating elephant numbers? — Afr. J. Ecol. 39: 1-9.

Bearhop, S., Hilton, G.M., Votier, S.C. & Waldron, S. (2004). Stable isotope ratios indicate that body condition in migrating passerines is influenced by winter habitat. — Proc. Roy. Soc. Lond. B: Biol. 271 (S4): 215-218.

Bergman, C.M., Fryxell, J.M., Gates, C.C. & Fortin, D. (2001). Ungulate foraging strategies: energy maximizing or time minimizing? — J. Anim. Ecol. 70: 289-300.

Bock, C.E., Vierling, S.L., Haire, S.L., Boone, J.D. & Merkle, W.W. (2002). Patterns of rodent abundance on open-space grasslands in relation to suburban edges. — Conserv. Biol. 16: 1653-1658.

Bonnet, X. & Naulleau, G. (1996). Are body reserves important for reproduction in male dark green snakes (Colubridae: *Coluber viridiflavus*)? — Herpetologica 52: 137-146.

Bost, C.A., Thiebot, J.B., Pinaud, D., Cherel, Y. & Trathan, P.N. (2009). Where do penguins go during the inter-breeding period? Using geolocation to track the winter dispersion of the macaroni penguin. — Biol. Lett. 5: 473-476.

Brattstrom, B.H. (1965). Body temperatures of reptiles. — Am. Midl. Nat. 73: 376-422.

Burnham, P.K. & Anderson, D.R. (2002). Model selection and multimodel inference. — A practical information-theoretic approach. — Springer, New York, NY.

Charnov, E.L. (1976). Optimal foraging, the marginal value theorem. — Theor. Popul. Biol. 9: 129-136.

Ciarniello, L.M., Boyce, M.S., Seip, D.R. & Heard, D.C. (2007). Grizzly bear habitat selection is scale dependent. — Ecol. Appl. 17: 1424-1440.

Clark, R.W. (2004). Timber rattlesnakes (*Crotalus horridus*) use chemical cues to select ambush sites. — J. Chem. Ecol. 30: 608-617.

Clark, R.W. (2006). Fixed videography to study predation behavior of an ambush foraging snake, *Crotalus horridus*. — Copeia: 181-187.

Comins, H.N. & Hassell, M.P. (1979). The dynamics of optimally foraging predators and parasitoids. — J. Anim. Ecol. 48: 335-351.

Diller, L.V. & Johnson, D.R. (1988). Food habits, consumption rates, and predation rates of western rattlesnakes and gopher snakes in Southwestern Idaho. — Herpetologica 44: 228-233.

Duvall, D., Goode, M.J., Hayes, W.K., Leonhardt, J.K. & Brown, D.G. (1990). Prairie rattlesnake vernal migration: field experimental analyses and survival value. — Nat. Geogr. Res. 6: 457-469.

Duvall, D., King, M.B. & Gutzwiller, K.J. (1985). Behavioral ecology and ethology of the prairie rattlesnake. — Nat. Geogr. Res. 1: 80-111.

Ernst, C.H. & Ernst, E.M. (2003). Snakes of the United States and Canada. — Smithsonian Institution, Washington, DC.

Fitch, H.S. (1949). Study of snake populations in central California. — Am. Midl. Nat. 41: 513-579.

Fortin, D., Fryxell, J.M., O'Brodovich, L. & Frandsen, D. (2003). Foraging ecology of bison at the landscape and plant community levels: the applicability of energy maximization principles. — Oecologia 134: 219-227.

Fryxell, J.M., Wilmshurst, J.F., Sinclair, A.R.E., Haydon, D.T., Holt, R.D. & Abrams, P.A. (2005). Landscape scale, heterogeneity, and the viability of Serengeti grazers. — Ecol. Lett. 8: 328-335.

Glas, A.S., Lijmer, J.G., Prins, M.H., Bonsel, G.J. & Bossuyt, P.M.M. (2003). The diagnostic odds ratio: a single indicator of test performance. — J. Clin. Epidemiol. 56: 1129-1135.

Glaudas, X. & Rodríguez-Robles, J.A. (2011). Vagabond males and sedentary females: spatial ecology and mating system of the speckled rattlesnake (*Crotalus mitchellii*). — Biol. J. Linn. Soc. 103: 681-695.

Greene, H.W. (1997). Snakes: the evolution of mystery in nature. — University of California Press, Berkeley, CA.

Gunnarsson, T.G., Gill, J.A., Newton, J., Potts, P.M. & Sutherland, W.J. (2005). Seasonal matching of habitat quality and fitness in a migratory bird. — Proc. Roy. Soc. Lond. B: Biol. 272: 2319-2323.

Heithaus, M., Dill, L., Marshall, G. & Buhleier, B. (2002). Habitat use and foraging behavior of tiger sharks (*Galeocerdo cuvier*) in a seagrass ecosystem. — Mar. Biol. 140: 237-248.

Horne, J.S., Garton, E.O. & Rachlow, J.L. (2008). A synoptic model of animal space use: simultaneous estimation of home range, habitat selection, and inter/intra-specific relationships. — Ecol. Model. 214: 338-348.

Huey, R.B. & Pianka, E.R. (1981). Ecological consequences of foraging mode. — Ecology 62: 991-999.

Johnson, C.N. & Jarman, P.J. (1987). Macropod studies at Wallaby Creek VI. A validation of the use of dung pellet counts for measuring absolute densities of populations of macropodids. — Austr. Wildl. Res. 14: 139-145.

Johnson, D.H. (1980). The comparison of usage and availability measurements for evaluating resource preference. — Ecology 61: 65-71.

Johnson, J.B. & Omland, K.S. (2004). Model selection in ecology and evolution. — Trends Ecol. Evol. 19: 101-108.

Karels, T.J., Koppel, L. & Hik, D.S. (2004). Fecal pellet counts as a technique for monitoring an alpine-dwelling social rodent, the hoary marmot (*Marmota caligata*). — Arct. Antarct. Alp. Res. 36: 490-494.

Keating, K.A. & Cherry, S. (2004). Use and interpretation of logistic regression in habitat-selection studies. — J. Wildl. Manage. 68: 744-789.

King, M.B. & Duvall, D. (1990). Prairie rattlesnake seasonal migrations: episodes of movement, vernal foraging and sex differences. — Anim. Behav. 39: 924-935.

Krebs, C.J., Boonstra, R., Nams, V., O'Donoghue, M., Hodges, K.E. & Boutin, S. (2001). Estimating snowshoe hare population density from pellet plots: a further evaluation. — Can. J. Zool. 79: 1-4.

Levin, S.A. (1992). The problem of pattern and scale in ecology. — Ecology 73: 1943-1967.

Lima, S.L. & Dill, L.M. (1990). Behavioural decisions made under the risk of predation: a review and prospectus. — Can. J. Zool. 68: 619-640.

MacArthur, R.H. & Pianka, E.R. (1966). On optimal use of a patchy environment. — Am. Nat. 100: 603-609.

Madsen, T. & Shine, R. (1996). Seasonal migration of predators and prey — a study of pythons and rats in tropical Australia. — Ecology 77: 149-156.

Madsen, T. & Shine, R. (2000). Energy vs. risk: costs of reproduction in free-ranging pythons in tropical Australia. — Austral. Ecol. 25: 670-675.

Martínez, J.A., Serrano, D. & Zuberogoitia, I. (2003). Predictive models of habitat preferences for the Eurasian eagle owl *Bubo bubo*: a multiscale approach. — Ecography 26: 21-28.

Massé, A. & Côté, S.D. (2009). Habitat selection of a large herbivore at high density and without predation: trade-off between forage and cover? — J. Mammal. 90: 961-970.

Mayor, S.J., Schaefer, J.A., Schneider, D.C. & Mahoney, S.P. (2007). Spectrum of selection: new approaches to detecting the scale-dependent response to habitat. — Ecology 88: 1634-1640.

Millspaugh, J.J. & Marzluff, J.M. (2001). Radio tracking and animal populations. — Academic Press, San Diego, CA.

Murphy, R.W., Fu, J., Lathrop, A., Feltham, J.V. & Kovac, V. (2002). Phylogeny of the rattlesnakes (*Crotalus* and *Sistrurus*) inferred from sequences of five mitochondrial DNA genes. — In: Biology of the vipers (Schuett, G.W., Höggren, M., Douglas, M.E. & Greene, H.W., eds). Eagle Mountain Publishing, Eagle Mountain, UT, p. 69-92.

Murray, D.L., Roth, J.D., Ellsworth, E., Wirsing, A.J. & Steury, T.D. (2002). Estimating low-density snowshoe hare populations using fecal pellet counts. — Can. J. Zool. 80: 771-781.

Mysterud, A., Larsen, P.K., Ims, R.A. & Østbye, E. (1999). Habitat selection by roe deer and sheep: does habitat ranking reflect resource availability? — Can. J. Zool. 77: 776-783.

Neff, D.J. (1968). The pellet-group count technique for big game trend, census, and distribution: a review. — J. Wildl. Manage. 32: 597-614.

Norris, D.R., Marra, P.P., Kyser, T.K. & Sherry, T.W. (2004). Tropical winter habitat limits reproductive success on the temperate breeding grounds in a migratory bird. — Proc. Roy. Soc. Lond. B: Biol. 271: 59-64.

O'Donnell, R.P., Shine, R. & Mason, R.T. (2004). Seasonal anorexia in the male red-sided garter snake, *Thamnophis sirtalis parietalis*. — Behav. Ecol. Sociobiol. 56: 413-419.

Orians, G.H. & Wittenberger, J.F. (1991). Spatial and temporal scales in habitat selection. — Am. Nat. 137: S29-S49.

Pierce, B.M., Longland, W.S. & Jenkins, S.H. (1992). Rattlesnake predation on desert rodents: microhabitat and species-specific effects on risk. — J. Mammal. 73: 859-865.

Pyke, G.H. (1984). Optimal foraging theory: a critical review. — Annu. Rev. Ecol. Syst. 15: 523-575.

Randall, J.A., Hatch, S.M. & Hekkala, E.R. (1995). Inter-specific variation in anti-predator behavior in sympatric species of kangaroo rat. — Behav. Ecol. Sociobiol. 36: 243-250.

Reed, R.N. & Douglas, M.E. (2002). Ecology of the Grand Canyon rattlesnake (*Crotalus viridis abyssus*) in the Little Colorado River Canyon, Arizona. — Southwest. Nat. 47: 30-39.

Reichwaldt, E.S. (2008). Food quality influences habitat selection in *Daphnia*. — Freshw. Biol. 53: 872-883.

Reilly, S.M., McBrayer, L.D. & Miles, D.B. (eds) (2007). Lizard ecology: the evolutionary consequences of foraging mode. — Cambridge University Press, Cambridge.

Reinert, H.K. (1992). Radiotelemetric field studies of pitvipers: data acquisition and analysis. — In: Biology of the pitvipers (Campbell, J.A. & Brodie Jr., E.D., eds). Selva, Tyler, TX, p. 185-198.

Reinert, H.K. & Cundall, D. (1982). An improved surgical implantation method for radio-tracking snakes. — Copeia: 702-705.

Reinert, H.K., Cundall, D. & Bushar, L.M. (1984). Foraging behavior of the timber rat-tlesnake, *Crotalus horridus*. — Copeia: 976-981.

Rodgers, A.R., Carr, A.P., Beyer, H.L., Smith, L. & Kie, J.G. (2007). HRT: home range tools for arcGIS v1.1. — Ontario Ministry of Natural Resources, Centre for Northern Forest Ecosystem Research, Thunder Bay, ON.

Ropert-Coudert, Y., Kato, A., Wilson, R.P. & Cannell, B. (2006). Foraging strategies and prey encounter rate of free-ranging little penguins. — Mar. Biol. 149: 139-148.

Roth, E.D., May, P.G. & Farrell, T.M. (1999). Pigmy rattlesnakes use frog-derived chemical cues to select foraging sites. — Copeia: 772-774.

Row, J.R. & Blouin-Demers, G. (2006). Kernels are not accurate estimators of home-range size for herpetofauna. — Copeia: 797-802.

Rundus, A.S., Owings, D.H., Joshi, S.S., Chinn, E. & Giannini, N. (2007). Ground squirrels use an infrared signal to deter rattlesnake predation. — Proc. Natl. Acad. Sci. USA 104: 14372-14376.

Schoener, T.W. (1983). Simple models of optimal feeding-territory size: a reconciliation. — Am. Nat. 121: 608-621.

Shine, R. (1980). "Costs" of reproduction in reptiles. — Oecologia 46: 92-100.

Shine, R., Sun, L.X., Kerney, M. & Fitzgerald, M. (2002). Why do juvenile Chinese pit-vipers (*Gloydius shedaoensis*) select arboreal ambush sites? — Ethology 108: 897-910.

Sih, A. (1984). The behavioral response race between predator and prey. — Am. Nat. 123: 143-150.

Skomal, G.B., Zeeman, S.I., Chisholm, J.H., Summers, E.L., Walsh, H.J., McMahon, K.W. & Thorrold, S.R. (2009). Transequatorial migrations by basking sharks in the western Atlantic Ocean. — Curr. Biol. 19: 1019-1022.

Stephens, D.W. & Krebs, J.R. (1986). Foraging theory. — Princeton University Press, Princeton, NJ.

Stones, R.C. & Hayward, C.L. (1968). Natural history of the desert woodrat. — Am. Midl. Nat. 80: 458-476.

Swaisgood, R.R., Rowe, M.P. & Owings, D.H. (1999). Assessment of rattlesnake dangerous-ness by California ground squirrels: exploitation of cues from rattling sounds. — Anim. Behav. 57: 1301-1310.

Taylor, E.N., Malawy, M.A., Browning, D.M., Lemar, S.V. & DeNardo, D.F. (2005). Effects of food supplementation on the physiological ecology of female Western diamond-backed rattlesnakes (*Crotalus atrox*). — Oecologia 144: 206-213.

Theodoratus, D.H. & Chiszar, D. (2000). Habitat selection and prey odor in the foraging behaviour of western rattlesnakes (*Crotalus viridis*). — Behaviour 137: 119-135.

Verdolin, J.L. (2006). Meta-analysis of foraging and predation risk trade-offs in terrestrial systems. — Behav. Ecol. Sociobiol. 60: 457-464.

Vestal, E.H. (1938). Biotic relations of the wood rat (*Neotoma fuscipes*) in the Berkeley hills. — J. Mammal. 19: 1-36.

Wallace, R.L. & Diller, L.V. (1990). Feeding ecology of the rattlesnake, *Crotalus viridis oreganus*, in northern Idaho. — J. Herpetol. 24: 246-253.

Wang, G.C.S. & Jain, C.L. (2003). Regression analysis: modeling and forecasting. — Graceway, Flushing, NY.

Wang, J., Gao, W., Wang, L., Metzner, W., Ma, J. & Feng, J. (2010). Seasonal variation in prey abundance influences habitat use by greater horseshoe bats (*Rhinolophus ferrumequinum*) in a temperate deciduous forest. — Can. J. Zool. 88: 315-323.

Ward, D. & Saltz, D. (1994). Foraging at different spatial scales: Dorcas gazelles foraging for lilies in the Negev Desert. — Ecology 75: 48-58.

Wasserman, L. (2000). Bayesian model selection and model averaging. — J. Math. Psychol. 44: 92-107.

Wirsing, A.J., Heithaus, M.R. & Dill, L.M. (2007). Fear factor: do dugongs (*Dugong dugon*) trade food for safety from tiger sharks (*Galeocerdo cuvier*)? — Oecologia 153: 1031-1040.