



10-8-2009

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Recommended Citation

Hamilton, Bryan T. and Nowak, Erika M. (2009) "Relationships between insolation and rattlesnake hibernacula," *Western North American Naturalist*. Vol. 69 : No. 3 , Article 5.

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RELATIONSHIPS BETWEEN INSOLATION AND RATTLESNAKE HIBERNACULA

Bryan T. Hamilton¹ and Erika M. Nowak²

ABSTRACT.—We examined the relationship between insolation, climate, and hibernacula of black-tailed (*Crotalus molossus*), Great Basin (*Crotalus lutosus*), and western diamondback (*Crotalus atrox*) rattlesnakes at 4 sites in Arizona, Nevada, and Utah. Hibernacula were located through a combination of visual searches and radio telemetry from 1995 to 2003. We used global information systems to calculate insolation and compared hibernaculum insolation values with random points representing available insolation of the surrounding habitat. Insolation reflects soil temperatures, and we predicted that hibernacula in cool climates, at high elevations, and at high latitudes would have higher insolation relative to their surroundings, while hibernacula in warmer climates would not differ from their surroundings in insolation. Coolest temperatures, highest elevations, and highest latitudes occurred on the *C. lutosus* and *C. molossus* sites, where hibernaculum insolation was higher than surrounding insolation. Temperatures were intermediate on the high-elevation *C. atrox* site, where hibernaculum insolation did not differ from random-point insolation. Temperatures were highest on the low-elevation *C. atrox* site, where hibernaculum insolation was unexpectedly lower than random-point insolation. Our observations suggest that rattlesnakes in cool climates utilize hibernacula with insolation values higher than those of their surroundings. Rattlesnakes in warm climates utilize hibernacula with insolation values lower than or similar to those of their surroundings.

Key words: black-tailed rattlesnake, Great Basin rattlesnake, western diamondback rattlesnake, communal hibernacula, insolation, *Crotalus molossus*, *Crotalus lutosus*, *Crotalus atrox*, *dens*.

Protection of overwintering habitat is a critical component of rattlesnake conservation. At high elevations and latitudes, rattlesnakes are underground in hibernacula for more than half the calendar year (Brown 1992, Martin 1993, Diller and Wallace 1996, Martin 2002), and populations reach their maximum densities at communal hibernacula (Woodbury 1951, Martin 1992, Brown 1993). Persecution of rattlesnakes by humans at hibernacula has led to extirpations (Hall 1929, Parker and Brown 1974, Brown 1993) and listing of several species as sensitive or endangered (Dodd 1993, Rubio 1998). Locating and protecting hibernacula is an increasingly important objective for land management agencies that protect rattlesnake populations. Understanding the physical characteristics of hibernacula is an important step in their protection. Hibernacula can occur across a wide range of topographic conditions (Klauber 1956), but most often they occur on rocky, steep, south-facing slopes, which receive relatively large amounts of insolation (solar radiation) and have relatively high soil temperatures. The cooler climates and longer winters of high

latitudes and elevations should limit suitable hibernacula to areas with more favorable subsurface temperatures and high solar radiation, while at lower latitudes and elevations, suitable hibernacula should be less limited by thermal constraints.

Snake hibernacula serve many biological functions (Gregory 1982, Beck and Jennings 2003), but their most important function is to protect snakes from mortality risks, such as predation and freezing (Gregory 1984, Aldridge and Duvall 2002). Overwintering mortality is documented in many rattlesnake species (MacCartney 1985, Charland 1989, Reinert and Rupert 1999, Ernst 2003, Kingsbury et al. 2003). Snakes failing to utilize hibernacula with sufficiently high soil temperatures may freeze to death (Gregory 1982, MacCartney 1985, Charland 1989, Shine and Mason 2004). Conversely, failure to overwinter at sufficiently low temperatures depletes energy reserves (Gregory 1982, Dorcas et al. 2004, W.H. Martin personal communication). The potential for overwintering mortality due to freezing or starvation suggests that rattlesnakes should

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select hibernacula within an optimal range of soil temperatures (Gregory 1982).

As a primary determinant of soil temperature (Miller and Gardiner 1998), insolation patterns strongly influence rattlesnake hibernaculum locations and overwintering strategies (Martin 1992, Sexton et al. 1992). On a global scale, variation in insolation results from the earth's tilt and rotation on its axis and its revolution around the sun (Stiling 1996). On a landscape scale, slope, aspect, elevation, and shadows create highly variable spatial and temporal insolation patterns (Dubayah and Rich 1995, 1996). Insolation increases with steeper slope, more-southerly aspect, and higher elevation (Barry and Chorley 1976, Brady and Weil 2002). In the northern hemisphere, during the winter, insolation decreases with increasing latitude. During the summer this relationship reverses and insolation increases with latitude (Barry and Chorley 1976). Topographic effects on insolation are most pronounced in the northern hemisphere during winter solstice, when the sun is at its nadir (Stiling 1996).

Given the importance of hibernacula to rattlesnake biology and conservation, the interest in predicting the locations of rattlesnake hibernacula, and the influence of insolation on overwintering ecology, we examined the relationship between insolation and hibernacula of 3 rattlesnake species at 4 study sites. Our objectives were (1) to examine variation in climate, topography, and insolation among sites and (2) to examine the relationship between hibernacula insolation and random-point insolation by site. We predicted that in cooler climates, (i.e. at higher elevations and latitudes), hibernaculum insolation would be relatively high, while in warmer climates, hibernacula would not differ from surrounding areas in insolation.

STUDY SITES

Study sites were located in Arizona, Nevada, and Utah (Fig. 1). Ecoregions follow Omernik (1987), and geomorphology and class definitions for rock size follow Rosgen (1996).

Crotalus molossus hibernacula were located in central and northern Yavapai County, Arizona, in the Arizona/New Mexico Mountains ecoregion. The area of the study site was 71,225 ha.

Topography was dominated by mountainous, granitic intrusions overlain with basalt and weathered into rugged hills. Climate data were taken from Prescott, Arizona (Western Regional Climate Center, www.wrcc.dri.edu; mean distance from hibernacula = 38 km). Plant communities included desert scrub, shrub, and woodland. Trees around hibernacula included Utah juniper (*Juniperus osteosperma*) and two-needle piñon (*Pinus edulis*). Shrubs and cacti included birchleaf mountain mahogany (*Cercocarpus betuloides*), Englemann's pricklypear (*Opuntia phaeacantha*), and turbinella oak (*Quercus turbinella*). All hibernacula were located at the base of large bedrock outcrops and ledges surrounded by boulders and cobbles. Bedrock comprising hibernacula was limestone, granite, or gneiss. Minimum numbers of *C. molossus* observed per hibernaculum ranged from 2 to 8. Other species of snakes utilizing these hibernacula included Arizona black rattlesnakes (*C. cerberus*) and western lyresnakes (*Trimorphodon biscutatus*).

Crotalus lutosus^a hibernacula were located in eastern Nevada and western Utah, in the Central Basin and Range ecoregion on a study site of 113,960 ha. Topography was dominated by north-south-trending mountain ranges and valleys. Climate data were taken from Great Basin National Park, Nevada (Western Regional Climate Center; mean distance from hibernacula = 37 km). The study site was characterized by shrub and woodland plant communities. Trees adjacent to hibernacula included single-leaf piñon (*Pinus monophylla*) and Utah juniper; shrubs included black sagebrush (*Artemisia nova*), bud sagebrush (*Artemisia spinescens*), shadscale (*Atriplex confertifolia*), cliffrose (*Cowania mexicana*), Nevada ephedra (*Ephedra nevadensis*), and spiny greasebush (*Forsellesia nevadensis*). Bedrock comprising hibernacula included limestone, basalt, or metamorphic gneiss. All hibernacula were closely associated with large bedrock outcrops and ledges surrounded by talus, boulders, and cobbles. Minimum numbers of *C. lutosus* observed per hibernaculum ranged from 2 to 83. Other species of snakes utilizing these hibernacula included desert striped whipsnake (*Masticophis taeniatus*) and gopher snake (*Pituophis catenifer*).

^aThe systematic relationships of *C. lutosus*, a taxon belonging to the *C. viridis* species complex, have been studied recently by several authors (Pook et al. 2000, Ashton and Queiroz 2001, Douglas et al. 2002), and herein we recognize this snake at the species level, following the recommendation of Douglas et al. (2002) and the convention of Claudas et al. (2008).

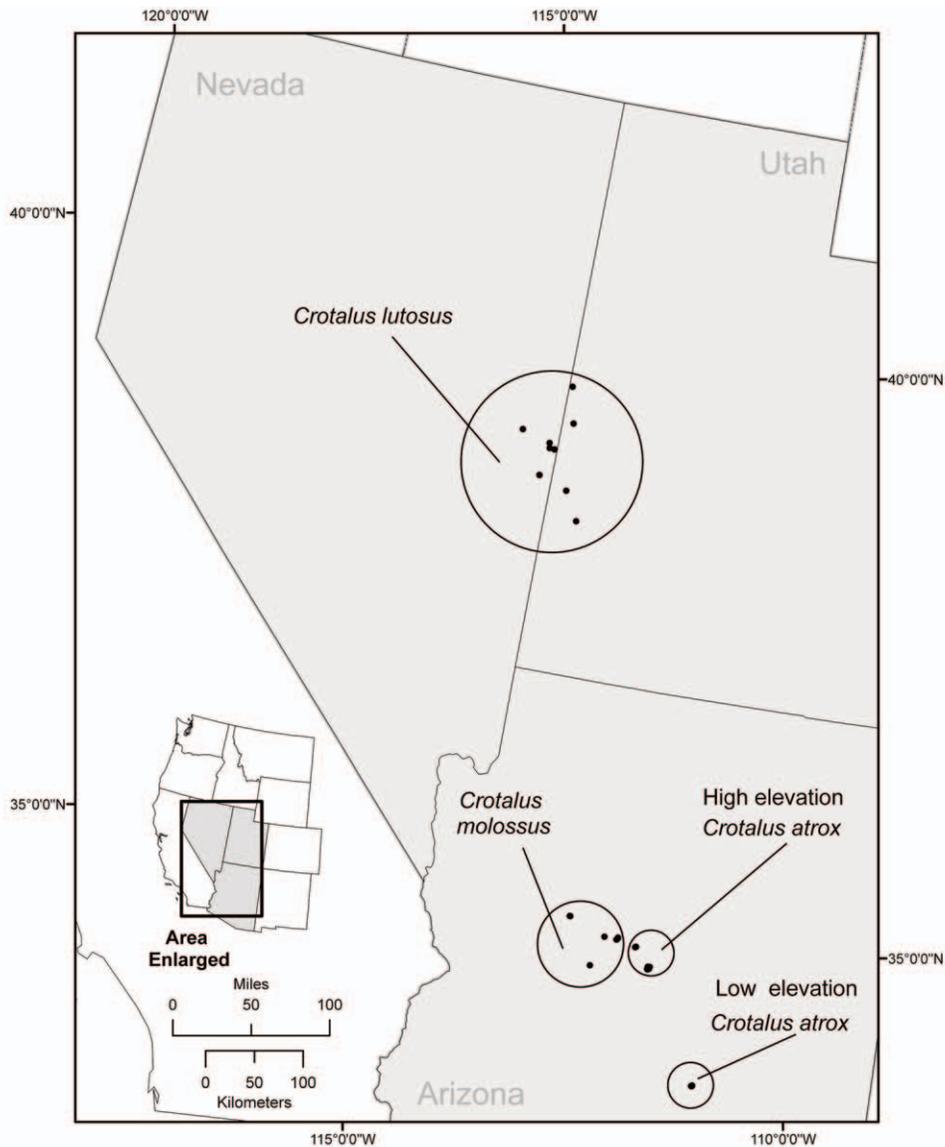


Fig. 1. Study sites and hibernaculum locations of 3 rattlesnake species.

High-elevation *Crotalus atrox* hibernacula were located on 2 ecologically similar national monuments in western Yavapai County in the Arizona/New Mexico Mountains ecoregion. This study site was 28,490 ha. Topography was dominated by limestone cliffs and mesitas rising from river valleys and floodplains. Lower hillsides were overlain with unconsolidated sandstone and basalt cobbles from ancient floodplains. Climate data were taken from Montezuma Castle National Monument, Arizona (Western

Regional Climate Center; mean distance from hibernacula = 6 km). Trees around hibernacula were primarily crucifixion thorn (*Canotia holacantha*) and velvet mesquite (*Prosopis velutina*) and shrubs included creosotebush (*Larrea tridentata*), featherplume (*Dalea formosa*), four-wing saltbrush (*Atriplex canescens*), and western mugwort (*Artemisia ludoviciana*). Most hibernacula were located at the base of large limestone or volcanic/sedimentary bedrock outcrops and ledges, with one hibernaculum located

TABLE 1. Selected climate variables, insolation, and topographic characteristics of hibernacula of 3 rattlesnake species at 4 sites in Arizona, Utah, and Nevada. Frost-free season is the number of days between spring and fall frosts (low temperature $> 0^{\circ}\text{C}$) within a 50th percentile. See text for detailed descriptions of study sites. Values for insolation, elevation, aspect, and slope are means with one standard error. Ranges are in parentheses.

Hibernaculum characteristics	<i>C. molossus</i>		<i>C. lutosus</i>		High-elevation <i>C. atrox</i>		Low-elevation <i>C. atrox</i>	
	n	range	n	range	n	range	n	range
Mean annual temperature ($^{\circ}\text{C}$)	12		9		16		20	
Mean January temperature ($^{\circ}\text{C}$)	2		-1		6		9	
Mean July temperature ($^{\circ}\text{C}$)	23		22		28		32	
Frost-free season (days)	148		124		183		319	
Annual precipitation (cm)	48		33		32		40	
Hibernaculum sample size	11		12		29		15	
Random-point sample size	483		746		194		103	
Hibernaculum insolation ($\text{watts} \cdot \text{m}^{-2}$)	2252 \pm 105 (1425–2645)		1551 \pm 111 (896–2178)		1515 \pm 54.2 (442–2359)		1256 \pm 118 (447–1844)	
Random-point insolation ($\text{watts} \cdot \text{m}^{-2}$)	1626 \pm 13.5 (453–2491)		1316 \pm 10 (310–2381)		1575 \pm 20.4 (427–2440)		1576 \pm 20.8 (779–2166)	
Hibernaculum mean elevation (m)	1458 \pm 43.9 (1432–1877)		1837 \pm 48 (1539–2088)		1014 \pm 5.2 (969–1060)		866 \pm 24.8 (756–1015)	
Random-point mean elevation (m)	1573 \pm 8.2 (1216–2110)		1853 \pm 10.8 (1482–3186)		1129 \pm 10.7 (915–1556)		758 \pm 11.7 (638–1170)	
Hibernaculum mean aspect ($^{\circ}$)	177 \pm 11 (102–237)		197 \pm 24 (103–342)		267 \pm 15 (0–345)		66 \pm 12 (15–342)	
Random-point mean aspect ($^{\circ}$)	358 \pm 13 (0–357)		48 \pm 5 (0–358)		180 \pm 43 (0–358)		210 \pm 21 (0–357)	
Hibernaculum mean slope ($^{\circ}$)	29 \pm 3 (12–48)		20 \pm 2 (6–34)		15 \pm 3 (0–39)		18 \pm 3 (3–42)	
Random-point mean slope ($^{\circ}$)	10 \pm 0.4 (0–50)		7 \pm 0.3 (0–45)		9 \pm 0.6 (0–43)		8 \pm 0.9 (0–43)	

under a historic rock building. Minimum numbers of *C. atrox* observed per hibernaculum ranged from 1 to 5. Other snake species utilizing these hibernacula included *C. molossus*, *M. taeniatus*, and *P. catenifer*.

Low-elevation *C. atrox* hibernacula were located in western Gila County in the Arizona/New Mexico Mountains ecoregion. The study site was 28,490 ha. Topography was dominated by rugged cliffs rising from washes. Volcanic extrusions and a dolomite layer capped siltstone and sandstone and formed tall outcrops from 1 to 25 m high. Talus slides were common on steep slopes and lower bajada areas, with floodplains and washes strewn with cobble and boulders. Climate data were taken from Roosevelt Dam, Arizona (Western Regional Climate Center; mean distance from hibernacula = 4 km). Vegetation around hibernacula included saguaro (*Carnegiea gigantea*), paloverde (*Parkinsonia* spp.), Barrel cactus (*Ferocactus cylindraceus*), cholla (*Opuntia* spp.), sotol (*Dasyllirion wheeleri*), jojoba (*Simmondsia chinensis*), hopbush (*Dodonaea viscosa*), and brittlebush (*Encelia* spp.). Most hibernacula were located at the base of large limestone or volcanic/sedimentary bedrock outcrops and ledges. Two hibernacula were located in nearly flat washes and 2 were under concrete walkways used by park visitors. Minimum numbers of *C. atrox* observed per hibernaculum ranged from 1 to 4. Other reptile species utilizing these hibernacula included *C. molossus*, *M. taeniatus*, *P. catenifer*, and Gila monster (*Helerma suspectum*).

METHODS

Hibernacula were located from 1993 to 2005 by 2 methods: (1) Rattlesnakes were observed within or immediately adjacent to hibernation crevices during spring emergence. For the purposes of this paper, hibernation crevices were considered synonymous with hibernacula. All *C. lutosus* and 8 *C. molossus* hibernacula were located by this method. Although this method has the potential to bias hibernaculum locations toward areas, such as south-facing slopes, where observers tend to focus their surveys, all topographic aspects in the study areas were searched, and sampled hibernacula were found across a wide range of aspects (Table 1). (2) Radio-tagged rattlesnakes were tracked to hibernacula. Three *C. molossus* and all *C. atrox*

hibernacula were located by this method. Hibernaculum locations were recorded with a handheld global positioning system unit. Horizontal precision was within a range of 0.6–15 m.

Global information systems (GIS) model insolation values for large numbers of pixels over large areas (Fu and Rich 1999). We calculated global insolation ($\text{watts} \cdot \text{m}^{-2}$) for each grid cell of a study site from 10-m digital elevation models (DEM) using the Solar Analyst (Fu and Rich 1999), an ArcView 3.2 extension. Global insolation is the cumulative insolation over a 24-hour period at a grid cell, and it incorporates slope, aspect, elevation, latitude, surrounding topography, and date, allowing standardized comparisons to be made across latitudinal gradients (Fu and Rich 1999). In the winter, more-southerly aspects, higher elevations, and steeper slopes receive more insolation than northerly aspects, low elevations, shallow slopes, areas shaded by surrounding topography, and northern latitudes. We also generated aspect, slope, and elevation grids from DEMs using the ArcView 3.2 Spatial Analyst extension.

We found 6 data sets of global insolation (October–March) to be highly correlated ($r^2 = 0.97$, $P < 0.001$) and chose to use a single global insolation value (1 January) because of the close proximity of this date to winter solstice. Insolation values are lowest in the northern hemisphere at winter solstice when the sun is at its nadir (Stiling 1996).

Insolation is a primary determinant of soil temperature (Miller and Gardiner 1998), which in turn strongly influences rattlesnake hibernaculum locations and overwintering strategies (Martin 1992, Sexton et al. 1992). Based on this correlation, we use soil temperature and insolation as loosely interchangeable but recognize that cloud cover, substrate albedo, soil moisture, and vegetation distort this relationship (Miller and Gardiner 1998, Fu and Rich 1999). Insolation calculations used in this study did not incorporate this distortion because of the difficulty of quantifying it at the landscape scale. Our study sites were located in relatively cloud-free climates typified by dry soils and sparse vegetation types (Omernik 1987; Western Regional Climate Center, unpublished data), and we assumed that distortion effects under these conditions were negligible.

To characterize the insolation of the study sites, we generated 100 random points in each

quadrangle for each study site and assigned insolation, aspect, slope, and elevation values at each random point and hibernaculum from DEMs (ESRI 1996a, 1996b). Due to a small border surrounding each DEM, some random points fell slightly outside the boundaries of the DEMs, so the numbers of random points by species and study site are not exact multiples of 100 (Table 1). We used the random points to characterize the range of insolation and topography available at the study sites and then contrasted these values against those from the locations of hibernacula.

For all hibernacula and random points, we calculated means and standard errors for insolation, elevation, aspect, and slope (Minitab 2004). Calculations of mean and standard error for aspect followed Fisher (1995), using the program NCSS (Hintze 2007). Due to the smaller number of hibernacula relative to random points, standard errors of hibernacula were much greater than those of random points. We were unable to transform the data to meet parametric assumptions of normality and equal variances, so we used nonparametric tests. Kruskal–Wallis tests were used to compare median insolation, elevation, and slope. Mann–Whitney U tests were used to compare median insolation of hibernacula and random points (Minitab 2004).

RESULTS

Insolation was calculated from DEMs based on slope, latitude, aspect, and elevation and was strongly correlated with these variables (multiple linear regression: $R^2 = 0.753$; $P < 0.001$ for all variables; Fig. 2).

The warmest temperatures and the longest growing season occurred at the low-elevation *C. atrox* site, and the coolest temperatures and shortest growing season occurred at the *C. lutosus* site (Table 1). The *C. molossus* and high-elevation *C. atrox* sites had intermediate temperatures and growing-season lengths (Table 1). Precipitation was highest at the *C. molossus* site, followed by low-elevation *C. atrox*, *C. lutosus*, and high-elevation *C. atrox* sites (Table 1).

Insolation contrasts on the landscape were striking (Fig. 3). As characterized by random points, insolation on *C. lutosus* sites was lower than it was on other sites ($H = 487.03$, $df = 3$, 1528 , $P < 0.001$). Insolation did not differ between other sites. Elevation differed between

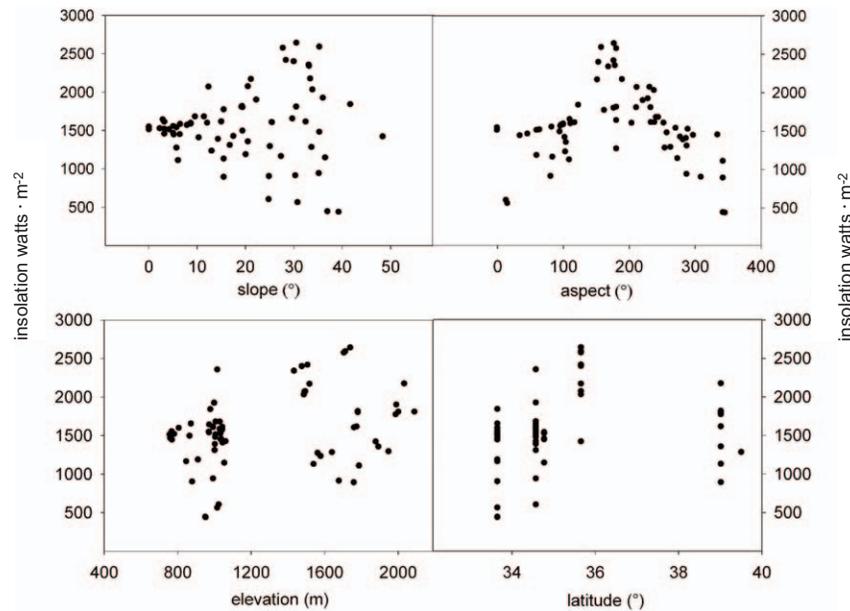


Fig. 2. Relationships between insolation, slope, aspect, elevation, and latitude for rattlesnake hibernacula in Nevada, Utah, and Arizona.

sites ($H = 897.6$, $df = 3$, 1454 , $P < 0.0001$), and was highest for *C. lutosus* sites, followed by *C. molossus*, high-elevation *C. atrox*, and low-elevation *C. atrox* sites (Table 1). Aspects also differed between sites (Table 1). Slope differed between sites ($H = 71.08$, $df = 3$, 1454 , $P < 0.0001$), with steepest slopes on *C. molossus* sites, followed by high- and low-elevation *C. atrox* sites and *C. lutosus* sites (Table 1).

Hibernaculum insolation of *C. molossus* sites was higher than that of other sites ($H = 20.99$, $df = 3$, 67 , $P < 0.0001$). Hibernaculum insolation did not differ between other sites. Hibernaculum aspects were more southerly for *C. molossus* and *C. lutosus* sites than for *C. atrox* sites (Table 1).

Pooled across sites, hibernaculum insolation was higher than random-point insolation ($W = 63493.0$, $P = 0.0066$, 95% CI = 36.0 – 200.0). However, this relationship also varied by site. Insulations of *C. molossus* and *C. lutosus* hibernacula were higher than those of random points on their respective study sites (*C. molossus*, $W = 14485.0$, $P = 0.0248$, 95% CI 19.9 – 442.9 ; *C. lutosus*, $W = 6071.5$, $P < 0.0427$, 95% CI 7.1 – 478.0 ; Fig. 4). Insolation of high-elevation *C. atrox* hibernacula did not differ from that of random points ($W = 2680.5$, $P = 0.0685$; Fig. 4). Insolation of low-elevation *C.*

atrox hibernacula was lower than insolation of random points ($W = 511.0$, $P = 0.0033$, 95% CI 47.9 – 298.0 ; Fig. 4).

DISCUSSION

In general, our prediction that hibernacula in cooler climates (i.e., at higher elevations and latitudes) would be higher in insolation than their surroundings was supported. *Crotalus lutosus* and *C. molossus* hibernacula were located in the coolest climates, highest latitudes, and highest elevations and were higher in insolation than their surroundings. Contrary to expectation, low-elevation *C. atrox* hibernacula were lower in insolation than their surroundings. These sites were located in the warmest climate, lowest latitude, and lowest elevation. These rattlesnake populations may utilize cool hibernacula as a strategy to conserve energy reserves during the overwintering period. Conversely, insolation values for the high-elevation *C. atrox* hibernacula were not different from values of random points. These observations suggest that rattlesnakes in cool climates utilize hibernacula with higher insolation values than those of their surroundings. Rattlesnakes in warm climates utilize hibernacula with insolation values lower than or similar to those of their surroundings.

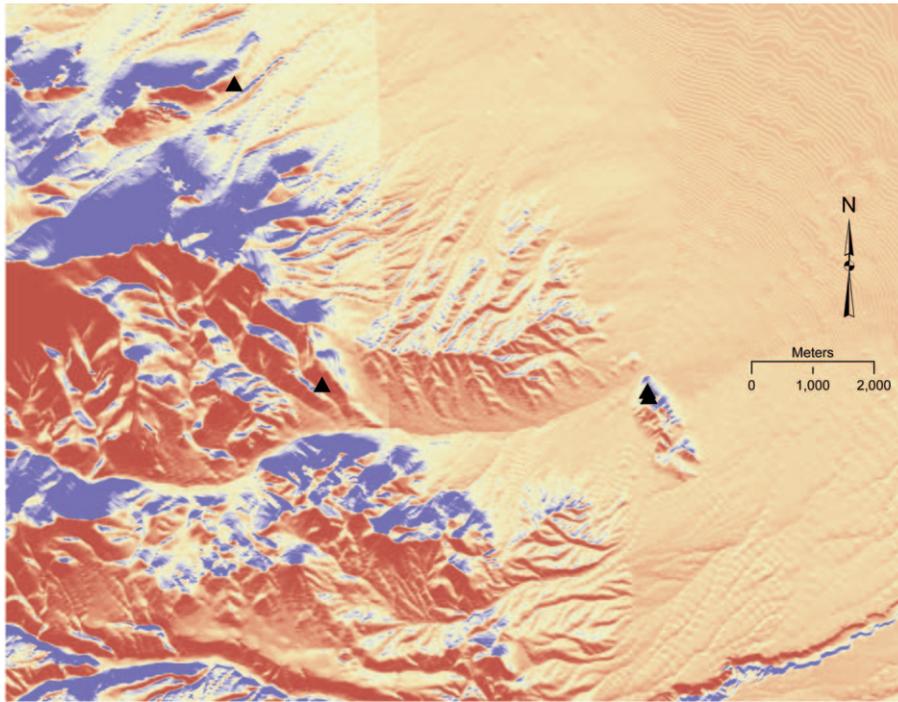


Fig. 3. Global insolation patterns on 1 January at a portion of the *C. lutosus* study site, eastern Nevada. Hibernacula are plotted with black triangles. Highest insolation is symbolized by dark red (2800 watts · m⁻²) and lowest by dark blue (55 watts · m⁻²).

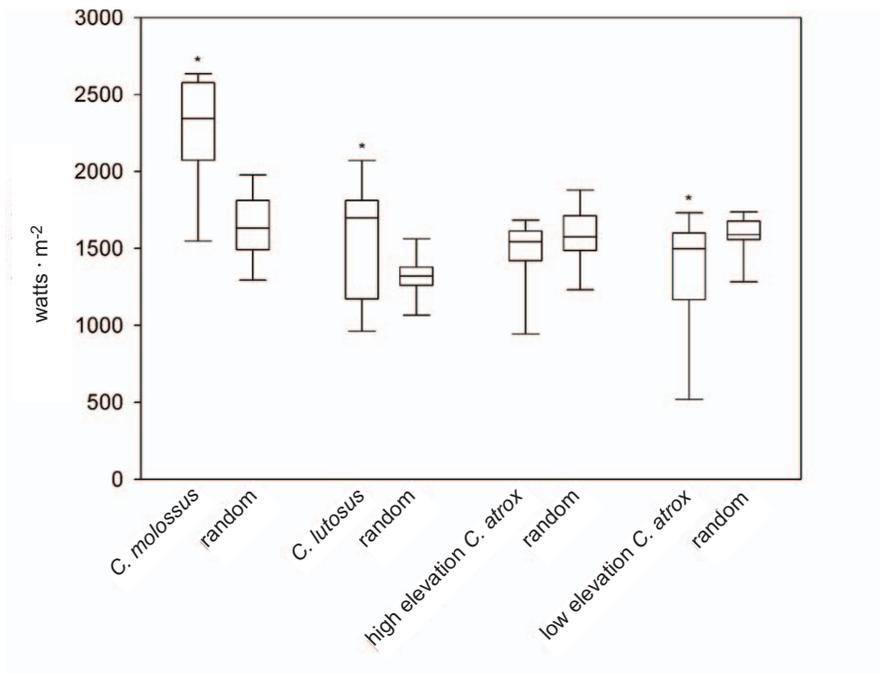


Fig. 4. Boxplots of global insolation (watts · m⁻²) for rattlesnake hibernacula and random points at 4 study sites. Hibernaculum plots marked with an asterisk (*) differed from random at $\alpha = 0.05$ (Mann-Whitney *U* tests).

Hibernaculum insolation values were strikingly similar between *C. atrox* and *C. lutosus*, in spite of the large temperature differences between these sites (Table 1). This similarity suggests that common factors pressure rattlesnakes across a range of climates to utilize hibernacula with similar insolation. Insolation is a primary determinant of soil temperature, moderated by cloud cover, plant cover, soil moisture, substrate type and reflectivity, and ambient temperature (Brady and Weil 2002), and the importance of soil temperatures to hibernating reptiles is well documented (Gregory 1982). Rattlesnakes failing to choose sufficiently warm hibernacula may freeze to death, while rattlesnakes that overwinter in hibernacula that are too warm may overutilize energy reserves and starve. Our observations are consistent with an optimal range of suitable overwintering temperatures for hibernating rattlesnakes. Similarity in insolation values across sites with widely differing climates may reflect this temperature range.

A brief discussion of soil-temperature dynamics may be useful in understanding the relationship between insolation and soil temperatures. During the fall, soil temperatures decrease with soil depth until a constant temperature, which approximates the mean annual soil temperature, is reached. As winter progresses, this isocline reverses and the coldest temperatures are found on the surface. During the spring, insolation raises soil temperatures. Isoclines that have moved toward the surface reverse, and warmer temperatures are again found on the surface (Sexton et al. 1992). Snakes underground in hibernacula thermoregulate by vertical orientation in the ground and can find cooler or warmer temperatures by moving up or down these thermal gradients.

Hibernacula with high insolation values should have a higher mean annual soil temperature than hibernacula with lower insolation values. In cold climates, snakes can access a warmer temperature at a shallower depth by choosing hibernacula with high insolation. Conversely, in warm climates snakes can access a cooler temperature at a shallower depth by selecting hibernacula with low insolation. More data are needed to clarify the relationship between soil temperatures, snake temperatures, and insolation values and to confirm the possibility that rattlesnakes across a range of climates overwinter within a similar temperature range.

While insolation and suitable soil temperatures are important to hibernaculum selection in rattlesnakes, access to that suitable range of soil temperatures through available holes, cracks, and fissures may be equally important. Prior and Weatherhead (1996) noted that subsurface characteristics which provide access to areas below frostlines were likely as important as surface characteristics in determining the location of communal hibernacula in *Elaphe obsoleta*. Beck and Jennings (2003) noted the strong influence of shelter availability on *Heloderma suspectum* habitat selection. However, Browning et al. (2005) found that topographic variables representative of insolation (slope, aspect, and elevation) contributed most heavily to the principal components in their modeling of *C. horridus* hibernacula in Arkansas, while soil variables representative of subsurface access (crevices and fissures) were less important.

We suggest a trade-off between insolation and subsurface access. Many areas of our study sites, such as steep alluvial fans underlain with shallow, impenetrable, calcic horizons, had suitable insolation values, but because there was minimal subsurface access, apparently no rattlesnake hibernacula occurred in these areas. However in areas with abundant outcrops, talus, and deep cracks and fissures, subsurface access is not limiting, and insolation and soil temperatures would be most important. Additional work is needed to define this interaction between insolation and access to suitable subsurface conditions.

Management Implications

GIS habitat models have been widely applied to wildlife management (Smith et al. 1991, Clark et al. 1993, Augustin et al. 1996, Knick and Dyer 1997, Mladenoff et al. 1999), and there is currently widespread interest in using similar models to predict the locations of rattlesnake hibernacula. Insolation is a parsimonious variable that captures most of the topographic variability used in modeling (i.e., slope, aspect, elevation, and latitude) and is directly related to soil temperature. Incorporating insolation into models will provide a useful, biologically meaningful, and easily interpretable variable.

As our data show, the relationship between insolation and rattlesnake hibernacula is complex and varies by site. Thus, models need to

be locally calibrated to an initial sample of hibernacula for each study site and analyzed relative to surrounding insolation values. Models will be most useful and will predict the largest number of hibernacula in the smallest area in sites where hibernaculum insolation greatly contrasts with that of the surroundings. This will most likely be at high latitudes, at high elevations, and in cool climates. As suggested by the low-elevation *C. atrox* data, models may also be useful in warmer climates if snakes are indeed choosing cool hibernacula.

While predictive models of rattlesnake hibernacula may prove useful for herpetologists and land management agencies, they will supplement rather than replace field-based methods. Radiotelemetry and searching based on topography will continue to be primary methods used to locate rattlesnake hibernacula and to ground-truth predictive models.

ACKNOWLEDGMENTS

We thank the following people for their help with this project: Jenny Hamilton, Matt Spille, Jim Fox, Doug Wynn, Daryl Hanks, Dan Carpenter, Dan Mulcahy, Jered Hansen, Terry Arundel, Roger Repp, Krupa Patel, Ben Roberts, Bart Wright, Rob Colvin, Gordon Schuett, Chuck Peterson, Josiah Hansen, Preston Hanks, Andrew Stock, W.H. Martin, Trevor Persons, Karl Sieglaff, Jack Sites, Kamiakin Richards, Jenny Richards, Carol Simpson, Jon Bortle, Christy Baumgartner, Ann DaVega, Kathy M. Davis, Paul Deshler, Shirley Hoh, Amyann and Patrick Madara-Yagla, John Reid, Manuel Santana-Bendix, Gretchen Baker, Neal Darby, Justin Schofer, and numerous National Park Service employees. Funding for the telemetry research at MOCA/TUZI and TONTO was provided by the monuments, the National Park Service's NRPP program, the USGS SIWD program, the USGS Southwest Biological Science Center, and the Western National Parks Association. We would particularly like to thank all the reviewers of this paper for their thorough reviews and thoughtful suggestions.

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Received 2 August 2008
Accepted 9 May 2009