Northern Pacific Rattlesnakes (*Crotalus oreganus*) use thermal and structural cues to choose overwintering hibernacula

C.M. Gienger and Daniel D. Beck

Abstract: Hibernacula play an important role in the ecology of high-latitude snakes, and communally denning species may occupy their hibernacula for half the year or more. Because of the long duration spent at hibernacula, such sites can provide multiple benefits to snakes including shelter from lethal overwinter conditions, social opportunities, and basking sites important in thermoregulation. Adequate hibernacula seem to be limited on the landscape and individuals travel several kilometres to use and reuse specific sites. We investigate orientation, physical structure, and thermal properties of sites used as hibernacula by Northern Pacific Rattlesnakes (*Crotalus oreganus* Holbrook, 1840), and compare them with random sites that appear to be similar but were not used for hibernation. Hibernacula occurred primarily on south-facing talus slopes, were oriented on less-steep slopes, and were composed of rocks that were intermediate in size to randomly occurring sites. Our results suggest that the orientation and physical composition of hibernacula allow them to be stable over time, allowing snakes to repeatedly locate the sites, as well as providing predictable overwinter refuge. Hibernacula were also warmer on the surface than north-facing random sites and provided increased basking opportunities for snakes thermoregulating in early spring after emergence from hibernation.

Résumé : Les hibernaculums jouent un rôle important dans l'écologie des serpents des hautes latitudes et les espèces qui occupent des tanières communautaires peuvent passer la moitié de l'année ou plus dans leurs hibernaculums. À cause de la longue période passée dans les hibernaculums, ces sites peuvent fournir de multiples bénéfices aux serpents et, en particulier, un gîte qui les protège des conditions létales pendant l'hiver, des occasions sociales et des sites pour lézarder, ce qui est important pour la thermorégulation. Les hibenaculums adéquats semblent être restreints dans le paysage et les individus se déplacent de plusieurs kilomètres pour utiliser et réutiliser des sites spécifiques. Nous examinons l'orientation, la structure physique et les propriétés thermiques des sites utilisés comme hibernaculums par les crotales de l'Ouest (*Crotalus oreganus* Holbrook, 1840) et les comparons à des sites choisis au hasard qui paraissent être semblables, mais qui ne servent pas à l'hibernation. Les hibernaculums se retrouvent principalement sur les talus d'éboulis orientés vers le sud, ils sont disposés sur des pentes moins abruptes et ils se composent de pierres de taille intermédiaire par comparaison aux sites répartis au hasard. Nos observations indiquent que l'orientation et la composition physique des hibernaculums leur donnent de la stabilité dans le temps, ce qui permet aux serpents de les retrouver à chaque fois, tout en fournissant un refuge prévisible pendant l'hiver. Les hibernaculums sont aussi plus chauds en surface que les sites aléatoires à orientation nord et ils procurent aux serpents plus d'occasions de lézarder au soleil pour leur thermorégulation après leur émergence de l'hibernation.

[Traduit par la Rédaction]

Introduction

One of the most spectacular mass congregations of vertebrate predators occurs at the overwintering hibernacula of high-latitude snakes (Woodbury 1954; Drda 1968; Klauber 1972; Parker and Brown 1973; Gregory 1977). Although most snakes live secretive and solitary lives, gathering conspicuously at hibernacula can be an important aspect of the biology of some species (Gregory 1982). High-latitude snakes often use hibernacula to both escape critically low winter temperatures (Macartney et al. 1989; Sexton et al. 1992) and for regulating physiological processes following spring emergence by basking (Gregory 1984).

Snakes that fail to choose winter hibernacula that provide suitable protection from harsh surface conditions will likely have a considerable risk of death. Therefore, communally denning snakes tend to exhibit a high degree of fidelity to specific hibernacula. Year-to-year return rates can be >90% (Hirth 1966; Brown and Parker 1976; Gregory 1977; Brown 1992) and individuals often travel several kilometres from seasonal territories to return to overwintering sites (Sehman 1977; Gregory 1984; Gannon and Secoy 1985; Graves and Duvall 1993). Even neonates, which are usually born away from hibernacula and thus have no previous knowledge of wintering sites, often use the same hibernacula as their parents (Graves and Duvall 1993; Clark et al. 2008). Neonates

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locate hibernacula by following chemical trails left by adult snakes during fall returns to den sites (Graves et al. 1986; Reinert and Zappalorti 1988; Cobb et al. 2005).

The high fidelity that snakes display towards specific hibernacula suggests that hibernacula have unique characteristics which allow them to be repeatedly relocated and features which may be critical in allowing overwinter survival (Burger et al. 1988; Prior and Weatherhead 1996; Harvey and Weatherhead 2006). Because of this, we investigate the hypothesis that Northern Pacific Rattlesnakes (*Crotalus oreganus* Holbrook, 1840) are able to distinguish potential hibernacula from sites unsuited for hibernation by assessing specific habitat features. We test the predictions that hibernacula used by rattlesnakes differ from randomly chosen (unsuitable) sites in (*i*) orientation, (*ii*) physical structure, and (*iii*) thermal regimes.

Materials and methods

We analyzed the physical features of 11 dens of rattlesnakes in Kittitas and Grant counties, Washington State, USA (46.9°N, 120.5°W), from fall 1998 through summer 1999. Rattlesnake hibernacula in the Pacific Northwest are often located in large rocky talus (basalt) complexes containing steep slopes and sparse vegetative cover (Sehman 1977; Wallace and Diller 2001), and these features have been shown to be good predictors of hibernacula in other rattlesnake species (Browning et al. 2005). We initially located field sites by revisiting historic areas known to contain complexes of snake hibernacula (Brady 1980). We located individual hibernacula by visual search ($n = 7$) or by following snakes that we equipped with radio transmitters ($n = 4$; Reinert and Cundall 1982; Beck 1995). Locations of overwintering sites were verified in spring by the observation of congregations of basking snakes (Fig. 1). Each congregation typically had between 5 and 100 individuals basking on the surface on any given day, usually within a concentrated area of 10 m^2 or less. All den sites used in this study are known to be well-established hibernacula with significant aggregations of individuals (50–500) returning year after year.

After emergence in the spring, snakes spend much of the day basking on the den surface and we determined the location of entrances to hibernacula by observing individuals moving out of hibernacula to bask. When openings leading to a single underground hibernacula could not be located (four sites total), the central area of congregation by the snakes early in the spring (late March to mid-April) was considered the entrance, even though some sites likely had more than one hibernaculum opening. The entrance was then used as the starting point for all measurements.

For comparison, each hibernaculum was paired with a visually similar random site available to snakes but not used as an overwintering den. Random sites were located within 300 m of the actual hibernaculum and were selected by taking a random distance between 10 and 300 m, using a random number table, and a random direction, using the sweep-second hand of a wristwatch. Our selection criteria for random sites additionally stipulated that random sites had to appear visually similar to hibernacula in structure and had to be contained on a talus slope (e.g., random sites could not occur in streams occurring along valley bottoms, flat grassy areas). For each hibernaculum and paired random location, we recorded eight variables that described orientation, slope, and aboveground physical structure (Table 1). We chose variables, in part, based on those used in other studies demonstrating the importance of physical structure and orientation in determining the suitability of hibernacula for other high-latitude snake species (Burger et al. 1988; Prior and Weatherhead 1996; Kingsbury and Coppola 2000; Harvey and Weatherhead 2006).

For some variables we recorded data at two different spatial scales; one that describes the local area directly surrounding the entrance(s), referred to as the minor scale, and a larger scale that described the entire slope containing the hibernacula or random site, referred to as the major scale. Minor-scale measurements were limited to a 1.78 m radius extending from the central hibernaculum or random-site entrance (10 m^2 area), whereas major-scale measurements were made in a 10.0 m radius (314 m^2 area; hereafter referred to as plots). Although measurements at these overlapping scales are not independent, analyzing site characteristics in this way provides a way to separate potential microhabitat differences associated with the hibernacula from those effects associated with the terrain surrounding the hibernacula. To avoid disturbing the snakes unnecessarily, measurements were made during early summer after the majority of the individuals had moved away from the hibernacula. We revisited random sites in the spring to verify that they were not used for hibernation by rattlesnakes; any use would be obvious because of congregating snakes.

Previous studies have suggested that rattlesnake hibernacula frequently occur on south-facing slopes (Nussbaum et al. 1983; Brown 1992; Clark et al. 2008). Because south-facing slopes tend to receive more solar radiation over the winter than north-facing slopes (Gates 1980; Hamilton and Nowak 2009), south-facing slopes may provide warmer overwintering temperatures to snakes. To investigate how thermal properties may influence choice in hibernacula and to explicitly test the thermal effect of slope exposure, we paired temperature logging at two south-facing hibernacula with two north-facing random sites. Data loggers were buried at the surface (in open areas free of vegetation cover) and at depths of 45 and 85 cm below the surface. Data loggers (HOBO® Temp; Onset Computers Corporation, Pocasset, Massachusetts, USA) were enclosed in 250 mL plastic containers (to avoid damage from moisture) and loggers recorded temperature at 1 h intervals from mid-November through March.

Statistical analysis

In nearly every case, data for structural variables failed to meet the assumptions for parametric testing (normally distributed errors, homogeneous between-group variance, etc.), even after attempting data transformations. We therefore used nonparametric Mann–Whitney *U* tests of nontransformed data to compare groups and we followed up comparisons using false discovery rate (FDR) procedures (Benjamini and Hochberg 1995). FDR procedures adjust the *P* values of tests to account for family-wise error rates when conducting multiple comparisons. We additionally used Watson U^2 tests to compare directional aspect and Fisher's exact test to analyze differences in the distribution of mean rock size between groups. To compare repeated measurements of temperature between hibernacula and random sites, we used random effects ANOVA

Fig. 1. Congregation of Northern Pacific Rattlesnakes (*Crotalus oreganus*) at hibernacula. Snakes occupy the hibernaculum for up to 6 months of the year and bask on the surface to regulate body temperature for 3–4 weeks before and after hibernation.

Table 1. Comparison of orientation, slope, and structural variables between hibernacula (n = 11) of Northern Pacific Rattlesnakes (*Crotalus oreganus*) and paired random sites (n = 11).

Variable (units)	Description	Plot scale	Hibernacula	Random sites	Statistic	P
Aspect (°)	Aspect of talus slope containing the plot; measured with compass	Major	183±23	175±110	$U^2 = 0.19$	0.04
		Minor	185±32	162±68	$U^2 = 0.14$	0.15
Slope (°)	Maximum slope of plot; measured with clinometer	Major	56±12	62±7	$U = 33.5$	0.04
		Minor	51±13	53±15	$U = 56.5$	>0.50
Vegetative cover (%)	Percent vegetative cover of plot. Measured by four line-intercept transects extending from center of plot in each cardinal direction	Major	13±17	9±9	$U = 42.5$	0.24
		Minor	7±7	3±5	$U = 38.0$	0.14
Rock volume (cm^3)	Mean of 50 randomly selected surface rocks within a plot; measured as L × W × H of each rock	Minor	7 652 ± 3 507	12 037 ± 18 021	$U = 44.0$	0.28
Refuge depth (cm)	Mean depth of 50 holes or crevices (>10 cm deep) leading to possible refugia or escape route from predation	Minor	20±3	19±7	$U = 45.0$	0.31
Refuge density (no./m)	Number of crevices (≥10 cm deep) leading to possible refugia or an escape route from predation; determined from four transects extending from center of plot in each cardinal direction	Minor	13±3	9±5	$U = 22.0$	0.01
Cover distance (m)	Distance to nearest shrub or tree that could be used for cover	Minor	3.1±2.9	4.2±3.5	$U = 50.5$	>0.50
Cover area (m^2)	Area of nearest shrub or tree cover object	Minor	26±30	81±206	$U = 55.5$	>0.50

Note: Values are means ± 1 SD and P values are corrected for false discovery rate.

(Gillies et al. 2006). Summary statistics are reported as mean ± 1 SD.

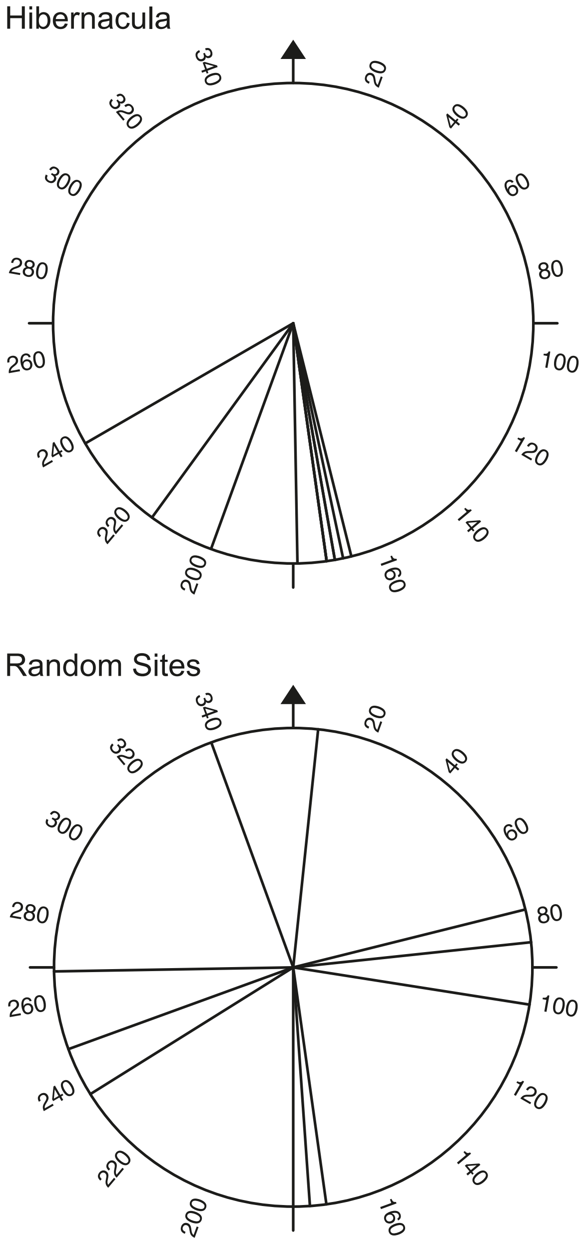
Results

We quantified orientation, slope, and physical structure of 11 hibernacula and paired random sites; data summaries and statistical comparisons are given in Table 1. At the landscape level, hibernacula (major scale) ubiquitously occurred in habitats with south-facing aspects (Fig. 2), whereas the distribution of random-site aspects was essentially random and did not differ from circular uniformity (Rayleigh's $Z = 0.28$; $P = 0.76$). At the scale of the hibernaculum entrance (minor scale), there was no significant difference in aspect between hibernacula and random sites; Watson's $U^2 = 0.14$, $P = 0.15$).

Major slopes of hibernacula were significantly less steep than random sites ($U = 33.5$, $P = 0.04$), but slopes at the minor scale showed no significant difference ($U = 56.5$, $P > 0.50$). Vegetative cover (both major and minor scales), rock volume, refuge depth, cover distance, and cover area all did not differ between hibernacula and random sites ($P > 0.05$ for each; Table 1). However, refuge densities were significantly greater at hibernacula than random sites (Mann–Whitney $U = 22.0$, $P = 0.01$).

Although there was no significant difference in the mean volume of rocks between hibernacula and random sites, the distribution of the means differed (Fisher's exact test, $P = 0.023$; Fig. 3). Mean rock volume of each site was categorized as either small (<7 000 cm^3), medium-sized (7 000 – 15 000 cm^3), or large (>15 000 cm^3). Random sites were

Fig. 2. Directional aspect of hibernacula used by Northern Pacific Rattlesnakes (*Crotalus oreganus*) and randomly occurring sites not used for hibernation. All hibernacula occurred on south-facing slopes, whereas the distribution of random sites did not significantly differ from a uniform circular distribution.



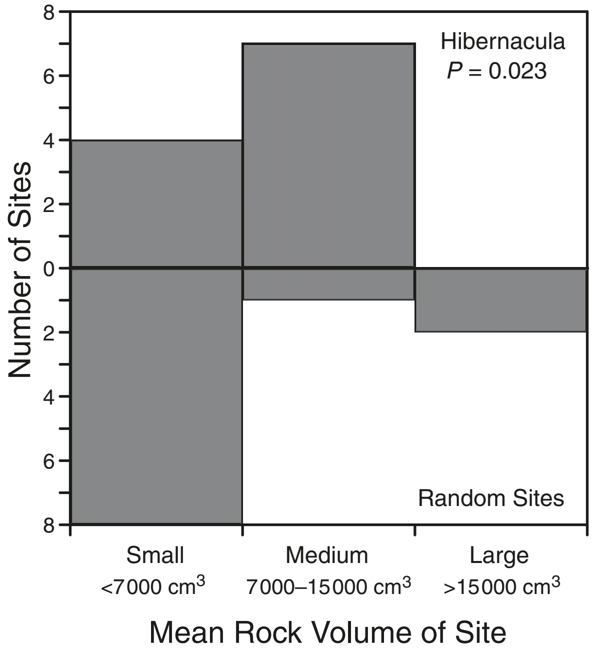
composed mostly of substrata with small and large rock volumes, whereas hibernacula were most commonly composed of intermediate-sized rocks.

On the surface, thermal regimes at south-facing hibernacula were significantly warmer than those of north-facing random sites (Fig. 4; $F_{[1,2]} = 93.6$, $P = 0.01$). Below the surface, temperatures were not significantly different between hibernacula and random sites at both 45 cm below ground ($F_{[1,2]} = 4.2$, $P = 0.18$) or at 85 cm below ground ($F_{[1,2]} = 1.4$, $P = 0.36$).

Discussion

Our data support the hypothesis that Northern Pacific Rattlesnakes use habitat features to choose overwintering hibernacula. Attributes related to site orientation, physical structure, and thermal properties all appear to be important in determining site suitability. Hibernacula are distinguished from random sites by having higher temperatures, south-facing orientations, gentler slopes, and a higher number of potential refuge sites. However, each of these characteristics may dictate site suitability in different ways.

Fig. 3. Distribution of mean rock volumes between hibernacula used by Northern Pacific Rattlesnakes (*Crotalus oreganus*) and randomly occurring sites. Although mean rock size did not differ between groups, the distribution of rocks between the sites was significantly different; hibernacula are primarily composed of medium-sized rocks (7 000 – 15 000 cm^3), whereas random sites were made up mostly of very small rocks and very large boulders.



South-facing slopes tend to receive more solar radiation than north-facing slopes (Gates 1980; Bonan 2002; Geiger et al. 2003), and as a result, temperatures at the surface of hibernacula were higher than surface temperatures of random sites (Fig. 4). However, below the surface, there were no statistically significant differences between temperatures of hibernacula and random sites. This suggests that subsurface thermal regimes, at the depths we measured them, may not be as important of a factor in determining overwintering site suitability than thermal diversity on the surface. At dens monitored in this study, snakes would likely have frozen during the second half of December at 45 and 85 cm below the surface (Fig. 4), and these depths would therefore not be thermally suitable habitat. To avoid lethally cold temperatures, rattlesnakes must move deeper below ground at hibernacula (Macartney et al. 1989), where conditions are more stable. In our region, the frost-free zone on talus slopes is near 1 m below ground, a depth at which rattlesnakes have been observed to hibernate at some of our dens (D. Beck, unpublished data).

Alternatively, rattlesnakes may choose sites on south-facing slopes for hibernacula because the warmer temperatures on the hibernacula surfaces provide increased opportunities for thermoregulation and basking activities relative to random sites. Overwintering Prairie Rattlesnakes (*Crotalus viridis*

Fig. 4. Mean temperature profiles for hibernacula used by Northern Pacific Rattlesnakes (*Crotalus oreganus*) and randomly occurring sites. Hibernacula are significantly warmer than random sites on the surface but not significantly different below ground (45 and 85 cm).

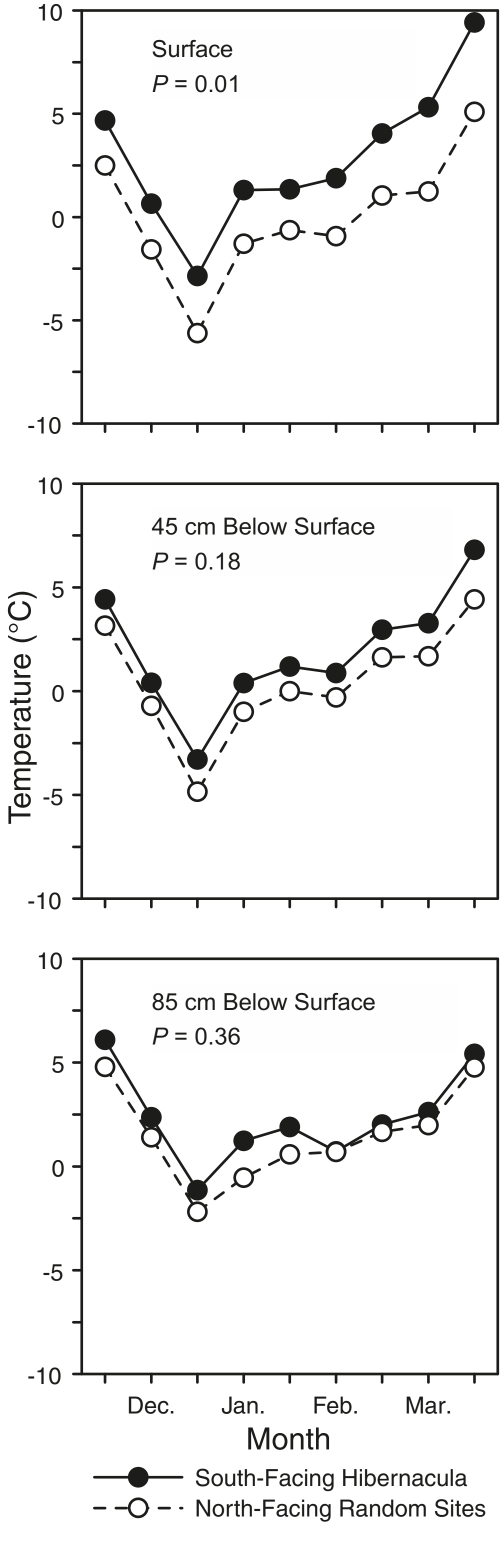
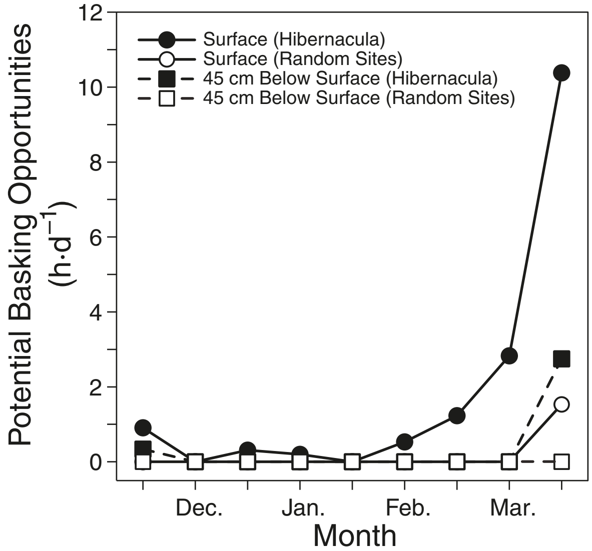


Fig. 5. Potential basking opportunities for Northern Pacific Rattlesnakes (*Crotalus oreganus*) at hibernacula (south-facing slopes) and random sites not used for hibernating (north-facing slopes). During spring emergence from hibernation (mid-March), snakes would be able to bask, on average, for >10 $h \cdot d^{-1}$ on the surfaces of hibernacula but would be able to bask for <2 $h \cdot d^{-1}$ at random sites.



(Rafinesque, 1818)) have been observed active and basking at hibernacula with body temperatures as low as 9–10 °C (Vetas 1951; Woodbury 1954; Jacob and Painter 1980), and basking may be important in helping restore function to quiescent physiological systems (e.g., digestion, reproduction) after 5–6 months of hibernation.

For example, female rattlesnakes emerging from hibernation may bask and regulate body temperature to facilitate ovarian follicle development (Aldridge and Duvall 2002), and once becoming pregnant, females maintain higher body temperatures to incubate developing embryos (Gier et al. 1989; Graves and Duvall 1993; Gardner-Santana and Beaupre 2009). Males disperse away from hibernacula in early spring to establish territories, and basking to achieve higher body temperatures may facilitate earlier or more successful dispersal (Christian and Tracy 1981).

If we assume 10 °C as a minimum temperature at which central Washington rattlesnakes could be active or bask, then during emergence from hibernacula in late March, rattlesnakes would be able to bask for >10 $h \cdot d^{-1}$ at hibernacula but would be limited to basking for <2 $h \cdot d^{-1}$ on north-facing random sites (Fig. 5). Thus, selecting overwintering sites for the thermal opportunities that they provide for snakes in spring may be at least as important as selecting hibernacula for escaping lethal temperatures during winter.

Hibernacula tended also to be located on rocky slopes that were less steep than slopes containing random sites. The angle of repose for talus slopes with rock sizes similar to those measured in this study is around 55° to 56° (Carson 1977), and slopes greater than this would likely experience subsurface shifting and frequent down-slope movement of talus material (Giani 1992). The movement of talus at the surface could make relocating entrances to hibernacula problematic, but more importantly, rocky material eroding and falling down-slope could potentially entomb or crush snakes occupying the site. At random sites, 10 out of 11 major slopes were >55° (mean = 62°), suggesting that nearly all random sites would be structurally too unstable to house aggregations of hibernating snakes.

Slope angle has likely also influenced other physical properties of talus substrate that dictate site suitability for snake hibernation. The distribution of mean rock size at hibernacula and random sites was significantly different, even though mean rock size did not differ (Table 1). Hibernacula tended to consist of medium-sized rocks (1000–2000 cm^3), whereas random sites tended to have a bimodal mix of small rocks (<1000 cm^3) and large boulders (>2000 cm^3; Fig. 3). Sites made up of large boulders would have large interstitial spaces, allowing snow and cold temperatures to penetrate farther below the surfaces (Pérez 1998), whereas sites with small rocks would have tightly packed substrate, potentially preventing snakes from penetrating the surface to belowground chambers. Sites where the mean rock size is intermediate of these extremes, such as hibernacula, may have neither problem, and snakes would be able to pass below the surface while still being protected from moisture and cold temperatures over the winter. This trade-off between thermal conditions and subsurface access has recently been shown to influence the distribution of snake hibernacula even at large scales and across species (Hamilton and Nowak 2009).

The importance of substrate packing in determining suitability of hibernacula is further supported by measurements of refuge density. Hibernacula (medium-sized rocks) have a higher density of refugia in surface basking areas than do random sites (mix of big and small rocks). Our criteria for determining a refuge was that the hole or crevice be ≥10 cm deep, and at this depth snakes would be both partially hidden from predators and still be able to bask and exploit the higher temperatures at the surfaces of hibernacula.

Although we have shown how hibernacula and randomly occurring sites differ in orientation, structural surface features, and thermal regimes, those attributes alone may not completely encompass the cues that Northern Pacific Rattlesnakes use in determining site suitability. In addition to providing critical habitat for overwintering and for thermoregulation in the spring, dens may also provide an important arena for courtship, mating, and parturition (Klauber 1972; Diller and Wallace 1984; Macartney and Gregory 1988; Macartney et al. 1989; Charland and Gregory 1990). The chemical signatures left by these social activities likely play a critical, yet uninvestigated, role in the selection of hibernacula by rattlesnakes. Rattlesnakes thus likely evaluate many other cryptic features of potential overwintering sites that were not investigated here, and our univariate approach only partially addresses the elements involved in the selection of hibernacula. A fruitful future direction would be to explicitly consider a multivariate context to address the interactions of habitat variables (Reinert 1993; Prior and Weatherhead 1996), physiological state (Blouin-Demers and Weatherhead 2001), and individual behavioral decisions (Downes and Shine 1998).

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