

Hibernation and Oviposition Sites of Great Basin Gophersnakes (*Pituophis catenifer deserticola*) near Their Northern Range Limit

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ABSTRACT.—Northern range limits for snakes may result from thermal constraints, especially for oviposition and hibernation. We characterized hibernation and oviposition sites for federally threatened Great Basin Gophersnakes (*Pituophis catenifer deserticola*) near the edge of their northern-range limit in south central British Columbia, Canada. During 2006 and 2007, most Gophersnakes (75.8%) hibernated alone. At our more northern study area, typical hibernation sites were in grassy hillsides, whereas at our southern study areas snakes hibernated in rocky outcrops. All snakes that denned in rock outcrops reused sites over years, but only 28.6% of snakes that hibernated in rodent burrows reused sites. Most female Gophersnakes (94%) laid eggs in sites that were not used by other females, and reuse of sites was rare (12.5%). Almost all of the oviposition sites were in grassy slopes, with any shrubs and trees more than 5 m away; females selected grassy or sage-steppe cover for oviposition. This pattern of mostly individual and single-use hibernation and oviposition sites suggests that hibernation and oviposition sites are readily available as components of the active-season range within the sage-steppe ecozone, although this habitat is rare and severely threatened within Canada. In terms of species conservation, areas of suitable habitat should be protected based on active-season use, rather than by attempting to find hibernation sites supporting large aggregations of snakes. This recommendation is unlike that for Rattlesnakes (*Crotalus* spp.) and Gartersnakes (*Thamnophis* spp.), which often congregate at hibernation sites.

The northern-range edges of temperate snake species are thought to be determined by thermal constraints (Gregory, 2009; Weatherhead et al., 2012). During the active season, snakes adjust temperatures behaviorally via habitat selection and timing of activity (Row and Blouin-Demers, 2006; Kearney et al., 2009; Harvey and Weatherhead, 2010). During hibernation, however, snakes rely on dens that are sufficiently insulated to protect against lethal cold, yet are also cool enough to reduce energetic expenditures and mass loss overwinter (Gibbons and Semlitsch, 1987; Harvey and Weatherhead, 2006; Gienger and Beck, 2011). Similarly, oviparous snakes require nesting sites with thermal properties that enable timely development of the embryos relative to the requirement for neonate snakes to reach hibernacula after hatching (Shine and Bonnet, 2009; Weatherhead and Madsen, 2009). The temperatures experienced by embryos during development affect hatchling survival (Lourdais et al., 2004), fitness, and locomotor performance (Booth, 2006). Indeed, short and cool summers may have driven the higher proportion of viviparous snake species at northern latitudes (Gregory, 2009) because females can thermoregulate actively whereas eggs cannot. The presence of thermally appropriate oviposition sites and hibernation sites likely affects range limits for oviparous species at northern latitudes.

Given this critical importance of thermal attributes for hibernation and oviposition sites, individual snakes in a given region presumably use the same habitat cues when choosing sites. If suitable hibernacula or oviposition sites are scarce on the landscape, it becomes likely that snakes will (a) show site fidelity, and (b) use sites that other snakes use, either conspecifics or individuals of other species. Use of sites by multiple individuals might occur simultaneously (i.e., denning together overwinter) or with time separation (i.e., multiple females laying eggs in an area at different times). Snakes selectively use sites with evidence of past successful hatching (Brown and Shine, 2005), and oviposition site fidelity may be more prevalent in communal nests than in single nests (Blouin-

Demers et al., 2004), both of which suggest that aggregation of oviposition sites may be common. Similarly, if hibernation sites are relatively scarce, it becomes more likely that snakes will both reuse sites and den with other snakes (Harvey and Weatherhead, 2006; Gienger and Beck, 2011).

Understanding snakes' use of oviposition and hibernation sites is also important for management and conservation, because snake movements are critically linked to the distribution of these sites within a landscape. In cases where either (or both) oviposition or hibernation sites are aggregated, many snakes will use these specific sites, then disperse for foraging. Specific habitat can be protected when such aggregations occur (e.g., British Columbia's Wildlife Habitat Areas protect areas around identified multisnake hibernacula; Williams et al., 2012), but aggregated oviposition or hibernation sites may challenge local population persistence if environmental disturbances or human activities damage these sites. Scattered oviposition or hibernation sites are more difficult to identify and manage.

There are thus critical ecological and conservation needs for understanding oviposition and hibernation sites for northern populations of snakes. The Great Basin Gophersnake (*Pituophis catenifer deserticola*; snake names follow Crother, 2012) is federally listed in Canada as Threatened (Committee on the Status of Endangered Wildlife in Canada [COSEWIC], 2002, 2013), and British Columbia (BC) has designated a number of Wildlife Habitat Areas around known hibernacula to help protect the species; the Provincial Recovery Strategy (Southern Interior Reptile and Amphibian Recovery Team, 2008) identifies information about habitats at oviposition and hibernation sites as well as the site fidelity that the Gophersnakes exhibit as knowledge gaps. The distribution of Great Basin Gophersnakes spans California and Arizona northwards into British Columbia's interior river valleys. In British Columbia, Shewchuk (1996) identified three hibernation sites in rock features, two of which were communal. Bertram et al. (2001) found three single hibernation sites that were associated with tunnels underground. Seven Great Basin Gophersnake oviposition sites in BC were on south-facing grassy hillsides of moderate slope, with fine, sandy soils (Shewchuk, 1996; Bertram et al., 2001). Shewchuk (1996) documented a few Gophersnake oviposition

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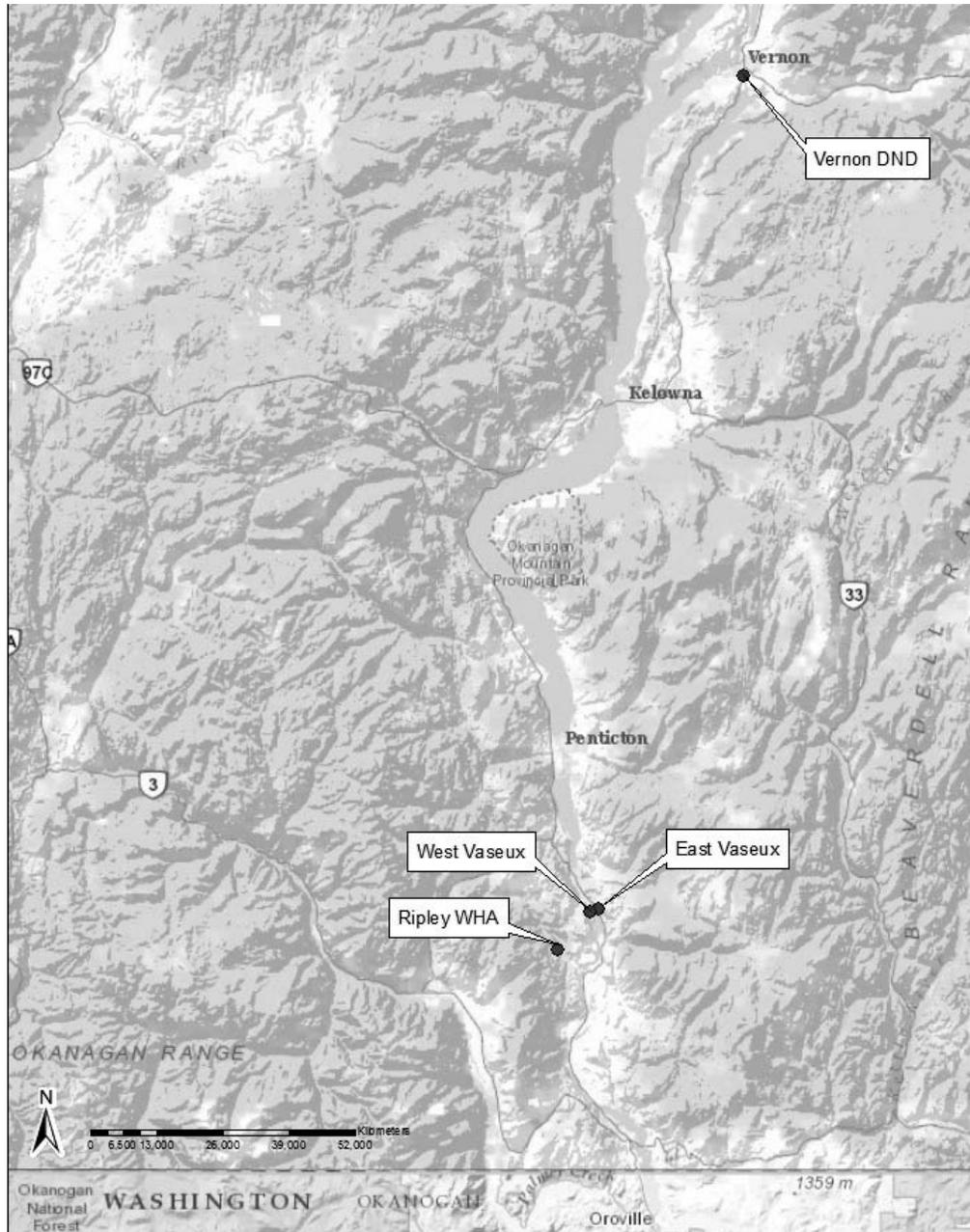


FIG. 1. The location of the study areas within south-central British Columbia, Canada.

sites that contained eggs of multiple individuals and snake species. Thus our understanding of oviposition and hibernation sites for this species is limited by small sample sizes from the few study populations these studies observed.

We characterize hibernation and oviposition sites of Great Basin Gophersnakes on four study areas near their northern range edge, in the Okanagan Valley of south-central BC. Our specific goals are to characterize both oviposition and hibernation sites with respect to 1) fidelity of snakes to these sites; 2) the proportion of sites used by single snakes, multiple conspecifics, or multispecies assemblages; and 3) aboveground habitat attributes around sites. We examined the likely thermal attributes of oviposition sites by recording temperatures at sites similar to observed oviposition sites. Given the scarcity of information on hibernation and oviposition sites for this subspecies, it is unknown what spatial scales of habitat

description are most relevant. We therefore sampled habitat variables at different spatial scales around each site to offer a baseline portrait of habitats at hibernation and oviposition sites.

MATERIALS AND METHODS

Four study areas were selected in British Columbia's Okanagan Valley (Fig. 1). Three sites were located in the southern Okanagan and one in the north. The northern site (Vernon) was roughly 140 km north of the southern study areas, but all four sites are within the northern range periphery of the species. Vaseux-Bighorn National Wildlife Area in the south Okanagan is owned by the Canadian Wildlife Service, and contained two sites, one on either side of Vaseux Lake. East Vaseux is a 40-ha site composed of a rocky bluff with grassy hills beside Vaseux Lake and Highway 97 (the primary highway

running north–south in the Okanagan), and West Vaseux is a 90-ha area composed of open ponderosa pine (*Pinus ponderosa*) forests, antelope brush (*Purshia tridentata*) meadows, talus slopes, rock faces, and wetlands at a lake edge. Ripley Wildlife Habitat Area (WHA) in the south Okanagan is designated around a protected snake hibernaculum, but the province does not release exact boundaries or areas of these WHAs, to prevent vandalism or destruction of hibernacula. At this site, we worked primarily in an area we knew to be just outside the WHA, consisting of 50 ha of mixed federal and private land. The dominant vegetation was grassland, open ponderosa pine forests, and exposed rock features; it was adjacent to several houses with nearby discarded automobiles and lumber piles that acted as refuges for Great Basin Gophersnakes. In the north Okanagan, the Vernon Department of National Defence site is 120 ha located on the Vernon Army Camp Grounds; the area was composed of highly disturbed and invaded grasslands, with infrequent shrubs and rock outcrops.

Field Methods.—Great Basin Gophersnakes were captured opportunistically through active searching on all sites (Williams et al., in press). Adult Gophersnakes (17 females, 22 males), mass ≥ 240 g, were surgically implanted with radio-transmitters (modified protocol from Reinert and Cundall, 1982; 12-g transmitter consisting of less than 5% of body mass; Holohil Systems Ltd., Ontario, Canada) between April and June of 2006 and 2007; remaining transmitters were removed at the completion of the study in April 2008. For all snakes, Metacam® (meloxicam 0.1 mg/kg) and Baytril® (enrofloxacin 5 mg/kg) were injected intramuscularly 24 h preceding surgery, at surgery, and 24 h postsurgery to reduce pain and swelling. Following a 24–48-h recovery period, each transmitter-equipped Gopher-snake was released at its location of capture.

Each transmitted snake was relocated approximately every second day throughout the active season (late March through mid-October). Tracking was typically between 0700 and 1900 hours. Homing techniques were used to relocate individuals, with the infrequent exception (< 5% of the time) of using triangulation methods when snakes were located in wetland or rock features that did not permit direct access. Snakes were often underground, but the signal was detectable from the receiver alone without a cable or antenna, thus indicating high accuracy of the location. Upon location of the individual, a GPS location was recorded (Garmin Map76S, accuracy of < 5 m).

Oviposition sites were identified from tracking records and the confirmation of oviposition derived from observations of the female (emaciation, skin folds). To determine oviposition site fidelity, we recorded site data for females tracked in both 2006 and 2007. Similarly, we judged that snakes showed fidelity to hibernation sites if they used sites in two winters that were within 10 m (surface distance) of each other. For all oviposition and hibernation sites, we recorded whether we observed other snakes at the sites. Because Great Basin Gophersnakes are federally threatened, we could not excavate oviposition or hibernation sites, and we may have underestimated the use of these features by more than one snake.

Habitat at Oviposition and Hibernation Sites.—With the use of aerial photographs and extensive ground-truthing, we first classified habitat at each site into one of six general habitat types: rocky outcrop, forest, wetland, grassland, shrub-steppe, and human modified. Human-modified habitats were areas that showed human disturbance, including roads and road edges as well as buildings and associated debris piles. Each hibernation

site and oviposition site was also classified into one of these six categories.

We then collected more specific habitat data at the hibernation and oviposition sites of each Great Basin Gophersnake, using variables common in other studies (Burger and Zappalorti, 1986; Burger et al., 1988; Bertram et al., 2001; Harvey and Weatherhead, 2006). Specifically, within 5 m of each site, we recorded the dominant habitat type, slope, and aspect. We recorded the maximum droop height of vegetation at each hibernation or oviposition site and the number of woody stems within a 1-m radius. Within this 1-m radius, we also recorded the percent ground cover composed of rock, soil, vegetation, and coarse woody debris. Within circles of 10-m radius, we recorded the number of shrubs < 2 m tall, number of trees > 2 m tall, number of fallen logs > 7.5 cm diameter, and number of rocks > 20 cm (we also collected these data in circles of 5-m radius; data were qualitatively similar and are not shown here). Finally, we calculated distances (if present within a 30 m radius) to the nearest log > 7.5-cm maximum diameter, tree > 2 m tall, shrub < 2 m tall, and rock > 20 cm in diameter.

To characterize the soil in which Great Basin Gophersnakes oviposited, we collected soil samples (> 17 g) from all oviposition sites used by transmitter-equipped snakes. To compare soils at oviposition sites to available but nonused sites, at each of the four study areas we collected soil samples at 10 random locations on south-facing slopes of moderate grade and comparable vegetative cover to determine if oviposition sites had different soil qualities than at available, but nonused sites. We conducted soil texture tests (Miller et al., 1996), and used a 2-mm mesh sieve (separates fine particles from gravel, Hubbard Scientific Co., Northbrook, Illinois) and balance (Mettler Toledo, Switzerland) to determine percent particle size by mass.

Temperatures at Simulated Oviposition Sites.—Temperature during incubation is maintained from solar heating of the ground around the eggs. As latitude increases, it may be necessary for female snakes to use steeper slopes to obtain the same amount of thermal units for incubation. In 2006, oviposition sites on different study areas had different slopes: slopes were steeper at our northern site ($43 \pm 3^\circ$, mean ± 1 SE) than in the southern sites ($32 \pm 1^\circ$). In 2007, we tested whether different slopes resulted in different soil temperatures. With the use of oviposition sites identified through telemetry during 2006, we determined the average aspect (157°) of these sites. Based on observations of some sites where eggs were visible from the tunnel mouth as well as two sites where eggs had been preyed upon, we assumed laying depth was 5–10 cm. We placed iButtons (calibrated and programmed with the use of a Dallas Semi Conductor 32-bit iButton viewer) at this depth and aspect, to record temperature every 2 h from the beginning of nesting season to the end of incubation. We used the two study areas at which we had the most females and the most nests from 2006, East Vaseux and Vernon, and we selected seven locations (at least 200 m apart) at each study site. At each replicate location we placed three iButtons, where local slopes were 32° , 39° , and 46° , which were based on the range of slopes at which Great Basin Gophersnakes oviposited in 2006. The site characteristics of these locations were similar to 2006 oviposition sites for aspect, soil type, soil texture, percent vegetative cover, and dominant vegetation type. We used the daily maximum temperature during the incubation period for each iButton as our temperature variable for analysis.

Statistical Analysis.—Spatial data were imported into ArcView v. 3.2 with Spatial Analyst (Environmental Systems Research

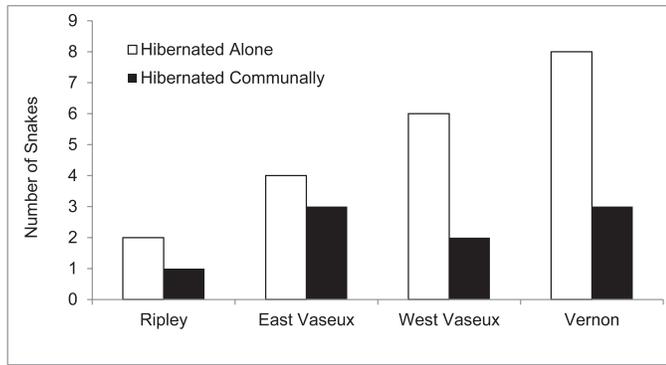


FIG. 2. Number of Great Basin Gophersnakes occupying communal and single hibernation sites in 2006 or 2007 by study area in the Okanagan Valley, British Columbia. Only one snake, from Vernon, used both a communal hibernation site and a single hibernation site—this snake was recorded on this graph only once, as belonging to a communal hibernation site.

Institute, 1999), and analyzed using several extensions, primarily the Animal Movement Analysis Extension (Hooge and Eichenlaub, 1997). Statistical analyses were performed in Microsoft Excel 2003 and 2008 with the Poptools add-in (Hood, 2000), and SPSS 12.0 and 16.0 for Windows (SPSS 2003, 2007). Aspect data were analyzed using circular statistics and the Watson-Williams test (Zar, 1984).

We compared the general habitat type of oviposition sites and hibernation sites to habitat availability by using Manly's alpha (Krebs, 1999):

$$\alpha_i = \frac{r_i}{n_i} \times \frac{1}{\sum r_j/n_j}$$

Here α_i is the preference for habitat type i , r_i and r_j are the proportions of habitats i and j used ($i, j = 1, 2, \dots, m$ types available), and n_i and n_j are the proportion of each habitat type available. Values of α sum to 1.0 and preference is indicated when $\alpha_i > 1/m$, with more preference indicated by higher values; similarly, avoidance is indicated for $\alpha_i < 1/m$. We also used Manly's alpha to assess whether female Great Basin Gophersnakes selected certain soil textures.

For more specific details of microhabitats directly around hibernation and oviposition sites, we used ANOVA to test whether there were differences by study area. For some variables, we used χ^2 tests or t tests to compare the three southern sites to the one northern site, to accommodate different sample sizes among sites or categories with < 5 observations. For the iButton temperature data, we compared study areas and slopes in a two-way repeated-measures ANOVA. We accepted statistical significance at the nominal level of $P < 0.05$.

RESULTS

Hibernation.—Of 39 radio-implanted Great Basin Gophersnakes, 12 were tracked to hibernation sites in both fall 2006 and 2007. Seven of the 12 (58.3%) reused the same hibernation site. There was a study-area difference in fidelity, as five of five snakes (100%) from the three southern sites reused their hibernation sites, whereas only two of seven snakes (28.6%) at the Vernon site in the north showed fidelity ($\chi^2 = 4.98$, $P = 0.026$).

Twenty Great Basin Gophersnakes hibernated singly, eight hibernated with at least one other snake (Gophersnake or other species), and one snake switched from a communal den in 2006 to a single den in 2007 (Fig. 2). In our southern study areas, 6 of 18 snakes hibernated communally (33%), whereas at the northern site (Vernon) 2 of 10 snakes did (20%; $\chi^2 = 0.097$, $P = 0.76$). In the south Okanagan study areas, other snakes sharing the hibernacula included Western Yellow-Bellied Racers (*Coluber constrictor mormon*), Western Rattlesnakes (*Crotalus oreganus oreganus*), Western Gartersnakes (*Thamnophis elegans*), and Common Gartersnakes (*Thamnophis sirtalis*). At Vernon, three Gophersnakes used dens that were used by other Gophersnakes or Yellow-Bellied Racers. Including Gophersnakes that switched hibernation sites between years, we found 8 communal hibernation sites and 25 single sites (24.2% of dens were communal).

Specific features of aboveground habitat at hibernation sites differed between study areas in the south compared to the north (Table 1). In the three southern areas, hibernation sites were located in rock outcrops, associated with either a talus slide or a fissured rock feature. Slopes were $28.4 \pm 2.1^\circ$ on average. Trees were typically found within 10 m. Rock was the primary ground cover within 1 m (averaging 48.3–85.0% at the three study southern areas), although at Ripley vegetation was also a common ground cover (33.3%). In contrast, at the northern Vernon study area, hibernation sites were located in much shallower slopes ($17.9 \pm 3.0^\circ$) accessed via rodent tunnels, although occasionally an emergent rock provided access below ground. The aspect varied among sites, with snakes at West Vaseux (in the south) having an average aspect of $215.2 \pm 22.6^\circ$ (mean \pm angular deviation), whereas snakes at the northern site and the other two southern sites averaged between 82.3 and 145.9° . Few trees or shrubs were located near the hibernation sites, and vegetation (mainly grass) and exposed soil were the dominant ground covers.

In the three southern study areas, all hibernation sites of Great Basin Gophersnakes had > 100 rocks (of > 10 cm diameter) within 10 m of the hibernation site. At Vernon, 5 hibernation sites had > 100 rocks, but the remaining 11 hibernation sites had anywhere from 0 to 42 rocks within 10 m ($\chi^2 = 16.0$, $P < 0.001$). Shrub density within 10 m of each hibernation site also varied: In the southern study areas, 14 of 19 hibernation sites had > 100 shrubs, whereas at Vernon only 4 of 16 hibernation sites had shrub densities that high ($\chi^2 = 6.41$, $P = 0.001$). Hibernation sites at Vernon were significantly less likely than at the southern study areas to have trees or logs within 30 m (trees $\chi^2 = 12.85$, $P < 0.001$; logs $\chi^2 = 4.64$, $P = 0.031$). When these features were present, they were about twice as far away at Vernon as at the southern study areas (Table 1). Almost all hibernation sites in all study areas had shrubs present within 30 m, but at Vernon shrubs were much further away (on average over 11 m compared to < 3.2 m).

Oviposition.—We observed five Great Basin Gophersnakes that oviposited in both 2006 and 2007 (Williams et al., in press). Only one female reused a nest site. Of the 16 unique oviposition sites we observed, we had 1 site for which egg shells laid in a previous year were excavated by the female. In 2006, all nine female Gophersnakes laid their eggs in single nests; in 2007, seven females laid singly, but one female laid in a nest where we observed two other nontransmitted Gophersnakes. Of the observed nests 6.25% were communal and 12.5% were reused between years.

TABLE 1. Habitat and physical attributes at hibernation sites for Great Basin Gophersnakes in the Okanagan Valley, British Columbia. Snakes were tracked in 2006 and 2007 (total $n = 35$) and values are means \pm 1 SE. Statistics are from ANOVAs comparing characteristics among sites. Vernon is the more northern site and the other three are in the south Okanagan. Some sample sizes are given when sites lacked a particular habitat feature.

	East Vaseux ($n = 8$)	West Vaseux ($n = 8$)	Ripley ($n = 3$)	Vernon ($n = 16$)	F	P
Slope	28.4 \pm 3.1	28.8 \pm 4.1	27.7 \pm 1.5	17.9 \pm 3.0	2.74	0.060
Aspect ^a	215.2 \pm 22.6	97.8 \pm 32.6	145.9 \pm 51.9	82.3 \pm 56.9	11.65 ^a	< 0.001
Maximum droop height (cm) of vegetation at plot centre	24.3 \pm 5.2 ($n = 4$)	38.7 \pm 8.4 ($n = 3$)	22.0 \pm 6.0 ($n = 2$)	22.6 \pm 3.3 ($n = 12$)	0.16	0.920
Number of woody stems within 1-m radius	2.0 \pm 0.8	3.8 \pm 2.4	10.0 \pm 10.0	0.7 \pm 0.7	2.26	0.101
Number of trees > 2 m tall within 10-m radius	4.1 \pm 1.3	12.6 \pm 2.5	28.7 \pm 24.3	0.5 \pm 0.3	6.18	0.002
Number of logs > 7.5 cm diameter within 10-m radius	4.3 \pm 1.2	18.3 \pm 7.1	9.0 \pm 8.5	0.5 \pm 0.3	5.36	0.004
Nearest distance (m) to feature (if within 30 m)						
Log > 7.5-cm diameter	4.7 \pm 0.8 ($n = 7$)	2.8 \pm 0.7 ($n = 7$)	3.4 \pm 2.1 ($n = 2$)	9.4 \pm 1.6 ($n = 7$)	4.24	0.013
Tree > 2 m tall	6.7 \pm 1.7 ($n = 7$)	2.7 \pm 0.7	4.8 \pm 2.3	8.7 \pm 2.2 ($n = 5$)	12.05	0.000
Shrub < 2 m tall	1.8 \pm 0.8	3.2 \pm 0.9	0.8 \pm 0.5	11.1 \pm 2.0 ($n = 15$)	6.50	0.002
Rock > 20-cm diameter	0.0 \pm 0.0	0.0 \pm 0.0	0.4 \pm 0.1	3.7 \pm 1.3	2.85	0.054
Percent ground cover within 1-m radius						
Rock	85.0 \pm 3.8	73.1 \pm 3.9	48.3 \pm 24.0	5.9 \pm 2.9	49.05	0.000
Coarse woody debris	0.0 \pm 0.0	3.8 \pm 2.1	1.7 \pm 1.7	0.0 \pm 0.0	3.49	0.027
Vegetation	9.3 \pm 3.1	16.9 \pm 4.9	33.3 \pm 15.9	72.2 \pm 9.0	11.86	0.000
Exposed soil	5.7 \pm 2.1	6.3 \pm 2.5	16.7 \pm 14.2	21.9 \pm 6.9	1.41	0.259

^a Aspect data were analyzed with the Watson-Williams test for angular data. Values are means and angular deviation.

Habitat characteristics of oviposition sites were averaged for the three study areas in the south and compared with those at the northern site due to the low number ($n = 9$) of southern oviposition sites observed (Table 2). All nest sites were in old rodent burrows except for one instance where a snake oviposited under a lone rock; this was the snake that reused her nest site. Oviposition sites were found on grassy slopes on south-facing hills, with slopes in the north significantly steeper ($42.7 \pm 1.2^\circ$) than those in the south ($32.4 \pm 0.3^\circ$). In most cases in both regions, shrubs, trees, and logs were > 5 m away from the oviposition sites; indeed, nests at the northern site did not have logs or trees within 10 m, but southern nest sites had a few. In all study areas, rocks were typically within 3.5 m or less of oviposition sites. Vegetation (mostly grass) and exposed soil were the dominant ground covers within 1 m of the nests. In the north, cheatgrass (*Bromus tectorum*) and dead tumbled mustard (*Sisymbrium* spp.) dominated the groundcover near nests, whereas in the south sand dropseed (*Sporobolus cryptandrus*) was the dominant plant cover.

Soils were statistically similar across all four study areas (data not shown) and therefore data were lumped across all four areas for the soils analysis presented here. On average, soils were $74.4 \pm 2.6\%$ composed of particles < 2 mm. Oviposition sites of Great Basin Gophersnakes averaged $71.4 \pm 3.0\%$ small particles and did not differ from the available soils ($t = 0.66$, $P = 0.51$). We collected soil texture data only in 2007. In these Okanagan Valley study areas, Gophersnakes selected three of the seven available soil types (Fig. 3). Sandy loam was relatively rare on the landscape (3 of 40 random samples), but 2 of 8 oviposition sites were in this soil type, resulting in a Manly's α value of 0.44 (well above the selection threshold of 0.14). Loamy sand and silty loam were also selected, whereas loam, silty clay loam, clay loam, and sand were avoided.

At a depth of 5–10 cm, which was consistent with observed nest depth at several of the 2006 nest sites, temperatures in the north were cooler than those in the south – the mean hourly temperatures in the north for all slopes was 24°C , while in the south it was 27°C . Although the northern study area was significantly cooler in daily maximum temperature (Fig. 4, ANOVA, $F_{1,2769} = 1003.14$, $P < 0.001$), there was no difference in temperatures among different slopes within each site (ANOVA, $F_{2,2769} = 0.56$, $P = 0.574$).

Habitat Type Selection.—Great Basin Gophersnakes showed strong selection for the general habitat type for both hibernation sites and oviposition sites (Table 3). Specifically, Gophersnakes strongly preferred to hibernate in rock features, especially in the southern study areas. At Vernon, our northern study area, rocky outcrops were quite rare. On this study area, most snakes hibernated in grassland or shrub-steppe, but the Manly's alpha selection index showed they strongly avoided grassland as a choice and used shrub-steppe nearly in proportion to its availability. Human-modified habitats were selected strongly relative to their availability because three snakes hibernated in steep human-modified rocky slopes associated with roads and a parking lot near a building on this site, although the footprint of this human-modified area was only 3.2% of the total area.

Great Basin Gophersnakes laid eggs almost exclusively in grassland or sage-steppe habitats at all study areas, with the exception of one snake that oviposited in a fine-soiled area within the human-modified habitat at the northern study area. Again, the selection index at this site shows strong preference for this habitat type for oviposition, as a result of the rarity of this habitat type coupled with the low sample size.

TABLE 2. Habitat and physical attributes at oviposition sites of Great Basin Gophersnakes during 2006 and 2007. We combined data from three southern study areas to compare to the northern study area (Vernon) and used *t*-tests to compare regions, but all of our study sites are in the northern range periphery for this species. Values are means \pm SE. Sample sizes are reduced for variables examining nearest distance to certain features if the feature was not present within 30 m; when sample sizes were below 5, statistical tests were not performed.

	Southern areas (<i>n</i> = 9)	Northern area (<i>n</i> = 7)	<i>t</i>	<i>P</i>
Slope	32.4 \pm 0.3	42.7 \pm 1.2	-2.47	0.027
Aspect ^a	170.0 \pm 29.4	143.3 \pm 23.7	3.21 ^a	0.095
Nearest distance (m) to feature (if within 30 m)				
Log > 7.5-cm diameter	6.6 \pm 1.4 (<i>n</i> = 4)	10.1 (<i>n</i> = 1)	—	—
Tree > 2 m tall	6.4 \pm 1.3 (<i>n</i> = 4)	16.2 (<i>n</i> = 1)	—	—
Shrub < 2 m tall	5.3 \pm 1.5 (<i>n</i> = 7)	8.6 \pm 1.2 (<i>n</i> = 6)	-0.13	0.895
Rock > 20-cm diameter	2.4 \pm 1.5 (<i>n</i> = 8)	3.3 \pm 1.0	0.64	0.530
% ground cover within 1-m radius				
Rock	4.0 \pm 2.2	0.0 \pm 0.0	1.71	0.109
Vegetation	51.0 \pm 7.4	50.0 \pm 9.4	0.09	0.927
Exposed soil	45.0 \pm 7.6	50.0 \pm 9.4	-0.46	0.650
Number within 10-m radius				
Shrubs < 2 m tall	19.0 \pm 10.6	6.3 \pm 5.6	0.97	0.348
Trees > 2 m tall	1.8 \pm 1.0	0.0 \pm 0.0	1.96	0.071
Logs > 7.5-cm diameter	7.8 \pm 3.1	0.0 \pm 0.0	2.18	0.047
Rocks > 20-cm diameter	66.8 \pm 13.6	32.1 \pm 10.1	1.94	0.073

^a Aspect data were analyzed with the Watson-Williams test for angular data. Values are means and angular deviation.

DISCUSSION

Great Basin Gophersnakes near the edge of their northern range limit in south-central British Columbia do not appear to be limited by either oviposition sites or hibernation sites within protected reserves of sage-steppe habitat. If hibernation or oviposition sites were limiting, snakes should show substantial site fidelity and many snakes should use the same sites. Instead, Gophersnakes reused 58% of hibernation sites and 12.5% of oviposition sites, and most snakes oviposited and hibernated alone. These results vary with study area: At the northern study area, Gophersnakes showed less site fidelity and less communal use of oviposition or hibernation sites than did Gophersnakes in the three southern study areas. The northern site was also slightly cooler than the southern areas (Environment Canada, www.weatheroffice.gc.ca). This varia-

tion in local habitat coupled with the differing behavior by snakes suggests oviposition and hibernation sites may be more limiting in the south than in the north of the Okanagan valley. This pattern also highlights that Gophersnakes use a range of habitats for these critical events. These results pertain to microhabitat availability and selection within protected sage-steppe habitat: The entire Okanagan Valley has undergone substantial habitat conversion, including human settlements, roads, and agricultural development (Cristine and Kerr, 2011), and the severe loss of sage-steppe habitat is a contributor to the listing of this species as threatened in Canada (COSEWIC, 2002, 2013).

Great Basin Gophersnakes selected rocky areas for hibernation. At our southern sites, this selection occurred even with the substantial rock outcrops and cliffs that made rocky sites highly available, as almost all snakes hibernated within these rock

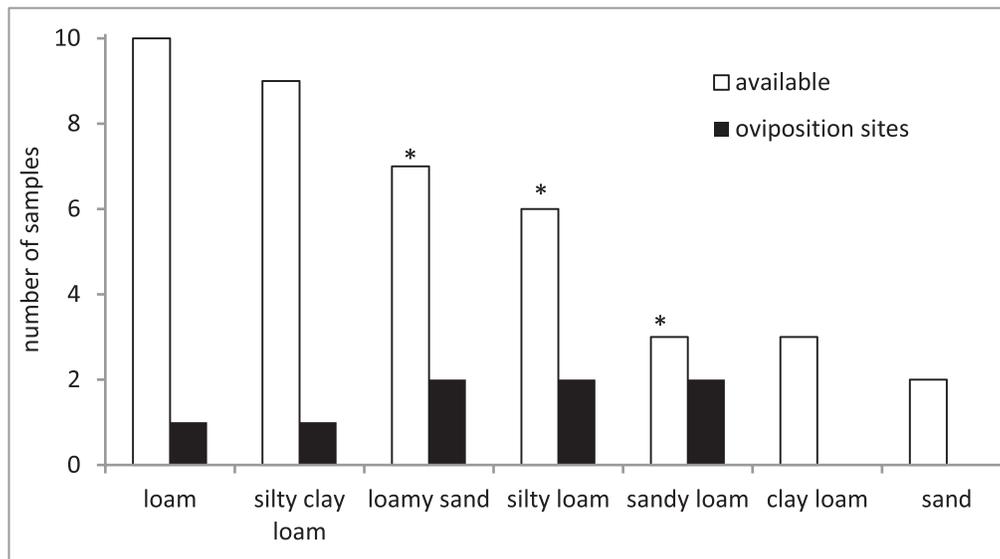


FIG. 3. Soil textures at oviposition sites of Great Basin Gophersnakes and available at the study areas. We sampled 40 random soil sites to determine availability, and in 2007 we assessed soil textures at eight oviposition sites. The asterisks indicate soil types that female Gophersnakes selected (Manly's $\alpha = 0.19$ for loamy sand, 0.22 for silty loam, and 0.44 for sandy loam; the threshold for selection is 0.14); the other four soil types were avoided.

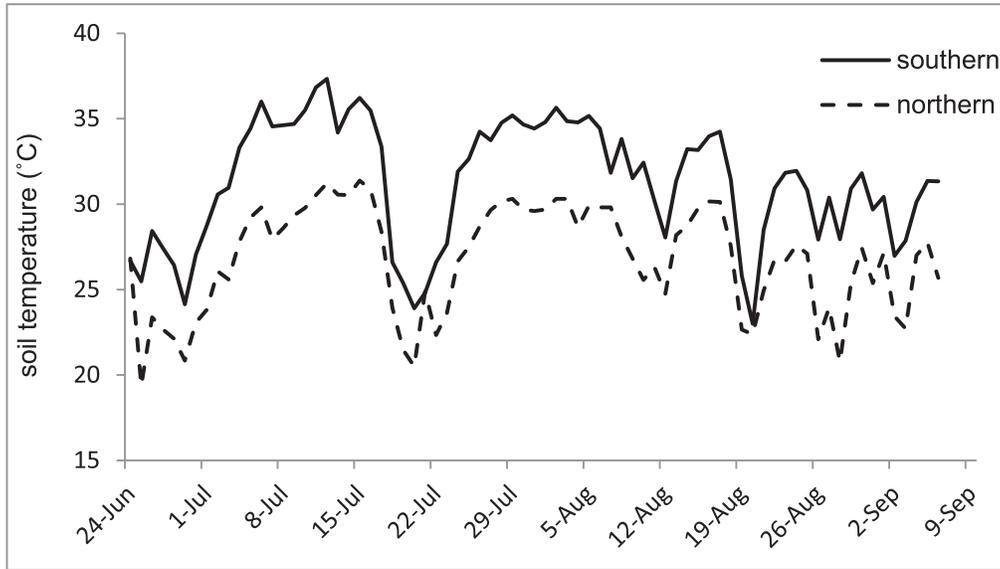


FIG. 4. Average maximum daily temperature 5–10 cm deep in soil. Values are averages from three different slopes in the south (Vaseux) and north (Vernon) Okanagan during the incubation period for Gophersnakes from late June to early September 2007. We did not track hatching dates, but the average incubation period was 73–74 d at a site slightly further south (Shewchuk, 1996). The median lay date of telemetry-equipped Great Basin Gophersnakes in 2007 was June 24; thus that was the start date for these 75 d of data.

features. The northern study area was essentially a wide grassy slope with few rock outcroppings, and here 3 of 16 observed hibernation sites were in human-created rocky slopes associated with a raised parking lot; another 2 hibernacula were located in the rare rock outcroppings.

In terms of aboveground habitat, we again observed strong differences in what Great Basin Gophersnakes used between southern and northern study areas. In the northern study area, Gophersnakes oviposited and hibernated belowground under the typical vegetation of the area: trees and shrubs were scarce,

rocks less common than in the south, and most of the aboveground cover consisted of bare soil or vegetation (mostly grass). In the southern study areas, Gophersnakes hibernated in the abundant rock features, but oviposited in grassy areas that were similar to those observed in the northern area. This pattern suggests that habitat attributes required for oviposition are more constrained than for hibernation in this species. Indeed, snakes at our northern site had hibernation sites closer to their range centers (Williams et al., 2012), suggesting hibernation sites were more available. Female snakes at the West Vaseux study

TABLE 3. Habitat selection by Great Basin Gophersnakes for hibernation and oviposition sites. The Vernon site is in the north and the other three sites are in the south Okanagan valley. Although we considered six general habitat types, no study area had all six types; only categories that were present at a site are shown. The α refers to Manly's alpha; values in bold indicate preference for a habitat type, values in italics show avoidance of a habitat type, values in roman type indicate use was close to availability, and 0 indicates complete avoidance. For East Vaseux and West Vaseux, the critical value of α is 0.20 (= 1/5 habitat types available), and for Ripley and Vernon it is 0.25 (= 1/4 habitat types available).

Habitat type	Available %	Hibernation sites	Hibernation α	Oviposition sites	Oviposition α
East Vaseux					
Rock outcrop	25	7	1	0	0
Grassland	20.9	0	0	3	0.75
Shrub-steppe	42.3	0	0	2	0.25
Human-modified	6.9	0	0	0	0
Wetland	4.8	0	0	0	0
West Vaseux					
Rock outcrop	14.7	7	0.94	0	0
Grassland/meadow	3.1	0	0	0	0
Shrub-steppe	31	1	<i>0.06</i>	3	1
Wetland	20.7	0	0	0	0
Forest	30.5	0	0	0	0
Ripley					
Rock outcrop	13.7	3	1	0	— ^a
Grassland/meadow	15.2	0	0	0	— ^a
Shrub-steppe	67.2	0	0	1	— ^a
Human-modified	3.9	0	0	0	— ^a
Vernon					
Rock outcrop	4.4	2	0.24	0	0
Grassland	81	6	<i>0.04</i>	5	<i>0.13</i>
Shrub-steppe	11.4	5	0.23	1	<i>0.19</i>
Human-modified	3.2	3	0.49	1	0.68

^a Manly's alpha was not calculated for oviposition sites on Ripley because we had only one site.

area traveled much further between hibernation and oviposition sites (on average 490 m in contrast to an average of 160 m at the other study areas, Williams et al., 2012). This particular study area was long and narrow because it was pinched between a cliff and a lake, which may have contributed to greater movements between suitable sites.

Hibernation Sites.—Lack of suitable hibernation sites may contribute to the formation of northern range limits for snakes (Gregory, 2009; Martino et al., 2012). For our populations of Great Basin Gophersnakes, this hypothesis does not appear to be supported. Gophersnakes made use of a number of single-occupant sites, including both rodent burrows and crevices amid rocky slopes, with many hibernation sites scattered throughout areas used during the active season. This pattern is akin to the hibernation sites observed for Massasaugas (*Sistrurus catenatus catenatus*) in southern Ontario; these snakes also used a variety of den sites (rodent burrows, crevices in rock piles, and root systems of trees) located throughout their active season ranges (Harvey and Weatherhead, 2006). In contrast, Northern Pacific Rattlesnakes (*Crotalus oreganus*) in northern Washington aggregate at locally uncommon rocky sites with suitable thermal and structural properties (Gienger and Beck, 2011) as do Common Gartersnakes in the Northwest Territories (Larsen and Gregory, 1989).

These disparate patterns in aggregated hibernation among species and regions may arise from the availability of suitable den sites, such that snakes in areas with abundant possible hibernation sites often hibernate alone and seldom reuse sites; alternatively, these patterns may reflect differences in snake biology with some species typically aggregating and others typically not doing so, no matter what the local habitat features are. We think the latter idea is more likely, as many species of Gartersnakes and Rattlesnakes hibernate communally throughout their geographic ranges (Gregory, 2009), whereas *Pituophis* species tend towards solitary hibernation (Burger et al., 1988; Rudolph et al., 2007). We did not find evidence for the idea that hibernation sites were limiting for Great Basin Gophersnakes near their northern range margin in BC; most Gophersnakes hibernated alone and they had high overwinter survival (Williams et al., in press).

These results also highlight the importance of understanding local habitat availability when managing Great Basin Gophersnake populations. At the northern study area, Gophersnakes typically hibernated singly in underground dens accessed via rodent burrows or from underneath the rare rock features. There were no identifiable large communal dens that could be protected, but rather the snakes denned throughout the area and seldom reused the same sites. In contrast, snakes in the southern study areas made use of the abundant rock features, with five of five snakes observed in both winters reusing the same feature. Southern Gophersnakes were observed in hibernacula with more species of snakes than we saw at Vernon, which could indicate that certain rock features were particularly suitable for hibernation. In the southern study areas, protection of identified multispecies hibernation sites could be possible, although even here two-thirds of the Gophersnakes hibernated singly. Our results confirm earlier findings based on smaller sample sizes: Shewchuk (1996) also observed Gophersnakes hibernating in rock features in the south Okanagan, whereas Bertram et al. (2001) found hibernating snakes in grassy hillsides of the Thompson-Nicola river valley near Kamloops, BC, in habitats similar to our Vernon study area.

Oviposition Sites.—Female Great Basin Gophersnakes seldom reused sites and seldom laid eggs in the same nests as other snakes. We interpret this pattern to mean that oviposition sites were not limiting to our study populations, although it is possible that sites degrade (e.g., thermally or structurally) after use in 1 yr. Although these particular study areas appear to support enough hibernation and oviposition sites, we again note that we specifically chose protected areas within the remaining sage-steppe habitats of the Okanagan, which are small remnants of a formerly much larger land cover.

Habitat at oviposition sites of Great Basin Gophersnakes were similar across the four Okanagan study areas, with sites typically in south-facing slopes of moderate grade with sparse grass cover. Trees and shrubs were typically more than 5 m and often more than 10 m away; although we did not excavate oviposition sites, this pattern suggests snakes may have avoided areas with woody roots or where the aboveground biomass would shade and cool the nest site. Gophersnakes typically made use of rodent burrows for their nests, so snakes may have been selecting these burrows rather than avoiding roots, but the effect in terms of nest site positioning is the same.

Compared to the soil that was available, Great Basin Gophersnakes used soil types that contained more sand or loam than clay or silt, suggesting that structural or thermal properties of these soil types are better suited either to nest creation or for embryo development. Soil texture was typically fine, composed primarily of particles < 2 mm in diameter. Soil temperatures at the typical nest depth were higher on average in the south than in the north. This temperature gradient was expected, as average daily air temperatures are warmer in the south Okanagan than the north (Environment Canada, www.weatheroffice.gc.ca). In 2007, the soil temperature at different slopes typical of Gophersnake oviposition sites did not differ within study areas, but temperatures were warmer in southern areas than in the northern study area. This pattern suggests that the local slope does not affect incubation temperature. General oviposition site characteristics—sandy/loamy soils, little vegetative cover, south facing aspects—were comparable to those characterized elsewhere for Great Basin Gophersnakes (Shewchuk, 1996; Bertram et al., 2001), as well as for other species of *Pituophis* (Burger and Zappalorti, 1986; Wright, 2008).

CONCLUSIONS

Although we did not examine thermal properties of hibernacula, our data loggers in mock nest sites showed that northern sites are a bit cooler than southern ones in this valley. It is possible Great Basin Gophersnakes are range limited via the lack of thermally suitable microsites even further north, as longer winters and shorter summers may mean snakes cannot acquire enough food during the active season to support hibernation, or that embryos cannot develop in time for the neonates to find hibernation sites (Williams et al., 2012). For Gophersnakes, we suspect instead that the northern range limit is related primarily to the locations of suitable sage-steppe or grassland habitat within the province; these vegetation types were restricted within BC even prior to the large-scale human-caused alteration of landscapes, but are now reduced severely in size and occurrence (Lea, 2008). Great Basin Gophersnakes do not occur in other habitat types within the province. It is unclear whether this strong habitat association is linked to thermal attributes, structural features, or other characteristics of the habitat (e.g., prey density, protection from predators).

Neither hibernation sites nor oviposition sites appear to be currently limiting for Great Basin Gophersnakes in the Okanagan Valley of BC in these protected areas, in large part because Gophersnakes use a variety of sites and often nest or den alone. This dispersed strategy means reduced dependence on one or a few key sites relative to species like Rattlesnakes or Gartersnakes. A few of our sites did have localized hibernation sites that snakes reused and that supported multiple snakes overwinter. If such sites are on Crown Land (i.e., publicly owned), they can be protected via BC's Wildlife Habitat Area designation, which designates buffer zones around identified hibernacula, although such reserves are likely too small to accommodate the high movement rates of Gophersnakes (Williams et al., 2012). Further, this strategy may not be effective for the many Gophersnakes that hibernated alone, depending on the configuration of protected areas. It is clear that for both hibernating and ovipositing, habitat conservation needs to include a substantial amount of the area used during the active season. This idea has been advanced previously for multiple populations of Canadian snakes near their northern range limits, based both on locations of hibernation and oviposition sites and on snake movements during the active season (Harvey and Weatherhead, 2006; Martino et al., 2012; Williams et al., 2012).

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