PHENOLOGY AND DEMOGRAPHY OF GREAT BASIN GOPHERSNAKES (*Pituophis catenifer deserticola*) at the Northern Edge of Their Range

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Abstract.—Northern range edges of snakes may arise due to short active seasons that challenge snakes to find enough resources to support growth, reproduction, and overwinter survival. We examined the demography and life-history timing for nationally listed as Threatened Great Basin Gophersnakes (*Pituophis catenifer deserticola*) near their northern edge of its range in south central British Columbia, Canada. In 2006 and 2007, we captured 157 snakes at four study sites and implanted radio-transmitters in 39 adults. Mortality was highest during the mating season in May, with 41% of observed mortalities. The main cause of death was predation (76%), but 18% was due to roadkill. The majority of females (89%) oviposited; all five females observed in both years oviposited in each year. The active season was ~200 days with snakes emerging in early April and retreating to hibernation sites in late September. Taken altogether, in suitable habitats, these northern populations of Gophersnakes occurred at high density with high reproductive rates and very low overwinter mortality.

Key Words.-body size; hibernation; mating; oviposition; peripheral population; survival

INTRODUCTION

Populations near northern edges of a geographic range often exhibit different body masses, demographic rates, and timing of life-history events than do populations in the range core (Gaston 2003; Hampe and Petit 2005; Eckert et al. 2008). Northern range-limits challenge populations with more pronounced seasonality and wider annual variation in weather than in southern parts of the range (Gregory 2009). Responses to range edge conditions include behavioral changes (e.g. foraging duration, choice of habitats), phenotypic or physiological changes (e.g. faster growth rates and larger body sizes), and selection for traits conducive to the harsher environments (Chevin et al. 2010; Sunday et al. 2011). In addition to basic ecological interest in understanding how population and individual attributes vary with range position and environmental conditions (Sexton et al. 2009), ecologists need to understand this variability to assess risk status of populations at the range periphery. project range shifts with climate change, and inform management (Lesica and Allendorf 2005).

For several snake species, body size increases with latitude, thus following Bergmann's rule (Ashton 2001; Tuttle and Gregory 2012). Body size affects the speed with which a snake gains and loses heat from the environment, as well as affecting energy stores available overwinter. Northern range-limits for snakes in the northern hemisphere are often ascribed to summers that are too cool or too short, thus preventing adequate

growth and reproduction (Gregory 2009; Weatherhead and Madsen 2009). The substantial range-wide variation observed in snake behavior, growth rates, and timing of life-history events derives primarily from these basic thermoregulatory requirements (Carfagno and Weatherhead 2008; Weatherhead et al. 2012).

Global warming induces temperature and moisture changes that may either challenge range edge populations or facilitate range expansions (Clusella-Trullas et al. 2011). Increases in the duration of the active season may potentiate higher growth rates or reproductive success (Gregory 2009; Shine and Bonnet 2009; Weatherhead et al. 2012), but may also expose snakes to higher predation risk and higher rates of mortality on roads. To forecast snake responses to climate change thus requires understanding the current variability in timing of life-history events of snake populations in their northern range margins, information that is lacking for the majority of northern snake populations (Weatherhead and Madsen 2009).

Our objective in this paper is to characterize the sex ratios, body sizes, population dynamics, and life-history timing of Great Basin Gophersnakes (*Pituophis catenifer deserticola*; Fig. 1) near their northern range limit in British Columbia, Canada. This subspecies occurs throughout the Great Basin ecosystems of the western United States (south to Arizona and New Mexico, and east to Wyoming and Colorado), and reaches its northern range limit in the southcentral arid and semi-arid valleys



FIGURE 1. A male Great Basin Gophersnake (Pituophis catenifer deserticola) with telemetry equipment surgically implanted in the Okanagan valley of southcentral British Columbia, Canada. The snake is basking in early spring. (Photographed by Kathleen Williams).

of British Columbia. Great Basin Gophersnakes are whether males and females are dimorphic in mass federally listed as Threatened in Canada due to their restricted Canadian range and the rapidly expanding human population and substantial habitat loss in this region (COSEWIC 2002, 2013; Southern Interior Reptile and Amphibian Recovery Team 2008). This subspecies is poorly known throughout its range, and especially at its northern range edge (Shewchuk 1996; Williams et al. 2012). The conspecific Bullsnake (P. c. savi), which occurs throughout the Great Plains and prairies, is better To date, Canadian work on P.c. savi has known. focused on habitat selection and movements (Martino et al. 2012; Gardiner et al. 2013), or oviposition sites (Wright 2008), rather than providing demographic analyses. In Wisconsin, Kapfer and colleagues have analyzed Bullsnake population estimates and mortality rates (Kapfer et al. 2008a), habitats and movements (Kapfer et al. 2008b; Kapfer et al. 2010), and factors impacting body temperatures (Kapfer et al. 2008c). Existing data on Bullsnakes are contradictory over whether there is a latitudinal gradient in body size and

(Iverson et al. 2008; Kapfer 2009), and such data are even more scarce for Great Basin Gophersnakes. In this paper, we develop a demographic portrait of Great Basin Gophersnakes near their current northern range edge, by analyzing body sizes, population attributes, survival, and the timing of life-history events such as emergence from hibernation, mating, oviposition, and immergence into hibernation.

MATERIALS AND METHODS

We used four sites in the Okanagan Valley of British Columbia, Canada to study population traits of Great Basin Gophersnakes (Fig. 2). East and West Vaseux in the south Okanagan are owned by Environment Canada and are part of the Vaseux-Bighorn National Wildlife Area. East Vaseux was a 40 ha area composed of grasslands and rock outcrops at elevations of 330-475 m; it rises from Vaseux Lake and a highway in the west to rock ridges and cliffs in the east. West Vaseux was a

90 ha area composed of open Ponderosa Pine (Pinus ponderosa) and Antelope Brush (Purshia tridentata) habitats at elevations of 330-595 m. The West Vaseux site is pinched between Vaseux Lake and a steep rock face, with wetlands at the northern end. Also in the south Okanagan, Ripley Wildlife Habitat Area was a 50 ha area owned in part by the British Columbia Ministry of Environment. It was composed of open Ponderosa Pine and grassland habitats at elevations of 435-645 m. Snakes hibernate on the hillsides and move downslope to fields and several private rural residences in the active season. In the north Okanagan, the Vernon site was a 120 ha area on the Vernon Military Camp owned by the Department of National Defence, composed of grasslands with invasive plant species, at elevations of 485-575 m. Several dirt roads, a nature center, and a firing range occurred within the Vernon site, which was bordered to the east with residential developments.

Snake captures and tracking via radio-telemetry.—We captured Gophersnakes via active searching in suitable habitats on all sites in 2006 and 2007. We weighed and determined the sex of each snake (by probing), measured the snout-vent length (SVL), and implanted a PIT tag subcutaneously. We did not determine the sex of neonates and small juveniles. We surgically implanted 12-g temperature-sensitive radio-transmitters (Model SI-2T, Holohil Systems Ltd., Ontario, Canada; Reinert and



FIGURE 2. Location of study sites in the Okanagan Valley, British Columbia, Canada.

Cundall 1982; Willson 2003) into 17 females and 22 males weighing ≥ 240 g. To reduce pain and swelling, we injected all snakes intramuscularly with Metacam® (meloxicam 0.1 mg/kg) and Baytril® (enrofloxacin 5 mg/kg) 24 h preceding surgery, at surgery, and 24 h post-surgery. Following 24 to 48 h of recovery, we released each transmitter-equipped Gophersnake at its capture location. We removed all remaining transmitters in 2008 following the same protocol.

located transmittered We each individual approximately every second day throughout the active season of late March through mid-October in 2006 and 2007. This tracking period started near emergence from hibernation and extended until after emergence. Tracking typically occurred between 0700 and 1900. We used homing techniques to locate individuals, with the infrequent exception (< 5%) of using triangulation when we located snakes in wetland or rock features that did not permit direct access. We recorded the location of individuals with a Garmin Map76S, which had an accuracy of < 5 m, except for rare cases near cliffs. To estimate mortality rates, we recorded dates and causes of deaths of transmitter-equipped Gophersnakes. То determine cause of death, we examined carcasses and transmitters, the location of the remains, and animal sign found near the remains.

Reproduction .- We derived the timing of mating from 10 observations of transmittered snakes that were combat dancing, scent tracking, coiled, or copulating with transmittered or un-transmittered snakes. On 10 further occasions, we observed male-female pairs of transmittered snakes underground or in dense shrubbery, which we inferred to be mating events. We are confident these events represented mating because malefemale pairs in such close proximity simply did not occur at other times of the active season. A few snakes hibernated together (most hibernated singly; Williams et al., in press), but the pairings here happened well after emergence and far away from the hibernacula. If a pair was observed together for two or more tracking occasions, the mating was inferred to have occurred on the last occasion.

We obtained oviposition dates by recording when females exhibited significant weight loss, obvious skin folds, and an emaciated appearance. We recorded the date that oviposition occurred and the length of time that each snake spent at her oviposition site. We checked oviposition sites once or twice a month thereafter to record predation.

Statistical analysis.—We imported spatial data into ArcView v. 3.2 with Spatial Analyst (Environmental Systems Research Institute, Redlands, California, USA), and we analyzed data using several extensions, primarily the Animal Movement Analysis Extension

TABLE 1.	Characteristics of	Great Basin	Gophersnakes	(Pituophis	catenife	• desertic	ola) captur	ed in the	Okanagan	Valley,	British C	olumbia,
Canada, in	2006 and 2007.	Values are	means ± SD.	We caught	157 sna	kes (four	not tagge	d because	e of small	size), in	addition	16 were
recaptures	in 2007 of snakes	initially caug	ht in 2006.									

Study site	Fomologimolog	Female	Male	Female	Male
Study site	remates.mates	Mass (g)	mass (g)	SVL (cm)	SVL (cm)
2006					
East Vaseux	10:6	340.2 ± 68.0	322.3 ± 112.5	90.4 ± 8.2	98.9 ± 10.4
West Vaseux	8:9	331.5 ± 83.1	393.2 ± 106.9	93.9 ± 9.3	102.1 ± 12.4
Ripley	2:9	371.0 ± 182.4	414.8 ± 125.1	95.5 ± 13.4	103.8 ± 12.9
Vernon	26:22	376.7 ± 115.0	437.0 ± 160.3	94.6 ± 8.7	105.0 ± 15.2
2007					
East Vaseux	7:8	342.0 ± 155.0	346.8 ± 70.1	95.8 ± 13.3	101.9 ± 8.0
West Vaseux	2:10	350.0 ± 141.4	327.4 ± 113.1	92.5 ± 14.8	100.9 ± 12.6
Ripley	1:4	390.0	293.5 ± 86.2	88.0	95.8 ± 13.7
Vernon	24:21	338.0 ± 102.5	392.5 ± 104.0	93.8 ± 12.5	102.8 ± 10.3
combined	80:89	352.3 ± 106.1	385.2 ± 125.2	93.7 ± 10.3	102.5 ± 12.1



FIGURE 3. Body length (snout-vent) and body mass of Great Basin Gophersnakes (*Pituophis catenifer deserticola*). For the same body length, females tended to be heavier than males (females, solid line; males, dotted line).

(Hooge and Eichenlaub 1997). We performed statistical analyses in Microsoft Excel 2003 and 2008 with the Poptools add-in (Hood 2000), and SPSS 12.0 and 16.0 for Windows (IBM, Armonk, New York, USA). Survival data were analyzed via staggered entry Kaplan-Meier estimates (Pollock et al. 1989). We used P < 0.05 as our significance value.

RESULTS

We captured and pit-tagged 92 Great Basin Gophersnakes in 2006 and 77 in 2007, of which 16 were recaptures from 2006 (Table 1). Across all sites, sex ratios were even (2006: 46 F:46 M, 2007: 34 F:43 M; $\chi^2 = 0.310$, P = 0.58), but we captured mostly males at



FIGURE 4. Kaplan-Meier survival estimates \pm 95% confidence intervals for Great Basin Gophersnakes (*Pituophis catenifer deserticola*) in 2006 (grey lines and diamonds) and 2007 (black lines and diamonds). Week 0 began April 1, and week 27 ended October 13.

the Ripley site in both years (2 F:9 M in 2006 and 1 F:4 M in 2007). Approximately half of the captured Gophersnakes were on the northern site (Vernon), and Ripley had the fewest snakes captured (16 total). We captured several Gophersnakes < 80 cm long, including two of the past fall's neonates and others that were probably between one and two years old; four were deemed too small for either tagging or sex determination (and are thus not included above) and several others were tagged but sex was not determined.

Females averaged 90.4–95.5 cm SVL across all sites and years, whereas male averages ranged from 95.8– 105.0 cm (Table 1). Female masses averaged 331.5– 376.7 g across site-years, and male masses averaged 293.5–414.8 g. For the same snout-vent length, females tended to be heavier than males (Fig. 3; females: mass = 8.71[SVL] - 463.7, $r^2 = 0.71$, males: mass = 9.11[SVL] - 548.0, $r^2 = 0.78$), but most females were < 110 cm long whereas a number of males reached snout-vent lengths in the 100–140 cm range and therefore were on average heavier.

Survival and causes of death.—During 2006 and 2007, we observed 17 mortalities of transmittered snakes (10 M, 7 F), proportions of which did not differ from the 22 M and 17 F with transmitters (G = 0.027, P = 0.870).

Seven (41%) deaths occurred in late May (i.e., late in the breeding season; Fig. 4). Six of the 10 male deaths we observed were in May, when male movement rates were much higher than female movement rates (Williams et al. 2012). Active season survival was 84.2% in 2006 and 61.6% in 2007. We did not observe any over-winter mortality in 2006–2007, but one snake died overwinter 2007-2008. Most snakes died of predation, although three were killed on the road by vehicles (Table 2). Seven snakes were killed by raptors (one by a Great Horned Owl, Bubo virginianus, two by Red-tailed Hawks, Buteo jamaicensis, and the other four likely by hawks), two were killed by Coyotes (Canis latrans), four were killed by unknown predators that were probably terrestrial (one was likely a Coyote, and the others might have been Domestic Cat, Felis catus, or some other small carnivore), and one snake died of unknown causes. There was no clear seasonality in the causes of death; for example, the roadkills occurred in 2007 on 24 April, 23 May, and 23 June.

Reproduction.—During 2006 and 2007, we observed or inferred 20 instances of mating between 5 May and 27 May, with 14 of the 20 mating events within the 10-day window of 10–19 May. Median mating dates were 15 May 2006 and 11 May 2007. Nine of 10 (90%)

TABLE 2.	Causes an	d timing of de	aths of	Great	Basin	Gop	hersna	ıkes
(Pituophis	catenifer	deserticola).	Data	from	2006	and	2007	are
lumped because of the few observed mortalities $(n = 17)$.								

Cause of death	April	May	June	July	Aug	Total
Road kill	1	1	1	0	0	3
Raptor	1	3	0	1	2	7
Mammalian	0	3	2	1	0	6
predator						
Unknown	0	0	0	1	0	1

telemetry-equipped females oviposited in 2006 and eight of nine (88.9%) in 2007. Of the five females we tracked both years, all oviposited in both years.

Females oviposited from late June into early July. In 2006, the median date of oviposition was 30 June (range 27 June - 4 July, n = 8), and in 2007, it was 24 June (range 19 June to 4 July, n = 8). The length of time individual females spent at their oviposition sites prior to laying varied, with some females found there only once whereas other females were tracked there up to nine times prior to laying eggs. During 2007, most gravid Gophersnakes moved to the site, laid eggs, and quickly moved on to their summer foraging areas, whereas in 2006 many females spent longer periods near their oviposition sites prior to laying. We recorded two predation events of eggs, one in each year. Both occurred within 48 h of oviposition, and the probable predator was a Coyote or other mid-sized mammal.

Hibernation.—Great Basin Gophersnakes emerged

from hibernation in late March and early April. In 2006, we observed six Gophersnakes near their hibernacula; three that were transmittered the previous year by others and three that were captured by us in the spring but then returned to the identical spot to hibernate in fall 2006. Of these six snakes, five emerged between 6 April and 15 April, while the remaining snake emerged sometime between 14 April and 26 April. In 2007, we observed 21 Gophersnakes close to emergence. Our tracking began 31 March at the southern sites and 7 April at the northern site; 62% of snakes had already left their hibernation site by these dates and had moved up to 90 m away (average 44 m). Of the 38% of transmittered snakes that were

 TABLE 3.
 Median dates of return of Great Basin Gophersnakes

 (*Pituophis catenifer deserticola*) to hibernation sites.

study site	median date	date range	n snakes	
2006				
East Vaseux	23 Sept	10 Sept - 5 Oct	4	
West Vaseux	9 Oct	24 Sept - 11 Oct	6	
Ripley	11 Oct	12 Sept - 11 Oct	3	
Vernon	28 Sept	18 Sept - 10 Oct	9	
2007				
East Vaseux	3 Oct	27 Sept - 14 Oct	4	
West Vaseux	27-28 Sept	18 Sept - 7 Oct	4	
Ripley	12 Sept	-	1	
Vernon	29 Sept	11 Sept - 5 Oct	9	



FIGURE 5. The timing and duration of the annual life history events of Great Basin Gophersnakes (*Pituophis catenifer deserticola*) near their northern range edge in south central British Columbia. The white areas between the labelled events are parts of the active season in which snakes move and forage.

still hibernating at the beginning of tracking, the last snake emerged at the northern site on 23 April, and at the southern sites on 11 April.

In the fall, most snakes returned to their hibernation sites in late September (Table 3). Snakes typically returned to their hibernation sites and then spent up to a month shifting around below ground, extending their activity into late October in some cases. The median dates that snakes were back at their hibernation sites were 30 September 2006 and 27 September 2007.

Annual life cycle.—Great Basin Gophersnakes hibernated from early October to late March (Fig. 5). Both emergence from hibernation and retreat to hibernation sites lasted about a month. Mating took place over about three weeks in May and oviposition during the last two weeks of June and into early July. We observed minor variation in timing between the two years, about a week different for mating and oviposition, and roughly two weeks different for the timing of emergence and retreat. If a Gophersnake hibernated from the last fall day to the first spring day on which we saw active snakes, 15 October - 31 March respectively, hibernation lasted 168 days. Duration of hibernation was variable, as some snakes emerged prior to our 31 March start to the field season, and hibernation could be even shorter if a snake also started hibernation late. Alternatively, snakes retreating earlier and emerging later would spend up to 4-6 weeks longer hibernating.

DISCUSSION

Although native habitats in the Okanagan Valley of British Columbia have been decimated, in remnant patches of sage-steppe or native grasslands, we found that Great Basin Gophersnakes are relatively common. Like many other snake studies, we had insufficient recaptures to obtain reliable population estimates, but we had a high number of captures, especially at the northernmost site. Gophersnakes are often locally common, so these study sites are not exceptional in that regard. For example, Sullivan (2000) found Gophersnakes and Western Rattlesnakes (Crotalus viridis) in California were an order of magnitude more common along 18 km of road than were nine other snake species in the region. In Arizona, Gophersnakes were common in a community of 17 species found on roads (Jones et al. 2011). Similarly, Gophersnakes were one of the most common of 17 snake species captured by pitfall traps in southern California (Rochester et al. 2010), and they were the second most common species out of 13 species captured in New Mexico (Bateman et al. 2009). In Wisconsin, the subspecies P.c. savi was estimated to have a density of 0.42 snakes/ha (Kapfer et al. 2008a). We observed even sex ratios, as did Kapfer et al. (2008a) for P.c. sayi.

We observed a complex sexual dimorphism in size. For the same SVL, females were heavier than males, but more males reached larger SVL and hence had higher body masses as well. Our results offer an interesting counterpoint to results from Bullsnakes. Iverson et al. (2012) reported no sexual dimorphism in Nebraska, although the largest snakes (both mass and SVL) were males. In contrast, Kapfer (2009) did find dimorphism in Wisconsin, with males reaching larger SVL than females. The Gophersnakes we observed had different relationships between SVL and mass in males and females, with males reaching the largest sizes for both mass and SVL. We suspect a similar pattern may occur in Bullsnakes and other Pituophis taxa.

The Great Basin Gophersnakes we captured near the northern range edge were larger than Gophersnakes in other populations, suggesting they follow Bergmann's rule. In New Mexico, 11 Gophersnakes averaged 56.1 cm long (SVL) and 17 snakes averaged 95.0 g (Bateman et al. 2009); in California, four males were 94-102 cm SVL and weighed 302–376 g (Rodriguez-Robles 2003). The snakes we observed were often 90-140 cm SVL and many weighed 350-700 g. This contrast likely is partly due to bias in the trapping methods (the New Mexico study used pitfall and funnel traps whereas we handcaptured snakes), but we think it also reflects genuine biological differences. Western Rattlesnakes (Ashton 2001) and Plains Garter Snakes (Thamnophis radix; Tuttle and Gregory 2012) show a similar pattern of larger individuals in northern populations. For P. c. savi, Kapfer (2009) reported 34 males with mean SVL 133.4 and 18 females with mean SVL 120.9 in Wisconsin; in Nebraska, Iverson et al. (2008) found means of 107.3 and 108.3 SVL for 294 females and 618 males, respectively. These authors reach opposite conclusions about latitudinal clines for *Pituophis* species (Iverson et 2008) and in Nebraska, with oviposition from 10 June to

al. 2012; Kapfer 2009). Our results support a latitudinal cline in body mass for P.c. deserticola.

Survival.--Mortality was highest during May, which is the mating season. This high mortality reflects high snake movements as males search for and then scenttrack females: six of seven snakes killed in May were males and males moved significantly more than females during the mating season (Williams et al. 2012). The high spring mortality is also related to the higher visibility of snakes during spring. Vegetative cover is lower in spring than later in the growing season, and snakes bask on the surface more in the cooler spring temperatures. The estimates of mortality rates may be high, because they derive from animals with surgicallyimplanted transmitters, which may increase morbidity.

The three roadkills represented 18% of the deaths we observed. As adult mortality in reptiles is often a leading factor in reducing population viability, road mortality may have important implications for these populations especially if it is additive (Gibbs and Shriver 2002; Row et al. 2007; Shepard et al. 2008). It is not yet clear if roadkills are a major threat for this species in this region, but given high movement rates of Gophersnakes (Williams et al. 2012), it is worth further research. The predators that killed Gophersnakes were the same as in other studies of P.c. deserticola and P.c. savi, namely raptors and Coyotes (Shewchuk 1996; COSEWIC 2002, 2013; Kapfer et al. 2008a).

We did not observe overwinter mortality, with the single exception of one snake during the 2007-2008 winter, after our main study period. This result contrasts with the high overwinter mortality that occurs in other northern snake populations. For example, Massasaugas (Sistrurus catenatus catenatus) in Ontario had overwinter mortality of 23% and active-season mortality of 21% (Harvey and Weatherhead 2006). Shine and Mason (2004) documented massive winter-kill from flooding severe freezing for Gartersnakes or (Thamnophis sirtalis parietalis) in large communal dens in Manitoba. Winter in the Okanagan Valley is much warmer than in these other regions, but overwinter mortality for Gophersnakes may be higher in years with more severe cold than the relatively mild winter we observed.

Reproduction.---We directly observed and inferred Gophersnakes mating from 5 May - 27 May and we observed ovipositing from 19 June - 4 July. We also observed one instance of male-male combat dancing, which has only rarely been observed in Pituophis (Beane 2012); we are not aware of previous reports of this behavior in P.c. deserticola. The oviposition date range was narrower than that for oviposition by P.c. savi in Alberta with laying dates of 12 June to 22 July (Wright 13 July (Iverson et al. 2012). This narrow oviposition window in the Okanagan Valley is consistent with the idea that post-laving thermal conditions are potentially limiting for embryos near the northern range edge. In 2006, female Gophersnakes spent up to several weeks at their eventual oviposition sites, whereas in 2007 females moved to their oviposition sites, laid eggs, and moved on to their summer foraging grounds. The spring of 2006 was cooler than 2007. When snakes reached their oviposition sites in 2006, perhaps their eggs had not yet developed sufficiently, explaining their subsurface basking period prior to laying. In contrast, a warmer spring in 2007 may have resulted in eggs being ready at the time of arrival at females' oviposition sites, resulting in their short stays. In support of this idea, the median date of laying was six days earlier in 2007 than in 2006.

Most of the females oviposited, with $\sim 90\%$ of females gravid each year and 100% of the snakes we saw in both years gravid in both years. Other studies have had lower percentages of gravid females, including studies in British Columbia on P. c. deserticola (Shewchuk 1996; Bertram, N.A., K.W. Larsen, and J. Surgenor. 2001. Identification of critical habitats and conservation issues for the Western Rattlesnake and Great Basin Gopher Snake in the Thompson-Nicola Region of British Columbia. Final Report for the British Columbia Ministry of Water, Land and Air Protection, British Columbia. Canada. http://www.bcreptiles.ca/docs/bertram%20et%20al%202 001.pdf) and P. c. savi in Nebraska (Iverson et al. 2012). Still, most studies report that well over 70% and often much higher percentages of Gophersnakes are gravid in any given year, suggesting that annual reproduction is the norm rather than the exception. Kapfer et al. (2008a) also report annual reproduction and high proportions of gravid females in P. c. savi. Reproduction does require high energetic expenditures, so reproduction is expected to be lower in years with poor conditions thermally or in terms of prev availability (Seigel and Ford 1987).

The annual cycle.—Gophersnakes near their northern range edge hibernated for 168–196 days, with most snakes either already hibernating or near their hibernation sites by late September and most snakes emerging in late March or early April. These dates may be a week or two earlier than peak emergence of Bullsnakes (*P. c. sayi*) in Wisconsin (Kapfer et al. 2008b). In the spring, some Gophersnakes repeatedly came to the surface to bask before moving substantive distances away from their hibernation sites. In the fall, some individuals returned to their hibernation sites early in September but then remained warm for several weeks, which could have enabled digestion, foraging, growth, or development of gametes.

Great Basin Gophersnakes near their northern range edge appear well able to manage the seasonal challenges

of this region. The high overwinter survival, annual reproduction, and large body sizes combine to suggest that individuals are doing well energetically. The impacts of predicted climate change on this demographic picture are considerably more uncertain. If warming leads to reduced time hibernating, energetic demands will increase. Whether snakes remain in energy balance would hinge on whether they warm sufficiently to hunt, as well as prey availability during the extended active season.

The timing of oviposition is affected both by the time needed for eggs to develop and neonates to make it to hibernation sites, and by the pre-laying energetic needs of female snakes. Climate change is likely to ease both constraints, increasing the summer-fall time suitable for development, and making it easier for females to acquire the necessary resources during spring. We did note a much shorter oviposition period than for two populations of *P.c. sayi* (Wright 2008; Iverson et al. 2012), which might indicate these northern populations currently have a more stringent constraint on development than those populations do.

Northern range edge populations of Great Basin Gophersnakes are primarily and seriously threatened by loss of habitat, with some concerns about road mortality and other human-caused mortality (COSEWIC 2002, 2013). Our results suggest that reproductive potential is high; previous studies with much smaller sample sizes had hinted at alternate year reproduction (Shewchuk 1996; Bertram et al. 2001 *op. cit.*) but our findings suggest annual reproduction is typical. Our results also strongly point to mortality during the active season as being far more important than overwinter mortality for these northern populations.

The implications of predicted climate change for these northern populations are less clear. We suspect climate change will be advantageous rather than damaging for these northern populations, but this assessment hinges on how energetically costly extending the active season might be (Kearney et al. 2009). Both timing and duration of life-history events are likely to change with climate change, and our results provide a baseline Gophersnake-year for this region that can be used for comparison with later years or other localities within their geographic range.

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