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C. L. Jenkins[1], C. R. Peterson[2], S. C. Doering[2], and V. A. Cobb[3]

Studies on geographic variation in reproductive characteristics can contribute to an understanding of the effects of environmental factors on animal population structure and dynamics. Using a ten-year mark–recapture data set (1994–2003), we studied microgeographic variation in reproductive characteristics (body condition, growth, age to maturity, pregnancy interval, fecundity, and size of offspring) among three Western Rattlesnake (*Crotalus oreganus*) populations within 40 km of each other. Significant differences existed among snakes from the different den sites in length, body condition, growth rate, fecundity, and size and body condition of offspring. Furthermore, there was a consistent pattern in the variation among populations. Individuals from the population in the most disturbed area, were shorter, had lower body condition, grew slower, had lower fecundity, and had shorter and lower body condition offspring compared to other populations. The results from this study have important applied implications for understanding fine scale variation in reproductive characteristics. This study suggests that some rattlesnake populations have reproductive characteristics that may make them more susceptible to future disturbances.

S TUDYING geographic variation in reproductive characteristics can provide a basis for understanding the influence of environmental factors on animal ecology (Stearns, 1992). The majority of studies on reproductive variation focus on broad spatial patterns (Radder, 2006). With the current global decline of biodiversity (Singh, 2002), it is increasingly important that we also understand patterns of microgeographic variation (scaled to the species' population structure) because it can help increase knowledge of how human impacts on the environment influence reproduction as well as identifying certain populations that may be more susceptible to disturbed environments. Studies on microgeographic variation in reproductive characteristics are also important because they can provide a better understanding of population structure (Hanski and Gilpin, 1997; Hanski, 1998). Reptiles are one group of animals that would benefit from a better understanding of microgeographic variation because they are currently experiencing widespread global declines (Gibbons et al., 2000). Similar to other taxa, the majority of studies on geographic variation in reptile reproductive characteristics occur at coarse spatial scales (Iverson et al., 1993; Du et al., 2005; Zuffi et al., 2009).

Some snake species/populations are considered capital breeders (i.e., animals that store energy for reproduction) and acquire and store energy over multiple years before producing offspring (Saint Girons, 1952; Bonnet et al., 2002; Shine, 2003). Capital breeding is a means for individuals to withstand disturbance (Jonsson, 1997). Any limiting factor that slows the rate of energy acquisition and storage in capital breeding snakes, such as prey availability or foraging time, could result in smaller body sizes, increased ages to maturity, increased pregnancy intervals, and lower fecundity (Andrén and Nilson, 1983; Beaupre, 1995; Madsen and Shine, 2000a; Bonnet et al., 2001a; Taylor et al., 2005; Taylor and Denardo, 2005). If energy acquisition and storage is reduced to a low enough level capital breeders can experience lower survival (Bonnet et al., 2002; Altwegg et al., 2005).

Crotalus oreganus is a good example of a capital breeding snake species that is threatened by human alterations to the environment. *Crotalus oreganus* in northern Idaho mature at approximately four years of age, have biennial to triennial pregnancy cycles, and litter sizes of three to eight (Diller and Wallace, 2002). The combination of livestock overgrazing and invasive plants in the range of *C. oreganus* has altered natural fire regimes, resulting in widespread landscape conversion from shrublands to grasslands (Whisenant, 1990). Lower prey availability in these disturbed landscapes has been shown to influence reproductive characteristics in sympatric mammalian and avian predators (Knick, 1990; Marzluff et al., 1997).

To evaluate microgeographic variation in reproductive characteristics of *C. oreganus*, we studied three populations in southeast Idaho that have been monitored for ten years by the Idaho State University Herpetology Laboratory (Pocatello, ID). Anecdotal observations suggest that snakes from the population in the most disturbed landscape may be smaller than snakes from the other two populations (Jenkins and Peterson, unpubl. data). The primary question addressed in this study is whether reproductive characteristics of *C. oreganus* vary among these three populations. Secondary questions addressed in this study are whether snakes from the most disturbed landscape are indeed smaller and if they have reproductive characteristics that suggest lower reproductive output. Our specific objectives included comparing a number of characteristics among populations, specifically, female body condition, growth, shedding rates, maximum female size, size at first reproduction, age to reproduction, pregnancy interval, fecundity, and size of offspring.

MATERIALS AND METHODS

Study area.—*Crotalus oreganus* were studied from three den complexes on the Idaho National Laboratory (INL: 112°46′11.76″W, 43°40′52.10″N). The INL is located in the Upper Snake River Plain of southeast Idaho and is admin-

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istered by the United States Department of Energy (DOE). Topography on the INL is generally flat with dispersed volcanic features including buttes, cinder cones, lava flows, and collapsed lava tubes. Soil types vary, but the majority of the INL is composed of loess, sand on basalt, and cinder cone soils. Climate is characteristic of cold deserts with high daily and annual fluctuations in temperature and low levels of precipitation (Anderson et al., 1996). The INL encompasses 2305 km² of predominately sagebrush (*Artemisia* spp.) habitats. The landscape has received minimal disturbance as compared to adjacent lands. The majority of the INL is inaccessible to the public for any use, with peripheral areas (approx. 40%) receiving grazing. Direct human fragmentation on the INL is limited to a low density of buildings and roads.

The three den complexes that are the focus of this study are in close proximity (mean distance between complexes = 34 km); however, there are notable differences in the habitat characteristics surrounding the den complexes. The first complex, Crater Butte (CRAB), is located in the southwest portion of the INL at 1,697 meters elevation. The vegetation surrounding Crater Butte is characterized by a Big Sagebrush (*A. tridentata*) overstory and a Bluebunch Wheatgrass (*Pseudoroegneria spicata*) understory (McBride et al., 1978). Crater Butte and the surrounding area receive human disturbance in the form of livestock grazing. Fires have burned a large portion of the area east, north, and south of Crater Butte. Seven rattlesnake dens are located around the rim of a large shield volcano (700 m by 200 m). The second complex, Cinder Butte (CINB), is located in the northern portion of the INL at 1,470 meters elevation. The vegetation in this area is characterized by an overstory of *A. tridentata* and an Indian Rice Grass (*Oryzopsis hymenoides*) and Northern Wheatgrass (*Agropyron dasystachyum*) understory (McBride et al., 1978) and is relatively undisturbed, receiving no grazing, minimal invasion by exotic plants, and no recent fires. At this site, 11 snake dens are located around the rim of a large shield volcano (800 m by 700 m). The third complex, Rattlesnake Cave (RCAV), is located in the southeastern portion of the INL at 1,596 meters elevation, and unlike the other two populations it has two dens located in the talus formed by a collapsed lava tube (150 m by 60 m). The vegetation surrounding Rattlesnake Cave is characterized by an overstory of *A. tridentata* and a Green Rabbitbrush (*Chrysothamnus viscidiflorus*) understory (McBride et al., 1978) and receives livestock grazing east of the den location. In addition, a recent fire has burned some areas to the west of the den. Overall, the landscape surrounding Crater Butte is more disturbed than the other two landscapes.

Snake mark–recapture.—Snake populations at Cinder Butte have been monitored since 1989 and populations at Crater Butte and Rattlesnake Cave have been monitored since 1994. To account for these differences in sampling periods, we only use data collected since 1994 for all analyses presented here. At each site, a variety of techniques were used to capture rattlesnakes. First, we placed four cross-shaped drift fence arrays (one in each cardinal direction) at each of the den complexes. One funnel trap was placed at the end of each arm of the drift fence array. We opened and closed traps to coincide with snake activity at den sites. In most years traps were opened on 1 May and closed on 15 June then opened again on 1 September and closed on 15 October. Traps were sunk approximately four centimeters into the

ground and covered with cardboard to prevent overheating or freezing of the snakes. In addition, traps were closed if overnight temperatures were forecasted to drop below freezing. Doors were constructed in the top of the traps to allow snakes to be removed without having to dig up the trap. Using these arrays alone, sampling was disproportionately high at Rattlesnake Cave because it is much smaller than either Cinder Butte or Crater Butte. To compensate for this, we placed funnel traps at den openings and conducted area constrained hand capturing at all three sites.

We placed all captured snakes in snake bags, which in turn were placed inside of white plastic nine-liter buckets to prevent overheating. Snakes were then returned to the Idaho State University Herpetology Laboratory to be processed. Once in the lab, snakes were marked by injecting a cylindrical shaped (1.2 cm long by 0.2 cm diameter) Passive Integrated Transponder (PIT) tag (AVID Microchip I.D. Systems, Folsom, LA) and their weight, snout–vent length (SVL), sex, and reproductive condition (females) were recorded. Reproductive condition was determined by palping the ventral side of female snakes. If detectable follicles/embryos were present, females were considered gravid and the number of follicles/embryos was then estimated. In addition, the proximal segment of each snake's rattle was painted with a sampling period specific (i.e., spring or fall of a given year) color to determine shedding rates. Colors were selected that were not conspicuous in the sage steppe environment to prevent increased predation rates. Snakes were then released at their point of capture approximately 48–72 hours after their initial capture.

Defining age classes.—We used SVL and the number of rattle segments to characterize each snake captured as a neonate, juvenile, or mature adult. Specifically, snakes with only one rattle segment (i.e., a button) were classified as neonates. Snakes with at least two rattle segments and SVLs smaller than their population's (i.e., CRAB, CINB, or RCAV) size at sexual maturity (based on the mean length of the ten smallest females) were classified as juvenile. Finally, snakes with SVLs equal to or larger than their population's average size at sexual maturity were classified as mature adults. A chi-square test of independence was used to determine if the proportion of females in each age class varied among snake populations.

Body condition and growth.—We estimated body condition and growth for snakes from each den complex. To estimate body condition and make comparisons among hibernacula, an Analysis of Covariance (ANCOVA) was used. We assessed how much variation in mass (i.e., the dependant variable) was due to each of a series of independent variables including SVL and hibernaculum. The significance of all interactions among independent variables was also assessed. Mass and SVL values were log transformed ($\log_{10}$) prior to analysis. The deviation from the best fit line between mass and SVL is an index of body condition because it represents how heavy a snake is relative to its length. It is important to note that our body condition index is an integrated measure that is influenced by multiple elements that are not accounted for (e.g., reproductive condition or time since last meal) and not an exact estimate of body reserves.

To estimate and compare growth, we calculated growth rates and shedding rates and developed growth curves. Growth rates for recaptured snakes were estimated by

dividing the change in SVL between the two capture periods by the number of growth days in between captures (i.e., the number of days between captures when a snake could be active). Only dates when snakes are generally active (1 May through 1 October) were considered in growth day calculations. ANOVAs and Tukey's *post-hoc* tests were used to determine if growth rates varied among hibernacula. Shedding rates were calculated as the number of molts per year as indicated by the number of unpainted rattle segments proximal to the last previously painted segment. We compared shedding rates among hibernacula using an ANOVA.

We used Von Bertalanffy growth curves to display patterns in growth among sites (Von Bertalanffy, 1957) because they are the most accurate and commonly used model with reptiles (Andrews, 1982). Specifically, growth curves were generated using the slope and x-intercept from a regression of change in SVL and average SVL for snakes captured in subsequent years. The x-intercept of the relationship between change in SVL and average SVL was the maximum length (L_{max}), and the slope was the rate of closure on the maximum length (β). We generated growth curves with L_0 = average neonate SVL using the following equation:

$$L_{t+1} = L_t + \beta(L_{max} - L_t).$$

Growth curves were compared using an ANCOVA to determine if there was a significant difference in change in SVL among populations using average SVL as a covariate.

Age to maturity and pregnancy intervals.—To estimate age to maturity, we needed to first estimate the age of snakes. Snake age was estimated for a subset of snakes (all snakes with the button portion of the rattle remaining) by dividing the total number of sheds for each snake by the average shedding rate per year for the population. Estimated ages were then used to examine reproductive histories of females and determined the age at first reproduction for a subsample of snakes from each population (CRAB n = 5, CINB n = 9, RCAV n = 7). Age to maturity was compared among hibernacula using ANOVA.

We estimated pregnancy intervals by calculating the ratio of sexually mature females with follicles present to mature females without follicles present and used a Chi-square test of independence to determine if proportions were different among hibernacula. For example, a 1:3 ratio of pregnant females to nonpregnant females, would mean an estimated frequency of pregnancy of every four years. We also examined pregnancy intervals for a subset of snakes from Rattlesnake Cave (n = 6) that were recaptured frequently.

Number and size of offspring.—We estimated the average fecundity of females in each population using the number of follicles detected during palping. We recognize that using palping to estimate the number of young can produce overestimates; however, we were comfortable using the method in this study because the estimates are standardized among the three den complexes. To determine if fecundity varied among hibernacula, an ANCOVA was used. Fecundity was the dependant variable and hibernaculum and snake SVL were independent variables in this analysis.

We estimated the size and condition of offspring by examining the SVL and residual mass of neonates from Crater Butte and Rattlesnake Cave that were born in the laboratory (CRAB = 21, RCAV = 12). To obtain neonates during the spring and summer of 2004, 16 pregnant

rattlesnakes were collected from Crater Butte and Rattlesnake Cave (eight from each site). Snakes were housed in environmental chambers that were kept at 30°C during the day and 28°C at night with a constant 15-hour light/9-hour dark cycle that approximated the natural amount of light the snakes would experience in the study area during June (Cobb, 1994). Once the females gave birth, they were kept with the young until each of the neonates had completed its first shed (typically 7–14 days). Neonates were then removed from the mother's cage, measured, and weighed. We used separate one-way ANOVAs to compare offspring SVL and residual mass between Crater Butte and Rattlesnake Cave. We also compared difference in neonate size in snakes born in the field by comparing snakes with only one rattle segment captured at den locations in the fall using ANOVAs.

RESULTS

Mark–recapture.—Over the course of the ten-year monitoring project (1994–2003), the Idaho State University Herpetology Laboratory made 2735 captures of *C. oreganus*. Of those, 1799 rattlesnakes were new captures and marked with PIT tags (616 at Crater Butte, 697 at Cinder Butte, and 486 at Rattlesnake Cave). Despite marking the fewest rattlesnakes at Rattlesnake Cave, recapture rates were highest at this den complex (CRAB 22%, CINB 35%, RCAV 44%). The high recapture rates are likely due to the small size of the den relative to the other sites. Sex ratios were female biased at Crater Butte, unbiased at Cinder Butte, and male biased at Rattlesnake Cave (Table 1; CRAB: n = 545, χ^2 = 6.38, df = 1, P = 0.011; CINB: n = 990, χ^2 = 0.58, df = 1, P = 0.446; RCAV: n = 431, χ^2 = 4.69, df = 1, P = 0.030). However, considering that most male *C. oreganus* are capable of breeding every year and females are not, operational sex ratios in all study areas are likely male biased (Duvall et al., 1991).

Defining age classes.—We found differences among hibernacula in the distribution of female snakes in different age classes. Female rattlesnakes from Crater Butte matured at smaller sizes than snakes from Cinder Butte or Rattlesnake Cave (Table 1; SVL of ten smallest pregnant females [cm]: $F_{2,27}$ = 8.75, P = 0.001). The Crater Butte population was comprised of a large proportion of juveniles and the Cinder Butte and Rattlesnake Cave populations had a relatively lower proportion of juveniles and greater proportions of neonates and adults (Table 2; n = 1328, χ^2 = 41.81, df = 4, P < 0.001).

Body condition and growth.—We found a strong relationship between mass and SVL ($\log_{10}$ mass [g] = 2.98·$\log_{10}$ SVL [cm] −3.20, r^2 = 0.97; df = 1, $F_{1,1322}$ = 39,904.00, P < 0.001). The relationship between rattlesnake mass and SVL was significantly different among hibernacula ($F_{2,1322}$ = 181.44, P < 0.001). However, a significant interaction between hibernaculum and SVL ($F_{2,1322}$ = 10.22, P < 0.001) indicates that the relationships are more complicated. Specifically, snakes from Rattlesnake Cave were consistently heavier for their length than Crater Butte snakes, whereas relatively short Cinder Butte snakes were similar in mass to Crater Butte and relatively long Cinder Butte snakes were similar in mass to Rattlesnake Cave snakes (Fig. 1). In addition, female snakes from Crater Butte reach significantly shorter lengths than snakes from Rattlesnake Cave or Cinder Butte (Table 1; $F_{2,27}$ = 51.67, P < 0.001).

Snakes from Crater Butte grew at a slower rate than snakes from Cinder Butte and Rattlesnake Cave. Growth rates were

Table 1. Reproductive Characteristics Summarized for the Three Populations in This Study. Standard errors are shown in parentheses and values with different superscript letters were significantly different at $P < 0.05$.

Characteristic	CRAB	CINB	RCAV
Sex ration (M:F)	0.85:1	1.06:1	1.18:1
Relative body condition (Fig. 1)	Low	Low to High	High
SVL of 10 largest females (cm)	74.70 (0.99)[a]	91.95 (0.99)[b]	88.86 (1.72)[b]
Growth (cm/year)	0.012 (0.001)[a]	0.018 (0.001)[ab]	0.022 (0.002)[b]
Shedding (sheds/year)	1.17 (0.06)[a]	1.41 (0.06)[b]	1.36 (0.05)[b]
Age to maturity (years)	5.20 (0.37)	4.33 (0.24)	4.29 (0.29)
Size of 10 smallest gravid females (cm)	56.65 (1.91)[a]	63.32 (0.68)[b]	64.03 (1.26)[b]
Range in age to maturity (years)	4–6	3–5	3–5
Pregnancy interval (years)	3–5	3–5	3–5
Proportion of females pregnant	0.22	0.27	0.25
Estimated fecundity (palped follicles)	4.51 (0.24)[a]	5.65 (0.24)[b]	5.89 (0.24)[b]
Neonate SVL born in lab (cm)	26.82 (0.30)[a]	—	28.10 (0.33)[b]
Neonate body condition in lab	−0.43 (0.22)[a]	—	0.92 (0.33)[b]
Neonate SVL born in field (cm)	26.32 (0.20)	26.17 (0.16)	25.68 (0.20)
Neonate body condition in field	−0.38 (0.16)	−0.76 (0.14)	0.59 (0.16)

significantly higher at Rattlesnake Cave than Crater Butte (Table 1; $F_{2,668} = 8.50$, $P < 0.001$). Snakes from Crater Butte shed significantly fewer times per year than snakes from Cinder Butte and Rattlesnake Cave (Table 1; $F_{2,423} = 4.08$, $P = 0.018$). Finally, among snakes captured in consecutive years, change in SVL was significantly related to average SVL ($F_{1,110} = 43.72$, $P < 0.001$) and change in SVL decreased at a significantly greater rate with increasing average SVL at Crater Butte relative to Cinder Butte and Rattlesnake Cave (Table 3; $F_{2,110} = 3.73$, $P = 0.027$). Population specific growth curves help to visualize these relationships (Fig. 2).

Age to maturity and pregnancy interval.—There were no significant differences in ages to maturity or pregnancy intervals among snakes from the three hibernacula; however, the trends are consistent with other results. Specifically, snakes from Crater Butte had later ages to maturity than snakes from Cinder Butte and Rattlesnake Cave (Table 1; $F_{2,18} = 2.65$, $P = 0.098$).

Overall, we estimated that snakes in our study area have three- to five-year pregnancy intervals. The proportion of pregnant females pooled across years indicated that snakes went four to five years between pregnancies, but there were no significant differences among hibernacula (Table 1; $n = 580$, $\chi^2 = 11.58$, df = 2, $P = 0.590$). Finally, a sub-sample of snakes from Rattlesnake Cave that were recaptured at least once per year showed a three- to five-year cycle ($n = 6$, Mean = 3.66, SE = 0.33, Min = 3, Max = 5).

Number and size of offspring.—Snakes from Crater Butte had significantly fewer offspring than snakes from Cinder Butte or Rattlesnake Cave (Table 1; $F_{2,139} = 3.89$, $P = 0.023$).

Table 2. The Number and Proportion (in Parentheses) of Neonate, Juvenile, and Adult Female Rattlesnakes from Three Hibernacula on the Idaho National Laboratory.

Age class	Crater Butte	Cinder Butte	Rattlesnake Cave
Neonate	53 (0.13)	116 (0.23)	97 (0.25)
Juvenile	199 (0.47)	172 (0.33)	111 (0.28)
Adult	170 (0.40)	224 (0.44)	186 (0.47)
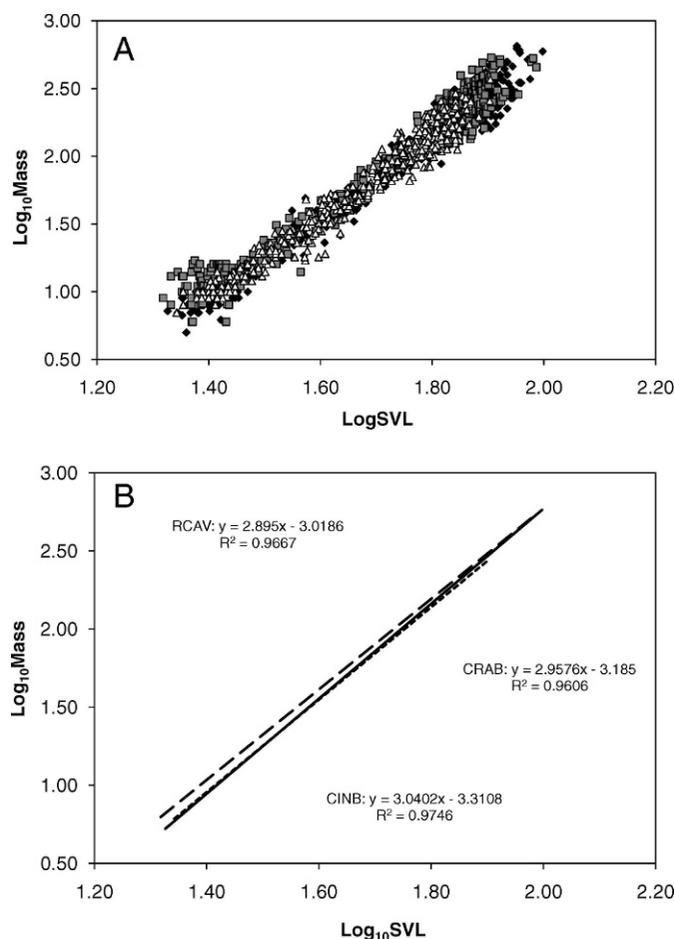
Fig. 1. (A) The relationship between $\log_{10}$ snout–vent length (cm) and $\log_{10}$ mass (g) for female rattlesnakes from three populations on the Idaho National Laboratory. White triangles represent Crater Butte (CRAB), black diamonds represent Cinder Butte (CINB), and gray squares represent Rattlesnake Cave (RCAV). (B) Equations of the line describing the relationships for CRAB (dotted line), CINB (solid line), and RCAV (dashed line).

RCAV: $y = 2.895x - 3.0186$
$R^2 = 0.9667$

CRAB: $y = 2.9576x - 3.185$
$R^2 = 0.9606$

CINB: $y = 3.0402x - 3.3108$
$R^2 = 0.9746$

Table 3. Slope and X-Intercept for the Relationship between Change in Snout–Vent Length and Average Snout–Vent Length.

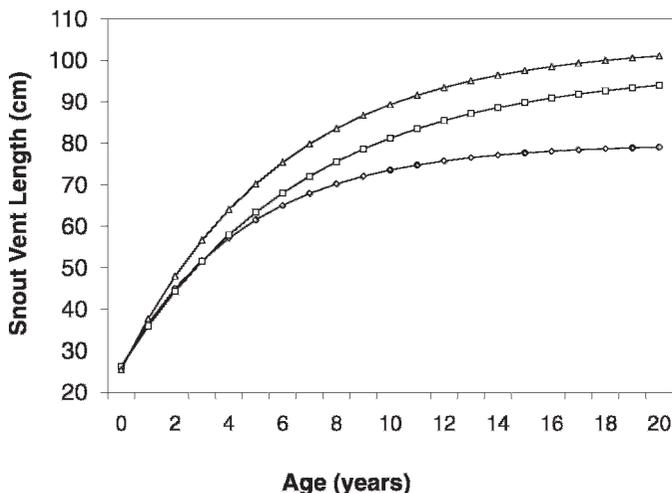| Population	Slope	x-intercept (cm)
Crater Butte	−0.19	79.80
Cinder Butte	−0.14	97.89
Rattlesnake Cave	−0.16	103.66

Additionally, when snake SVL was accounted for, there was a significant positive relationship between SVL and fecundity ($F_{1,139} = 14.94$, $P < 0.001$) and fecundity increased at a significantly greater rate with SVL at Rattlesnake Cave as compared to Crater Butte (Fig. 3).

Length and body condition of offspring was significantly different between Crater Butte and Rattlesnake Cave. Specifically, Rattlesnake Cave snakes born in the laboratory had significantly greater SVLs ($F_{1,31} = 9.87$, $P = 0.004$) and greater residual mass values ($F_{1,31} = 11.03$, $P = 0.002$) than laboratory born Crater Butte snakes. The lab results for residual mass were consistent with data on neonate captures at den sites in the field where we observed significantly greater residual mass at Rattlesnake Cave ($F_{2,382} = 23.52$, $P < 0.001$). However, field born snakes from Rattlesnake Cave tended to have lower SVL than snakes from Crater Butte ($F_{2,380} = 3.02$, $P = 0.053$).

DISCUSSION

To our knowledge, no studies exist examining variation in reproductive characteristics of *C. oreganus*; however, Ashton (2001) found that the size of female *C. oreganus* varied across the range in relation to temperature; specifically, populations in warmer areas had females with greater snout–vent lengths. Two of the studies from which Ashton (2001) summarized snake sizes also examined reproductive patterns (Macartney and Gregory, 1988; Diller and Wallace, 2002) and a third study summarized by Ashton (2001) occurred on the INL (Sehman, 1977). When comparing reproductive
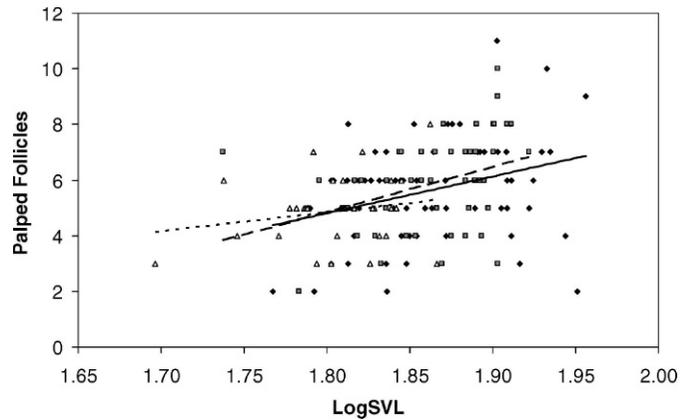
Fig. 3. The relationship between snout–vent length and the number of palped follicles for pregnant rattlesnakes from the Idaho National Laboratory. White triangles and the dotted line represent Crater Butte (CRAB), black diamonds and the solid line represent Cinder Butte (CINB), and gray squares and the dashed line represent Rattlesnake Cave (RCAV).

characteristics between our site and sites in northern Idaho and British Columbia, we see differences but not a consistent pattern with temperature gradients (Table 4). In addition, the variation we observed in fecundity among the three INL sites is greater than the variation between the INL sites and the northern Idaho and British Columbia sites. These patterns in variation among populations of *C. oreganus* suggest that factors at microgeographic scales can have a strong influence on rattlesnake reproductive characteristics and life histories.

The results from this study have important applied implications for the conservation of snake populations. Snake species with later ages to maturity, longer pregnancy intervals, and lower fecundity are more susceptible to declines (Webb et al., 2002). We found that populations of *C. oreganus* in close proximity can vary considerably with respect to these reproductive characteristics, and thus some populations may be more susceptible to declines. In our study area snakes from the most disturbed area, Crater Butte, were the smallest and had reproductive characteristics that would indicate the lowest reproductive output. The two populations that were less disturbed, Cinder Butte and Rattlesnake Cave, had similar reproductive characteristics that would indicate relatively higher reproductive output. The observed reproductive characteristics at Crater Butte may be

Fig. 2. Simulated Von Bertalanffy growth curves for snakes from three rattlesnake populations on the Idaho National Laboratory. Triangles represent Crater Butte (CRAB), diamonds represent Cinder Butte (CINB), and squares represent Rattlesnake Cave (RCAV). Slopes and x-intercepts of change in snout–vent length on average snout–vent length used to develop curve are displayed in Table 3.

Table 4. Comparison of Reproductive Characteristics Found in This Study to Studies from Northern Idaho and British Columbia. Temperatures reported in Ashton (2001) for each site are INL: 7.85°C, British Columbia: 8.85°C, and North Idaho: 9.85°C.

	INL			British Columbia	North Idaho
	CRAB	CINB	RCAV		
Age to maturity (years)	5.2	4.3	4.3	5–7	3–6
Pregnancy interval (years)	3–5	3–5	3–5	2–3+	1–3
Proportion of females pregnant	0.22	0.27	0.25	0.51	0.66
Estimated fecundity	4.5	5.6	5.8	4.6	4.8

due to higher disturbance levels and may make snake populations in the area more susceptible to future disturbance.

Future studies should examine the extent to which different factors are responsible for the observed microgeographic variation in *C. oreganus*. Environmental factors that influence a capital breeding snake's ability to acquire and store energy can result in the type of microgeographic variation we observed (Madsen and Shine, 1992; Bonnet et al., 2001b). First, any factor that directly influences the availability of prey can result in lower energy acquisition and lower reproductive output (Beaupre, 2008). Snakes in particular display a great deal of phenotypic plasticity in response to the availability of food (Seigel and Ford, 1991). Generally, juvenile snakes put energy into growth and adult snakes put energy into storage for reproduction (Madsen and Shine, 2002). Higher growth rates at early life stages can have long term impacts on snake reproduction because it allows individuals to eat larger prey at an early age (Madsen and Shine, 2000b). Food availability influences reproductive output by affecting female body size (Madsen and Shine, 1993; Shine and Madsen, 1997). Specifically, higher prey availability increases body condition and growth (Forsman and Lindell, 1997), litter mass (Lourdais et al., 2002), frequency of pregnancy, and number of young (Bonnet et al., 2001b). Second, factors that decrease the amount of time snakes have available for activity can result in less time for foraging, ultimately resulting in lower energy acquisition. The physical environment can influence the time available for activity (Lourdais et al., 2004). Beaupre (1995) found that snakes at a relatively hot, low elevation site had less available time for activity, grew at a slower rate, and had smaller adult body sizes. Other factors such as inter- and intraspecific competition can also influence snake activity (Forsman and Lindell, 1997; Himes, 2003).

Snake populations can also become locally adapted to their environments over time. Studies on terrestrial Garter Snake (*Thamnophis elegans*) life histories by Bronikowski and Arnold (1999) found that snakes grew slower in mountain meadow environments (colder physical environment) and faster in lake environments (warmer physical environment). However, a subsequent common garden experiment found that snakes from the colder environment grew faster in the cold and that snakes from the warmer environment grew faster in the warmth, suggesting that snake growth had become locally adapted in these populations (Bronikowski, 2000). Similarly, studies on *Vipera berus* in Switzerland suggest the existence of a dwarf mountain ecotype characterized by cryptic coloration, smaller body size, and lower fecundity (Monney et al., 1995). Specifically, cryptic snakes are not able to thermoregulate as well as black snakes and thus do not grow as fast or have as high reproductive output (Capula and Luiselli, 1994). Future studies should examine environmental factors and local adaptation in these rattlesnake populations.

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