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Population Estimate, Survivorship, and Generation Time of the Northern Pacific Rattlesnake (*Crotalus o. oreganus*) at its Northern-most Range Limits

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***Abstract.*—The Northern Pacific Rattlesnake (*Crotalus o. oreganus*) is restricted in its occurrence in Canada to British Columbia (B.C.) and is listed nationally as a Species-at-risk, yet there is a lack of demographic information, including baseline information on density, survivorship, generation time, and distribution necessary for evaluating the impacts of threats on the population. Here we report the first population and demographic parameters for rattlesnakes in over 30 y at this latitude, which is also the northern-most limit of the global range for this species. We used capture-mark-recapture (CMR) results from an 11-y study (2002–2012) to determine a density estimate for the Northern Pacific Rattlesnake on a 4.5 km^2 area within the Okanagan Valley of B.C., Canada. The adult population had an 11-y mean density of 58.2/km^2 (mean population size = 262; upper 95% Highest Density Interval (HDI) = 433; lower 95% HDI = 149) and a mean annual survivorship of 0.85. The smallest sexually mature female was 540 mm SVL and the estimated age at maturity for female rattlesnakes was 4.9–8.5 y, with a mean generation time of 13.7 y.**

Key Words.—conservation; *Crotalus o. oreganus*; demographic studies; density; growth rate; mark-recapture; population estimate; snake; species at risk

Introduction

Demography and survival rates of wildlife populations are critical components of species conservation efforts (Selman and Jones 2017). Such demographic information is becoming increasingly important for quantifying the impact of major threats such as habitat loss, climate change, and invasive species, and can be critical for conservation-based approaches (tools) including population viability analysis (Coulson et al. 2001; Jones et al. 2017). Typically, demographic studies derive information from the capture, mark, and recapture of free-ranging individuals within a population (Pike et al. 2008). However, at times, this can be logistically challenging, especially if the target species, for example, most snakes, is difficult to capture and monitor due to its ecology and cryptic behavior.

Snakes and other reptiles are exhibiting dramatic global population declines due to habitat loss and degradation, pollution, diseases, climate change, continued human persecution, and, for some species, overharvesting (Gibbons et al. 2000; Kjoss and Litvaitis 2001; Durso et al. 2011; Saha et al. 2018). Cascading effects from this are likely, as snakes play a critical role in ecosystems in which they live, occupying mid-to-high levels of the trophic food web (Lind et al. 2005) that render them a crucial vector for energy and nutrient movement. Furthermore, snakes can be used as important indicator species for ecosystem health and potential change in trophic dynamics. Often changes observed in snake behavior or populations can be linked to alterations in the local environment (Beaupre and Douglas 2009). For example, adult female Timber Rattlesnake (*Crotalus horridus*) survival decreased in

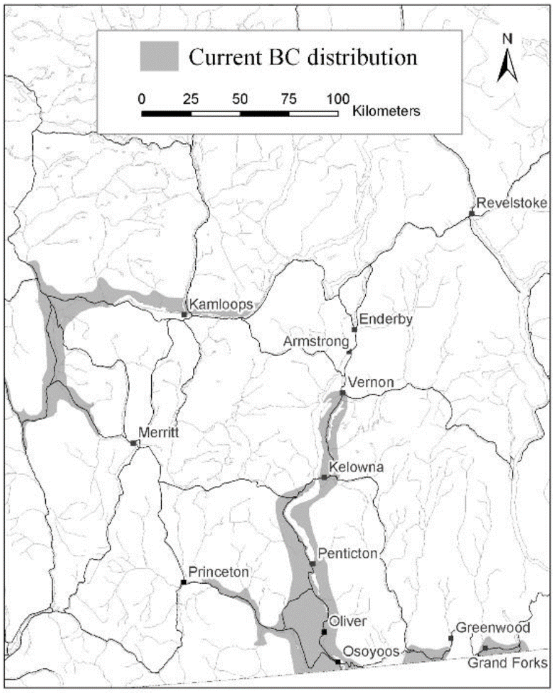

Figure 1. Current range distribution of the Northern Pacific Rattlesnake (*Crotalus o. oreganus*) in southern British Columbia, Canada, showing four main geographical populations. The Osoyoos Indian Reserve (OIR) study site was located near Osoyoos.

response to a 50% decline in prey species abundance (Olson et al. 2015), and declines in garter snakes (*Thamnophis* spp.) have been linked to reductions in amphibian prey (Matthews et al. 2002). Snakes are also effective indicators for environmental contaminants (Stafford et al. 1976; Olendorf et al. 1988; Bishop and Rouse 2000; Bishop et al. 2016). However, due to their cryptic nature, patchy distribution, and often nocturnal behavior, reliable long-term data on snake population size and densities are scarce and difficult to obtain (Fraga et al. 2014; Ward et al. 2017). Consequently, this taxon is often under-represented in the literature: a recent meta-analysis of wildlife population trends in Canada revealed usable data for only 46 of 102 reptiles and amphibians occurring in the country (45%; World Wildlife Fund Canada 2017; see also Seigel 1993; Bonnet et al. 2002; Lind et al. 2005).

The case of the Northern Pacific Rattlesnake (*Crotalus o. oreganus*) in Canada is similar to many northern reptiles because it has a limited geographic range and locations of overwintering den sites are generally well known (Southern Interior Reptile and Amphibian Recovery Team 2016). Federally listed as Threatened (Committee on the Status of Endangered Wildlife in Canada [COSEWIC] 2015), the species is under increasing pressure from habitat loss and fragmentation as well as direct mortality from road traffic and continued human persecution (Southern Interior Reptiles and Amphibian Recovery Team 2016). Despite this situation, relevant population estimates or demographic parameters from within the range of this species are lacking, an impediment to the development and assessment of conservation measures. Justifying and subsequently planning management of Northern Pacific Rattlesnake populations will require information on demographic parameters and trends.

Southern British Columbia (B.C.) encompasses the northern-most limits of the global range of the Northern Pacific Rattlesnake (Southern Interior Reptile and Amphibian Recovery Team 2016) where the species occurs solely in four disjunct populations in valley systems within the province of B.C. (Fig. 1). Moreover, the Okanagan Valley, which includes most of the rattlesnake range in B.C., is experiencing one of the fastest rates of urban and agricultural growth in Canada (Okanagan Valley Economic Development Society 2013; Statistics Canada 2014). The impact of these alterations to the habitat of Northern Pacific Rattlesnake is unknown because the last systematic survey and population estimates for this species in Canada occurred in the Okanagan Valley over 30 y ago (Macartney 1985).

We used 11 y of capture-mark-recapture data from a long-term population study of Northern Pacific Rattlesnakes in southern B.C. Given that habitat loss and rattlesnake population declines continue to be of high concern, the over-arching goal of this study was to attain demographic data on a northern rattlesnake population, thereby providing reference population data that will aid future monitoring and conservation efforts for this species. Our specific objectives were to determine estimates of the adult population size and density, annual survivorship of the local population, and determine generation time and female age at reproductive maturity.

Materials and Methods

Study site.—We conducted an intensive capture-mark-recapture study on the Northern Pacific Rattlesnake (*Crotalus o. oreganus*) between 2002–2012 on the Osoyoos Indian Reserve (OIR) near Osoyoos, B.C. This area is located within the Okanagan Valley approximately 4.5 km north of the Canada-USA border (Fig. 1). The 4.5 km^2 study site was comprised of low elevation (about 300–400 m elevation) shrub-steppe vegetation, primarily dominated by Antelope-brush (*Purshia tridentata*) and Big Sagebrush (*Artemisia tridentata*), as well as mid to high elevation rocky mountain slopes (Brown et al. 2009; Lomas et al. 2015). The site was bounded on the west by the shore of Osoyoos Lake, and to the east, rocky slopes that contained most of the communal hibernacula used by the snakes at (500–650 m elevation) and higher elevation mountains (Anarchist Mountain, elevation 1,491 m).

During our study years, extensive landscape developments and human activity were concentrated to the south and west portions of the study area (about 1 km^2). At the outset of our project, the natural area of the study site was bordered by a campsite with no other development. Over the following 11 y, a condominium resort, cultural centre with interpretive trails, parking lots and expanded roads were built in the southwest portion of the study area. Human presence remained very limited and restricted in the large northern and eastern portions of the study site, which continued to remain in a natural state.

Data collection, population estimates, and survivorship.—We collected field data between April and October of each year. We captured rattlesnakes and marked them using sterile passive integrated transponder (PIT) tags (Biomark Model TX1411SSL; Biomark, Boise, Idaho, USA). To measure snout-to-vent length (SVL; mm), we safely secured approximately ¼ the length of each individual body in a plastic restraining tube and then measured the snake. We also recorded weight (g), sex, and reproductive status (non-gravid, gravid, post-partum for females) for each captured individual. To determine female reproductive status, we palpated the ventral side of individuals and if detectable follicles/embryos were present, we considered females gravid. We processed captured snakes in a laboratory located within the study area. We measured and released snakes within 4–24 h at their capture locations (Brown et al. 2009).

To estimate population size, we used the Rcapture package (Baillargeon and Rivest 2007) in R (R Development Core Team 2016). We ran an open-population mark-recapture model using the opennp function. This function fits a Jolly-Seber population model to the data following the log-linear approach described by Cormack (1985, 1989) and produces estimates of population size and survivorship. Following Baillargeon and Rivest (2007), we examined the model fit using a visual inspection of the Pearson residuals and frequency of capture. Large residual values represent poorly-fitted data; when this was detected, we limited the frequencies of captures in the analyses and quantified the subsequent impact on the parameter estimates (Baillargeon and Rivest 2007).

Variation in the number of overall captures (i.e., sampling effort) across each year reflected annual variations in research methods including differences in survey timing (start date, length of field season, etc.), and individual field crew bias on an annual basis. Although the model estimates capture probabilities, we attempted to further account for any error associated with this unequal sampling and obtain a more robust confidence interval on model parameters using a bootstrapped resampling approach. Given uneven recapture events per individual snake and per year, resampling is likely to provide a better estimate of the confidence intervals. For each year we randomly sampled the data so that the number of captures per year was equal to the lowest observed in the field (n = 48). Subsequently, we rebuilt the capture history estimated model parameters for each resampled capture history. We estimated the model parameters and their confidence intervals from the sampling distributions of 999 permutations. The distribution of many of the survivorship estimates generated in Rcapture was non-normal and thus confidence intervals based on standard deviation were invalid. We therefore used the mode and 95% Highest Density Interval (HDI) estimates using the BEST package in R (Kruschke 2013).

We made population and survivorship estimates using the capture histories of adults only (≥ 540 mm SVL). Over the course of the 11-y study period, we made 223 juvenile captures (< 540 mm SVL) compared to 1,130 adult captures (see Results). Given that juvenile snakes are under-represented in population samples, even in hibernacula surveys (Macartney 1985; Larsen and Gregory 1989), we believe that this low capture rate is more of a function of capture bias rather than a representation of the juvenile component of the population; therefore, we omitted juveniles from our population and survival estimates. Furthermore, demographic changes to populations of long-lived species are mainly the result of adult survival, irrespective of changes in juvenile survival (Legendre 2004; Waldron et al. 2013). To calculate population density (individuals/km^2), we estimated the total area of our study site using previous radio-telemetry studies, the area covered by surveys, and the distribution of captures on the landscape (Brown et al. 2009; Lomas et al. 2015), which gave us a study area size of 4.5 km^2.

Growth.—To determine individual growth, we avoided using multiple data points for the same individual by only using the first and second captures for each snake to retain independence of observations (Blouin-Demers et al. 2002). Due to the slow growth rates of northern snake species, Blouin-Demers et al. (2002) excluded captures of less than one active season. However, many snakes that we recaptured were within the same year and were not captured in subsequent years. Thus, we excluded recaptures of individual snakes within the same year if the recapture interval was approximately less than a third of an active season (about Δt < 55 d). This allowed us to maintain adequate sample sizes for calculating growth rates.

We first examined growth by calculating rattlesnake instantaneous growth rates using a modification of Brody's formula (Brody 1945):

Table 1. Modified capture-mark-recapture analogues of nonlinear growth models used in a study of Northern Pacific Rattlesnakes (*Crotalus o. oreganus*) in Canada. Parameters are: *a* – asymptotic size, *k* – characteristic growth rate, *t* – age (in years), L_R – snout-vent-length at second capture, L_C – snout-vent-length at initial capture, and e is the natural logarithm.

Model	Modified Mark/Recapture Analog
Von Bertalanffy	$L_R = a - (a - L_C)e^{-k\Delta t}$
Logistic	$L_R = \frac{a * L_C}{(L_C + (a - L_C)e^{-k\Delta t})}$
Gompertz	$L_R = a\left(\frac{L_C}{a}\right)^{e^{-k\Delta t}}$

$$\Delta GR = (log_e SVL_2 - log_e SVL_1)/((t_2 - t_1)/167) \quad (1)$$

In this equation, log_e is the base of the natural logarithm, SVL_1 is the individual size at initial capture, SVL_2 is the individual size at second capture, t_1 is the time of first capture and t_2 represents the time at second capture. The constant (167) represents the length (days) of an active season, or period of growth. To calculate this number, we assumed that no growth occurred during hibernation. We used previous radiotelemetry studies at this site (Brown et al. 2009) and observations of snakes around the den sites (1 April to 15 September) to obtain an average annual active period of 167 d.

Estimating age-related parameters using mark-recapture interval data is becoming a common conservation tool, especially when the exact ages of individuals are unknown (Smith et al. 2010; Waldron et al. 2013; Dreslik et al. 2017). We deployed modified versions of three nonlinear growth models commonly used in herpetological studies (Smith et al. 2010; Sung et al. 2015; Dreslik et al. 2017; Table 1). Using methods originally developed by Fabens (1965) to accommodate mark-recapture data where exact ages are typically unknown, we reparameterized these models to allow us to use time intervals between subsequent captures of individual snakes (in this case first and second capture), thus projecting lifetime individual growth when ages were unknown (Table 1). We used nonlinear least squares regression procedures to characterize these models. We then plotted lifetime growth trajectories predicted by these models for a 285 mm neonate (average neonate size at age 0; Charland 1989) to generate expected sizes at specific ages. We assessed model suitability using Akaike's Information Criteria adjusted for small sample sizes (AIC_c) and AIC_c weights (AICcmodavg package; R Development Core Team 2016) to select the most parsimonious model.

Generation time.—We calculated generation time, using the following equation (International Union for Conservation of Nature [IUCN] Standards and Petitions Committee 2014):

$$1/\text{mortality rate} + \text{age at maturity} \quad (2)$$

This equation is appropriate if annual mortality after the age of first reproduction is well known, and mortality and fecundity do not change with age after the age of first reproduction (i.e., no senescence, IUCN Standards and Petitions Committee 2014). For species exhibiting senescence (i.e., mortality increasing and fecundity decreasing with age), this formula will tend to overestimate generation time. Snakes are perfect candidates for this equation: for example, older and longer female rattlesnakes in B.C. appear to reproduce at a more frequent rate (biennial compared to triennial) than smaller, younger snakes. Also, the only data available on female rattlesnake fecundity in B.C. shows that length (size) does not appear to be correlated to litter size (Macartney and Gregory 1988). Thus, we calculated three estimates of generation time based on the minimum, maximum, and average mortality rates and average age at maturity. To estimate minimum mortality rates, we used survivorship generated from the population estimate models run in Rcapture (Baillargeon and Rivest 2007).

Results

We captured 1,139 adult rattlesnake of 619 individuals over the course of the study period. Of those, we captured 400 at least once (35.1%). The number of individual adult rattlesnakes captured in each year ranged from 14–164 during the 11-y study period and after excluding the first year, the proportion of new individuals captured ranged from 0.38–0.92 (Table 2). Using complete capture histories for all individuals, the yearly adult population size estimates ranged from 146–512, with a mean of 305 individuals. Pearson residuals for individuals with histories involving more than six captures were large and removing these individuals produced a better fit (i.e., lower AIC), but the abundance estimates remained similar with a mean population size of 331 individuals across years.

Our bootstrapped resampling estimates (2003–2011) produced similar but lower estimates of the adult population size (Table 3). Population size estimates across years ranged from 114–419 individuals with an overall average population estimate of 262 individual adults (58.2/ km^2; upper 95% HDI = 433; lower 95% HDI = 149; Table 3). As with population size, survivorship estimates were similar whether using the full dataset or

Table 2. Annual sample sizes of captured adult Northern Pacific Rattlesnakes (*Crotalus o. oreganus*) near Osoyoos, British Columbia, Canada (2002–2012).

Year	Number of New Individuals	Total Number of Captures	Proportion New Animals in Sample
2002	14	14	1.00
2003	66	72	0.92
2004	99	133	0.74
2005	115	164	0.70
2006	81	145	0.56
2007	32	80	0.40
2008	35	93	0.38
2009	27	61	0.44
2010	19	48	0.40
2011	95	146	0.65
2012	40	67	0.60

Table 3. Bootstrapped results from population model showing population estimates for adult Northern Pacific Rattlesnakes (*Crotalus o. oreganus*) near Osoyoos, British Columbia, Canada (2002–2011; mode with upper and lower 95% Highest Density Intervals HDIs).

Year	Mode	Lower HDI	Upper HDI
2002	—	—	—
2003	114	76	253
2004	212	109	390
2005	419	233	619
2006	385	233	584
2007	264	171	456
2008	252	155	429
2009	358	191	504
2010	114	62	207
2011	244	110	458
Mean	262	149	433

the bootstrapped resampled distributions, and thus we only report on the latter. Survivorship estimates for adults ranged from a high of 1 to a low of 0.29, with a mean survivorship of 0.85 (upper 95% HDI, 0.94; lower 95% HDI, 0.54; Table 4).

Between 2002–2012, we captured 266 rattlesnakes over a time interval greater than 55 d. This was reduced to 172 animals when only first and second captures were used. Overall, smaller rattlesnakes had higher instantaneous growth rates, and growth declined with increasing size ($F_{1,170} = 54.73$, $P < 0.001$, $r^2 = 0.24$; Fig. 2). For example, an average sized neonate was expected to grow 70 mm/year in its first year. Growth rates slowed for an average juvenile to 38 mm/year, whereas average adult rattlesnake growth was 13 mm/year. Negative growth rates were likely a result of measurement error. However, we elected to retain these negative errors because we were unable to identify the positive errors that were probably as ubiquitous (Blouin-Demers et al. 2002). All three nonlinear growth models showed little differentiation, with predicted asymptotic (a) size ranging between 723–735 mm SVL and characteristic growth rates (k) between 0.001032–0.001438 (Table 5, Fig.3). Based on AIC_c we selected the von Bertalanffy model (Table 6) and used this to determine the estimated age of maturity for female rattlesnakes in our study.

The average SVL of gravid females in our study was 604 mm SVL (± 32.7 SD; range, 540–631 mm). Incorporating these values into the growth trajectory of a 285 mm SVL neonate, the von Bertalanffy model indicated an average age of maturity as 7.1 y (range, 4.9–8.5 y) for rattlesnakes at this study site. We calculated corresponding adult mortality rates as 1 minus the survivorship rate (1 - 0.85) resulting in an adult mortality rate of 0.15, with upper and lower limits of 0.06–0.46. Based on these estimates, and the average age of female maturity, we calculated minimum generation time as 9.3 y (1/0.46 + 7.1), maximum generation time as 23.7 y

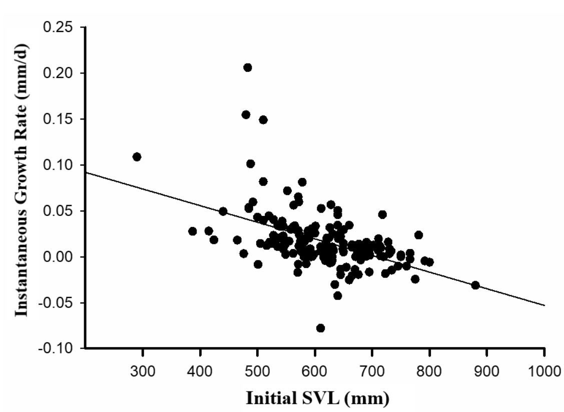

Figure 2. The relationship between instantaneous growth rate and initial snout-vent-length (SVL) of the Northern Pacific Rattlesnake (*Crotalus o. oreganus*) near Osoyoos, British Columbia, Canada (2002–2012).

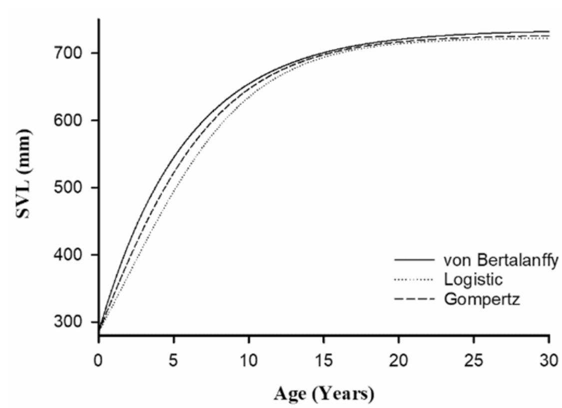

Figure 3. Nonlinear growth models for the Northern Pacific Rattlesnake (*Crotalus o. oreganus*) near Osoyoos, British Columbia, Canada, based on a 285 mm SVL neonate living during the study period of 2002–2012.

Table 4. Bootstrapped results from population model showing survivorship estimates for adult Northern Pacific Rattlesnakes (*Crotalus o. oreganus*) near Osoyoos, British Columbia, Canada (2002–2011; mode with upper and lower 95% Highest Density Intervals, HDIs).

Year	Mode	Lower HDI	Upper HDI
2002 → 2003	1.00	0.75	1.00
2003 → 2004	0.74	0.54	1.00
2004 → 2005	1.00	0.65	1.00
2005 → 2006	1.00	0.56	1.00
2006 → 2007	0.61	0.45	1.00
2007 → 2008	0.99	0.54	1.00
2008 → 2009	0.99	0.61	1.00
2009 → 2010	0.29	0.17	0.50
2010 → 2011	1.00	0.62	1.00
2011 → 2012	—	—	—
Mean	0.85	0.54	0.94

(1/0.06 + 7.1), and average generation time as 13.7 y (1/0.19 + 7.1).

Discussion

This study provides a detailed, long-term demographic analysis of a threatened rattlesnake population at the northern limits of its range. Consequently, there are very few density estimates by which to compare our results. Furthermore, direct comparisons of snake densities may not be entirely valid across spatial and temporal scales due to specific population requirements as well as differences in ecotypes, prey, and active period lengths (Gregory and Larsen 1996; Blouin-Demers et al. 2002). Near Vernon, B.C., in the northern part of the Okanagan Valley (approximately 140 km north from our study site; Fig. 1), Macartney (1985) estimated population densities of 160 and 250 total individuals/km^2 (adults and juveniles) in two neighboring sub populations during 1981–1983. Although this estimate includes both juveniles and adults, this is still a striking difference compared to our estimate of 58.2 adults/km^2. Techniques in this study were similar to ours; intensive mark-recapture field procedures and Jolly-Seber open population multiple sample mark-recapture models were used to estimate population sizes (as well as survivorship). However, area used in density estimates was solely determined through summer captures of snakes when they had dispersed from their respective dens, whereas our study area was determined by 11 y of mark-recapture occurrences as well as 9 y of radio-telemetry spatial data. On face value, comparing our results to those provided by Macartney (1985) suggests a potentially dramatic difference in snake densities between the two sites and points in time when the data were collected. However, their study was in a different locality in the Okanagan Valley with concomitant differences in rattlesnake habitat and climate, so natural, inherent, regional differences in rattlesnake abundance cannot be ruled out as factors affecting density.

Table 5. Parameter estimates (± SE) for all models used to describe individual lifetime growth from capture-mark-recapture (CMR) data of the Northern Pacific Rattlesnake (*Crotalus o. oreganus*) near Osoyoos, British Columbia, Canada (2002–2011). Parameters are: *a* is the asymptotic size and *k* is the characterisitic growth rate.

Model	Parameter Estimates
von Bertalanffy	$a = 734.8 \pm 16.99$, $k = 0.001032 \pm 1.592\times10^{-4}$
Logistic	$a = 723.1 \pm 13.15$, $k = 0.001438 \pm 1.786\times10^{-4}$
Gompertz	$a = 727.3 \pm 14.53$, $k = 0.001244 \pm 1.688\times10^{-4}$

Preston (1964) worked closer in proximity to our study site (approximately 8 km north), and estimated rattlesnake population densities at 135.9–163.0 individuals/km^2 (adults and juveniles). Again, we must add a caveat to this comparison, as work by Preston was based on two neighboring hibernacula populations, and he calculated the area of his study site similar to that done by Macartney (1985). Furthermore, all rattlesnake captures were recorded within an approximate area of 0.8 km^2. On our study site, our observations and those of our colleagues (Lomas et al. in press) found mean distances that adult male rattlesnakes travelled from their hibernacula was about 976 m, and average home ranges were between 10–36 ha (Lomas et al. in press). Therefore, the likelihood that individual snakes from these hibernacula moved out of this area or that snakes from other hibernacula moved into this area were high, therefore potentially biasing the estimates.

Although fraught with problems, the comparisons we make do not indicate any significant increase in rattlesnake densities across the Okanagan Valley, and it highlights a need for updated, current population estimates and monitoring for this species. However, our data on their own suggest that despite habitat loss and fragmentation occurring in the study site, the rattlesnake population appeared to remain stable over the course of the 11 y. This does not suggest that the population is secure however, as recent work by Lomas et al. (2015)

Table 6. Model selection criteria (AIC_c) for nonlinear growth fitting for mark/recapture data of the Northern Pacific Rattlesnake (*Crotalus o. oreganus*) near Osoyoos, British Columbia, Canada (2002–2011). Abbreviations are *P* = number of parameters; AIC_c = Akaike's information criterion adjusted for small sample sizes; ΔAIC_c = difference lowest AIC and model; AIC_cWt= Akaike weight; LL = log-likelihood.

Model	*P*	AIC_c	ΔAIC_c	AIC_cWt	LL
von Bertalanffy	3	1757.80	0.00	0.95	-875.90
Logistic	3	1770.33	12.53	0.00	-882.17
Gompertz	3	1763.93	6.14	0.04	-878.97

shows that body condition of rattlesnakes in our study site tends to be lower with an increase in landscape disturbance.

Similar to populations of other rattlesnake species (Gregory 1982; Diller and Wallace 2002; Jones et al. 2012; Olson et al. 2015), annual adult survivorship on our study site was high. Previously in B.C., Macartney (1985) estimated minimum annual survivorship in adult rattlesnakes ranging between 0.71–1.00, which is comparable to our survivorship estimates. Survivorship in snakes has been observed and hypothesized to be dependent on many factors, including prey population and abundance (Forsman and Lindell 1997; Olson et al. 2015), reproduction and post parturition behavior (Madsen and Shine 1993; Sperry and Weatherhead 2009), presence of human activity (Sealy 2002), and overwintering conditions (Shine and Mason 2004; Maida et al. 2017). Our results suggest that like many other *Crotalus* species (e.g., Eastern Diamondback Rattlesnake, *C. adamanteus*: Waldron et al. 2013), Northern Pacific Rattlesnakes can demonstrate high annual survivorship in areas where anthropogenic threats are minimized. In some areas of the Okanagan Valley, up to 90% of natural vegetation types have been lost (Lea 2008) primarily through the conversion of natural grasslands to urban and agricultural areas (Lomas et al. 2015; McAllister et al. 2016). Although our study site has experienced dramatic landscape alterations and an influx in human involvement, our results suggest the remaining portions of natural or undisturbed vegetation types on our study site are maintaining a high level of survival and stable population numbers within this decade.

Our mean estimate of 7.1 y for female maturity rates are at the upper limits of previous estimates (4–6 y in Idaho: Diller and Wallace 1984; 5–7 y in B.C.: Macartney and Gregory 1988; 4–6 y in Idaho: Jenkins et al. 2009). Like population density and survivorship, growth rates and age of sexual maturity probably vary both spatially and temporally. Subtle variations in estimates between the studies could be linked to population size, genetic variability (Macartney and Gregory 1988), as well as accuracy and differences in methodologies and models. The previous studies used known-aged snakes and Gompertz models (Macartney and Gregory 1988), rattlesnake size and follicle detection (Diller and Wallace 1984), and von Bertalanffy growth trajectories to determine rattlesnake age and female sexual maturity (Jenkins et al. 2009). Our model selection approach of determining rattlesnake growth and rooting neonate rattlesnake sizes into the growth curve (von Bertalanffy) to estimate individual growth trajectories and ages is a widely used and likely an improved and more accurate method of determining growth and age.

Possibly the most notable findings of our results is the discrepancy between the length of mature females between our study site and that observed in Macartney and Gregory (1988). Previous management plans and baseline biological concepts in B.C. state that rattlesnakes are deemed to be juvenile until 650 mm SVL (COSEWIC 2015; Southern Interior Amphibian and Reptile Recovery Group 2016); however, this does not appear to be an accurate province-wide assessment of rattlesnakes in B.C. Size can certainly differ substantially between populations of the same species of snakes (e.g., Common Garter Snake, *Thamnophis sirtalis*, Gregory and Larsen 1996; Western Rattlesnake, *C. viridis*, Ashton 2001), although whether a distance of 140 km would allow site-specific growth rates to occur is unclear. With similar survival rates (see above), differences in female size due to truncated lifespans at our study site seem less likely. Potentially, female rattlesnake growth has changed significantly in the last 30 y and females do not grow as long before becoming capable of reproduction in the Okanagan Valley anymore. Evidence of reduced growth in rattlesnakes due to disturbance (Jenkins et al. 2009; Lomas et al. 2015) and in other snake species across the globe (Wolfe et al. 2018) supports this theory. Another likely cause is a sizeable discrepancy in female growth and maturity across temporal scales in the northern-most limits of the range of this species. Furthermore, Macartney and Gregory (1988) measured individual snakes by stretching them out along a meter stick (standard measurement of SVL according to Bertram and Larsen 2004), which appears to generate higher estimates of SVL compared to more recent methods (i.e., squeezebox or tubing individuals).

Our observations on the lengths of female maturation (540 mm SVL) are similar to those previously reported by Diller and Wallace (1984, 2002) in Idaho (555 and 632 mm SVL: stretched snakes to measure, approximately 350 km south of our study site). More recently, the length of mature females in Idaho was identified to range between 567–640 mm SVL on three different study sites (mean of 10 smallest gravid females on each site: tubed snakes to measure- Jenkins et al. 2009) approximately 400 km south of the original Diller and Wallace (1984) study site. Snakes typically show a negative association with body size and increasing latitudes (Ashton and Feldman 2003), but based on these comparisons, that trend is not supported by female reproductive size in rattlesnakes. This may be due to the small scale of change in latitude between the studies and/or not accounting for the potential continued growth of these females throughout their life history. However, once mature, growth in reproductively active females is typically negligible (Macartney and Gregory 1988). Regardless, based on these comparisons, there are clear spatial differences in female size of maturity across the northern limits of this species range.

Estimating generation time is a key demographic component to assist species conservation and population monitoring. Individual longevity and generation time are important indicators to project or quantify how a species or population may react, respond or recover from disturbance-related declines on the landscape (Dodd et al. 2006). Our mean generation time estimate of 13.7 y for the Osoyoos population was slightly lower than the estimated 15.6 y (using the same calculation presented herein: 1/annual mortality rate + age of maturity) previously applied to the entire B.C. population of Northern Pacific Rattlesnakes in the province (COSEWIC 2015; IUCN Stands and Petitions Committee 2014). The minimal discrepancy between the two estimates likely will not greatly affect conservation efforts and ultimately adds support to each result. Our generation time is the first produced estimation for a specific population based on intensive, long-term capture-mark-recapture data likely making our estimate more accurate than the blanket estimation produced for all rattlesnakes across B.C.

The results of this study provide important baseline demographic information for future studies and conservation planning efforts for rattlesnakes in B.C. and other parts of the northern limits of range of this species. We did not find any changes to adult rattlesnake survival and population estimates over the 11-y period, suggesting that despite the growth in development and human involvement at our study area, the rattlesnake population remained stable. However, the ability to distinguish fluctuations in survival and population sizes due to anthropogenic causes are difficult in long-lived species. Our study did not span the length of more than one generation, potentially limiting our ability to detect changes to survival and population size. Life-history attributes such as generation time, age at maturation, and survival can influence the lag time between anthropogenic disruptions and population loss or extirpations (Waldron et al. 2013). Furthermore, the presence of rattlesnakes on the landscape may not indicate long-term population health. As mentioned, rattlesnakes living in more disturbed sections of our study area exhibit decreased body conditions (Lomas et al. 2015), an observation consistent with reported trends of slower growth and fewer offspring in populations occupying more disturbed areas of Idaho (Jenkins et al. 2009). Continued long-term monitoring of rattlesnake populations exposed to a changing anthropogenic environment contains promise for understanding convoluted population dynamics and influences, and potentially realizing the long-term consequences to indirect effects of disturbance on this long-lived species.

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