

NEONATAL GROWTH IN CAPTIVE DUSKY RATTLESNAKES (*CROTALUS TRISERIATUS*) FROM TWO POPULATIONS IN CENTRAL MÉXICO

CRECIMIENTO NEONATAL DE LA SERPIENTE DE CASCABEL TRANSVOLCÁNICA (*CROTALUS TRISERIATUS*) CAUTIVAS DE DOS POBLACIONES DEL CENTRO DE MÉXICO

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Resumen.— En las serpientes, el tamaño corporal tiene implicaciones importantes en su ecología, y éste a su vez, depende de la tasa de crecimiento de los individuos. En este estudio, analizamos el primer año de crecimiento en cautiverio de individuos de dos poblaciones de la víbora de cascabel transvolcánica (*Crotalus triseriatus*). Empleamos modelos lineales para estimar las tasas de crecimiento individual, así como para comparar estas tasas entre poblaciones y sexos. La talla al nacer fue mayor en machos que en hembras, y este patrón se mantuvo a lo largo de todo el experimento. La tasa de crecimiento promedio para todos los individuos fue de 7.66 mm/mes. Mientras que el cambio absoluto promedio fue de 79.8 mm. No se detectaron diferencias significativas en las tasas de crecimiento entre poblaciones ni entre sexos. Esto podría indicar que la variación en este atributo puede ser mayor dentro de poblaciones que entre poblaciones.

Palabras clave.— Tamaño corporal, crecimiento corporal, víbora de cascabel, cautiverio, experimento.

Abstract.— Body size has important effects on snake ecology, and in turn, body size is dependent on the rate at which individuals grow. In this study, we analyzed first year captive growth of individuals from two populations of the Mexican dusky rattlesnake (*Crotalus triseriatus*). We used linear models to estimate individual growth rates as well as to compare growth rates between populations and sexes. Birth body size was greater in males than in females, and this pattern remained throughout the experiment. Average growth rate for all individuals was 7.66 mm/month. While the average absolute change was 79.8 mm. No statistical differences were detected in growth rates between populations or sexes. This could indicate that the variation in this attribute may be greater within populations than between populations.

Keywords.— body size, body growth, captivity, rattlesnake, experiment.

INTRODUCCION

Body size shapes many aspects of the ecology of organisms (Calder, 1996). In animals, body size is related to the survival and reproduction of individuals (Stearns, 1992; Roff, 2002). Particularly in reptiles, it is related to reproductive effort in females and reproductive success in males (Shine, 2003; 2005). Characterizing the body size that individuals maintain throughout their life cycle is thus important for the study of the life history and ecology of reptiles.

Ecology and life history data are sometimes difficult to obtain for many snake species in the field because of their secretive nature and low densities (Seigel et al., 1987). Our knowledge of snake ecology has grown extensively in recent years, and there are now several taxa that are well studied (e. g. Bonnet et al., 2001a; Baron et al., 2010; Michel & Bonnet, 2010; Luiselli et al., 2011; Madsen et al., 2020). However, most of these studies have been conducted in North American, European, and Australian snake species (Mullin & Seigel, 2011). Basic data on snake body growth are always valuable to collect because helps to understand the variation in population dynamics and determining how natural selection shapes life history strategies.

Individual body growth is determined by genetic factors, as well as environmental factors such as food availability and, especially in reptiles, environmental temperature (Andrews, 1982; Calder, 1996). Due to behavioral thermoregulation, growth in snakes can vary widely between and within populations (Andrews, 1982). Life-history traits are highly related to fitness. Different environments can favor either slow or fast growers for different selective causes (Ferguson & Brockman, 1980). Nevertheless, phenotypic variation in different environments may not be good evidence for genotypic difference due to genotype-environment interactions. Hence, experimental studies that control environmental conditions are of great importance for evolutionary biology (Stearns, 1992).

Crotalus triseriatus (Wagler, 1830) is a rattlesnake that lives in the mountains of the Trans-Volcanic Mexican Belt (TVMB; Bryson et al., 2014). It inhabits an altitudinal range from 2500 to around 4000 m a.s.l., which is dominated by coniferous forests and subalpine grasslands (Campbell & Lamar, 2004). Consequently, most of its populations are isolated in the mountains of the TMVB, separated by the valleys of central Mexico. This geographic isolation results in little to no genetic flow between distant populations within its distribution (Sunny et al., 2015; 2018; 2019). These characteristics make it a great system for exploring variation in life history strategies between populations living at

different, isolated sites, as isolation might lead to changes in life history traits, such as individual body growth rates, between populations. This type of intraspecific variation in life history traits has been documented in populations of other species of reptiles (Ferguson & Brockman, 1980; Gregory & Larsen, 1993; Tinkle et al., 1993; Plummer, 1997; Bronikowski & Arnold, 1999; Aldridge et al., 2008; Hileman et al., 2010).

Currently, no studies have characterized body growth in *Crotalus triseriatus* in the field nor in captivity. Here, we analyze first-year growth in captivity of individuals from two populations of *C. triseriatus*. Although individuals experienced the same conditions in captivity (temperature, quantity and frequency of food), due to a degree of potential genetic determination, we expect that there might be differences in the growth rates in individuals from different populations.

MATERIAL AND METHODS

Study species and sites. *Crotalus triseriatus* is a small-sized rattlesnake species, adults commonly exceed 600 mm snout-vent length (SVL) (Campbell & Lamar, 2004). It occurs from central Veracruz to east Michoacán and is considered locally abundant (Bryson et al., 2014; Pérez-Mendoza et al., 2018). *Crotalus triseriatus* holds the highest-altitude record for a snake in the Americas, reaching 4,573 m a.s.l. (Mani & Giddings, 1980). We worked with two populations. Site 1 (Cumbres del Ajusco National Park; 19.22° N, -99.28° W) is located within the limits of Mexico City and corresponds to the mountain chain that closes the southern part of the Valley of Mexico. Site 2 (La Malinche National Park; 19.24° N, -97.99° W) is located in the state of Tlaxcala, bordering the state of Puebla. This National Park covers the area of a volcano isolated from other mountain formations, making it an island for high mountain flora and fauna in the region.

Sampling. During late winter and spring of 2015 (late stage of gestation; Campbell & Lamar, 2004), we collected pregnant females of *C. triseriatus* in both study sites (5 from site 1 and 5 from site 2). These were kept in the laboratory until parturition. The size and weight of the neonates were recorded (between 0 and 5 days later; reproductive traits of these litters are reported in Pérez-Mendoza et al., 2018). Forty randomly selected newborns were kept in captivity for the experiment (11 from site 1 and 29 from site 2).

The snakes were kept individually in 40×20×20 cm plastic terrariums with ad libitum access to water. The air temperature in captivity was maintained between 20–30°C for all individuals throughout the study, and the light cycle was 12 h light: 12 h

dark. The neonates were fed every twelve days with mice (*Mus musculus*; average mice weight: 2.8 g, standard error: 0.04 g; range of weights through the study: 1.08-8.04 g); these were introduced alive to stimulate feeding. A record was kept of the amount and weight of the food items consumed to ensure that the individuals consumed the same amount of food throughout the experimental period. Snout-vent length (SVL), tail length, total length (TL) and mass were measured monthly from June–July 2015 (depending on the date of birth) until June 2016.



Figura 1. Imagen de muestra que muestra cómo se tomaron las medidas del tamaño corporal de un *Crotalus triseriatus* juvenil utilizando un software de procesamiento de imágenes.

Figure 1. Sample image demonstrating how measurements of body size were taken from a juvenile *Crotalus triseriatus* using image processing software.

All measurements were made by the first author. Tail length was measured to the nearest mm with a Vernier caliper. To avoid excessive handling of individuals, the total length was obtained through photographic records and analysis in an image processing software (Snake Measure Tool; downloaded in <https://sourceforge.net/projects/snakemt/>). Photographs were taken from a 90° angle to minimize errors in measurements (Astley et al., 2017; e.g., Figure 1). SVL was calculated by subtracting the tail length from total length. Mass was determined on a precision scale to the nearest 0.01 g. The birth characteristics of the neonates' part of this study were published in Pérez-Mendoza et al. (2018).

Statistical analysis. The growth rate analysis was carried out by means of linear models. We used the method called “Derived variable statistics,” also known as “response variable analysis”

(Crowder & Hand, 1990; Diggle et al., 1994; Davis, 2003). We performed linear regressions for each of the individuals with time as the independent variable and the SVL or mass as dependent variables. The slopes (β) obtained were taken as the individual growth rates; these were grouped by population and sex, and differences were evaluated by Student's t-tests (parametric assumptions were met). Also, growth rates (β) were analyzed by a generalized linear model with population and sex as factors to evaluate interactive effects.

In addition, we analyzed growth using two other methods: the absolute change in SVL (ABS = final SVL - initial SVL) and the relative change in SVL (REL = [final SVL - initial SVL] / initial SVL) of the individuals. Since growth could vary as a function of initial size and the amount of food consumed, we performed correlation tests between these variables and the ABS and REL growth variables. If there was a correlation, we used the initial size or the amount of food as a covariate in the following analyzes (GLM's). We analyzed these variables (ABS and REL) using Student's t-tests and generalized linear models to test for population and/or sex effects. We decided to execute these last analyzes only with the SVL and not the mass because SVL is a better indicator of growth in this group. Analyses were performed with package “stats” in R version 4.1.0. (R Development Core Team 2020).

RESULTS

Eight snakes died during the study; thus, the analyses were restricted to the remaining 32 individuals, who were healthy and active throughout the experiment (8 from site 1 and 24 from site 2). Although the data were normally distributed, we also performed the non-parametric version of the t-test (Mann-Whitney U) in addition to the GLM's because of the small sample sizes. As the results of all analyses were consistent in terms of the statistical decision, we only report the results of the parametric and GLM analyses. We found a barely significant relationship between mortality and size at birth ($t = 2.09$, $P = 0.04$). On average, individuals who died before the end of the experiment had a lower SVL at birth. We did not find a relationship between mortality and sex ($\chi^2 = 5.67e-32$, $P \approx 1$).

Most of the neonates showed strong feeding responses during the experiment. During the first 3 feeding events, some individuals that did not react to food after one complete day were force-fed. After the fourth feeding event, all individuals ate on their own. The average weight of the mice consumed throughout the study did not vary significantly between populations or sexes ($t_{pop} = 0.89$, $df = 7.09$, $P = 0.39$; $t_{sex} = -0.17$, $df = 13.68$, $P = 0.86$).

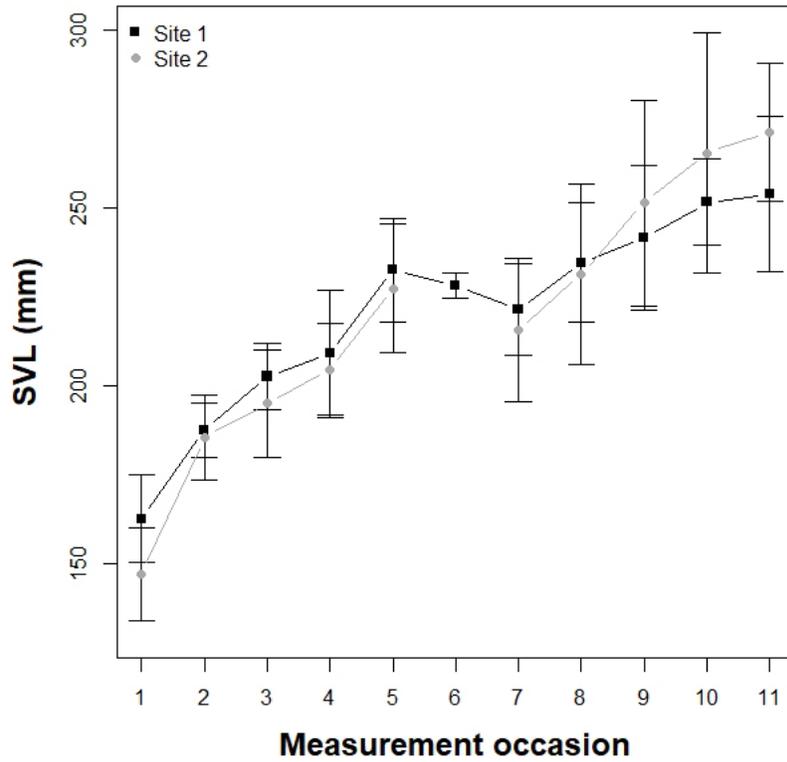


Figura 2. Trayectorias de crecimiento en cautiverio de neonatos de *Crotalus triseriatus* de dos sitios de estudio.
Figure 2. Growth trajectories of captive neonates of *Crotalus triseriatus* from two study sites.

Tabla 1. Medias de la LHC inicial y final, la longitud de la cola, la tasa de crecimiento de la LHC, la tasa de crecimiento de la masa, el cambio absoluto (ABS), y relativo (REL) en la LHC de neonatos de *Crotalus triseriatus*.

Table 1. Mean of initial and final SVL, tail length, SVL growth rate, mass growth rate, and absolute (ABS) and relative (REL) change in SVL for neonates of *Crotalus triseriatus*.

Site	N	Initial tail length (mm)	Final tail length (mm)	Initial SVL (mm)	Final SVL (mm)	SVL growth rate (mm/m)	Mass growth rate (gr/m)	ABS
1	8	24.33	29.33	168.83	254.16	9.32	1.24	77.6
2	24	21.32	28.76	185.22	271.38	7.11	1.06	80.6
Sex								
F	12	20.93	24.77	180.97	258.38	9.04	1.06	0.77
M	20	24.02	32.08	186.23	271.92	9.39	1.29	0.82



Tail size did not differ between populations or sexes at birth ($t_{\text{sex}} = 1.92$, $P = 0.07$; $t_{\text{pop}} = -2.25$, $P = 0.05$; $t_{\text{pop} \times \text{sex}} = 1.78$, $P = 0.09$). Nevertheless, it did vary between sexes at the end of the experiment ($t_{\text{sex}} = 4.00$, $P = 0.001$; $t_{\text{pop}} = -0.23$, $P = 0.81$; $t_{\text{pop} \times \text{sex}} = 1.03$, $P = 0.31$). At birth, the average SVL was higher in males than in females ($t = -6.20$, $df = 13.38$, $P < 0.001$), and this pattern held until when the last measurements were taken ($t = -3.21$, $df = 7.89$, $P = 0.012$; Table 1). The individual SVL range varied little during the study. In general, the longest snakes at the beginning of the study remained the longest at the end. Moreover, the initial SVL of the individuals was correlated with their final SVL ($r^2 = 0.51$, $P = 0.01$).

The average SVL growth rate for all individuals was 7.66 mm/month ($SE = 0.85$). The average SVL growth rates for sites 1 and 2 were 9.32 and 7.11 mm/month, respectively ($SE_1 = 0.63$, $SE_2 = 0.91$). The female growth rate was 9.04 mm/month, and the male growth rate was 9.39 mm/m ($SE_f = 0.77$, $SE_m = 0.70$). However, no significant differences were detected in the SVL growth rates between populations or between sexes ($t_{\text{pop}} = 1.72$, $df = 25.94$, $P = 0.09$; Fig 2; $t_{\text{sex}} = -0.32$, $df = 14.13$, $P = 0.74$). The monthly increase in mass varied less, which was 1.24 and 1.19 gr / m for sites 1 and 2, respectively ($SE_1 = 0.10$, $SE_2 = 0.14$; $t_{\text{pop}} = -0.32$, $df = 14.13$, $P = 0.74$), and 1.06 and 1.29 gr / m for females and males, respectively ($t_{\text{sex}} = -1.66$, $df = 15.84$, $P = 0.11$; Table 1).

No significant effects for the population \times sex interaction on the SVL growth rates ($t_{\text{pop} \times \text{sex}} = -0.12$, $P = 0.90$) or mass ($t_{\text{pop} \times \text{sex}} = 0.009$, $P = 0.99$) were detected by the GLMs. Furthermore, there were no significant differences between populations and sexes in the SVL growth rate ($t_{\text{pop}} = 0.59$, $P = 0.55$; $t_{\text{sex}} = 0.26$, $P = 0.79$).

The average absolute change in SVL was 79.8 mm, and the relative change was 0.43 mm. The absolute and relative changes in SVL also did not show significant differences between populations or sexes (ABS: $t_{\text{pop}} = -0.33$, $df = 8.27$, $P = 0.74$; $t_{\text{sex}} = -0.46$, $df = 12.02$, $P = 0.64$; REL: $t_{\text{pop}} = 0.69$, $df = 7.81$, $P = 0.50$; $t_{\text{sex}} = -0.09$, $df = 11.48$, $P = 0.92$; Table 1; Figure 2).

DISCUSSION

The mortality observed during the experiment was mainly associated with individuals who did not feed on their own or were delayed in feeding on their own. We do not assume that this was associated with the type of food offered during the experiment because most of the neonates fed without difficulty. Most rattlesnake species are known to prefer feeding on rodents, although they are often generalists in early life stages (Campbell & Lamar, 2004).

It has been documented that the first three months in captivity are the most critical in terms of survival and adaptation in wild caught snakes (Braz et al., 2012). Although born in captivity, we observed this pattern with *Crotalus triseriatus*, the frequency of mortality was higher during the firsts months after birth. The inability to adapt to the captive environment, known as Maladaptation syndrome, has been recognized as the major cause of death in captive reptiles (Cowan, 1980). This syndrome is defined as the pathological effects of stress on an animal related to the captive environment (Cowan, 1968), and it may cause anorexia and emaciation among other consequences. We found that on average, individuals with smaller SVL at birth were more likely to die than larger individuals ($P = 0.04$). However, there were relatively small individuals who survived the entire study and individuals with higher SVL at birth who did not.

We found that size at birth was higher in males than in females, and this difference was maintained throughout the experiment. Sexual dimorphism in SVL has been observed in neonates of *Storeria dekayi* and *Thamnophis sirtalis*. Females exceeded males in SVL in *S. dekayi*, while males exceeded females in *T. sirtalis* (King et al., 1999; Krause & Burghardt, 2007). In rattlesnakes, Beupre et al. (1998) did not find sexual dimorphism in SVL in neonates of *Crotalus atrox*, and Taylor & Denardo (2005) later confirmed this pattern. We did not find sexual dimorphism in tail length in neonate rattlesnakes; however, there were differences in tail length at the end of the experiment. In the last measurement, males had longer tails than females (Table 1). Many snake species exhibit sexual dimorphism in adult stages; however, it is not as common at birth (King, 1989; Shine, 1993; Bonnet et al., 2011). Sexual dimorphism in tail size is related to the caudal position of the hemipenis, and this pattern is consistent in most species (Shine, 1993).

There was a decrease in average SVL in individuals from both snake populations on two measurement occasions (Fig. 2). This may have been caused by measurement error; however, all measurements were made by the same observer and with the same methodology. These observations occurred during the winter period (from January to February); some reptiles have been observed to decrease in size under suboptimal conditions (Wikelski & Thom, 2000), such as low temperatures and food scarcity. Nevertheless, studies in snakes are not conclusive on whether they can shrink; in most cases, apparent shrinkage is a result of measurement error (Madsen & Shine, 2001a; Blouin-Demers, 2003; Luiselli, 2005). We evaluated intra-observer error by analyzing the variances of each measurement occasion with ANOVA, and found no significant differences. The laboratory conditions were identical for all the individuals within the

experiment, however there was a small variation in temperature in the winter period, in which lower temperatures in the laboratory (closer to 20 °C) were detected more frequently than during the other seasons of the year.

Individual growth rates are determined by extrinsic and intrinsic factors. In this experiment, we reduced as possible the environmental factors (extrinsic) that affect growth under natural conditions to detect differences in factors related to the genetics of individuals (intrinsic), such as belonging to a particular population or to a certain sex, which we hypothesized might shape differences in growth rates. However, our results did not support this hypothesis. This might be explained for two reasons. First, because sample sizes were small and unequal between sites, we might not have had sufficient statistical power to resolve intrinsic differences in growth rates. Ideally, the effects of population, sex and litter would be tested simultaneously. However, we did not include litter as a factor because of the low sample size. Second, with the exception of mass at birth (Pérez-Mendoza et al., 2018), no local adaptation in growth rates has been observed in the studied sites, in contrast to other life history attributes in these same populations (e.g., litter size, size at birth).

In snakes, these attributes can be highly plastic and vary widely within and between populations (Ford & Seigel, 1989; Gregory & Larsen, 1993; Gregory & Prelypchan, 1994; Gregory & Farr, 2018). Under the same captivity conditions, we did not find differences in neonatal growth rates between the two populations studied. Growth plasticity in snakes may be an adaptation to variable environments and might be more responsive to resource availability (Forsman & Lindell, 1996; Bonnet et al., 2001b; Taylor & Denardo, 2005).

Although the differences between population growth rates were not statistically significant ($P = 0.095$), there was a slight difference in growth rates between populations. Specifically, individuals from site 1 grew slightly faster on average ($GRS_1 = 9.3$ mm / year; $GRS_2 = 7.1$ mm / year). Site 1 (Ajusco National Park) has lower operative temperatures and therefore habitat with lower thermal quality (Jaramillo-Alba et al., 2020). Such thermal conditions might favor the selection of fast-growing individuals even under harsh conditions or that optimizes growth under the time windows when conditions are optimal; whereas, other populations inhabiting sites with higher thermal quality, such as site 2, may not favor faster or slower growth, as thermal environment is optimal during longer periods (Jaramillo-Alba et al., 2020). However, this hypothesis needs to be tested with a greater number of populations and a larger sample size

while controlling for other factors that might affect individual growth rate variation. As most life history theory has been derived from interspecies studies; intraspecies-level patterns of variation are expected to not be as predictable based on current theory (Dunham et al., 1988). Studies between populations of the same species are particularly important, as such studies permit genetic and non-genetic factors to be distinguished. Widely distributed species or species with isolated populations are particularly valuable because they may show greater diversity in life history attributes (Gregory & Larsen, 1993).

Studies that have analyzed rattlesnake body growth in the wild have shown that this attribute can be highly variable. Macartney et al. (1990) found differences in growth rates between sexes in *Crotalus viridis*, males grew at a higher rate than females. In addition, they found differences in growth between different populations, growth rates varied in relation to latitude (differences in activity and hibernation periods between southern and northern populations). They also reported differences in growth rates between years related to variation in annual precipitation. Wittenberg & Beaupre (2014) reported differences in growth rates between populations of *Crotalus horridus*. They report that prey abundance had the strongest effect in growth rates. Other studies have indicated that prey availability has a greater effect on snake growth than genetic differences among individuals (Madsen & Shine, 1993, 2000; Forsman & Lindell, 1996). Field studies are needed to determine the relative magnitude of these effects in *Crotalus triseriatus*.

Data on rattlesnake growth rates for both neonates and adults are especially useful. Few studies have analyzed individual growth in snakes (especially in tropical areas; e.g., Madsen & Shine, 2000; Madsen & Shine, 2001b; Brown et al., 2017), and studies in such regions are particularly important because variation in individual growth between size classes is key for understanding population growth rates.

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CITED LITERATURE

- Aldridge, R.D., B.C. Jellen, M.C. Allender, M.J. Dreslik, D.B. Shepard, J.M. Cox & C.A. Phillips. 2008. Reproductive biology of the Massasauga (*Sistrurus catenatus*) from South-central Illinois. Pp. 403-412. In W. Hayes, K. Beaman, M. Cardwell & S.P. Bush (Eds.), *Biology of the Rattlesnake*. Loma Linda University Press, Loma Linda, California, USA.
- Andrews, R.M. 1982. Patterns of growth in reptiles. Pp. 273-320. In C. Gans & F.H. Pouch (Eds.), *Biology of the Reptilia*, Volume 13. Physiology D. Physiological Ecology. Academic Press, London, New York, Paris, San Diego, San Francisco, São Paulo, Sydney, Tokyo, and Toronto.
- Astley, H.C., V.E. Astley, D. Brothers & J.R. Mendelson, III. 2017. Digital analysis of photographs for snake length measurement. *Herpetological Review* 48:39-43.
- Baron, J.P., J.F. Le Galliard, T. Tully & R. Ferrière. 2010. Cohort variation in offspring growth and survival: prenatal and postnatal factors in a late-maturing viviparous snake. *Journal of Animal Ecology* 79:640-649.
- Beaupre, S.J., D. Duvall & J. O'Leile. 1998. Ontogenetic variation in growth and sexual size dimorphism in a central Arizona population of the western diamondback rattlesnake (*Crotalus atrox*). *Copeia* 1998:40-47.
- Blouin-Demers, G. 2003. Precision and accuracy of body-size measurements in a constricting, large-bodied snake (*Elaphe obsoleta*). *Herpetological Review* 34:320-322.
- Bonnet, X., G. Naulleau, R. Shine & O. Lourdais. 2001a. Short-term versus long-term effects of food intake on reproductive output in a viviparous snake, *Vipera aspis*. *Oikos* 92:297-308.
- Bonnet, X., R. Shine, G. Naulleau & C. Thiburce. 2001b. Plastic vipers: influence of food intake on the size and shape of Gaboon vipers (*Bitis gabonica*). *Journal of Zoology* 255:341-351.
- Bonnet, X., S. Lorigou, D. Pearson, F. Aubret, D. Bradshaw, V. Delmas & T. Fauvel. 2011. Which proximate factor determines sexual size dimorphism in tiger snakes?. *Biological Journal of the Linnean Society* 3:668-680.
- Braz, H.B., M.M.T.D. Rocha & M.D.F. Furtado. 2012. Maintaining rear-fanged snakes for venom production: an evaluation of mortality and survival rates for *Philodryas olfersii* and *P. patagoniensis* in captivity. *Journal of Venomous Animals and Toxins including Tropical Diseases* 18:164-172.
- Bronikowski, A.M. & S.J. Arnold. 1999. The evolutionary ecology of life history variation in the garter snake *Thamnophis elegans*. *Ecology* 80:2314-2325.
- Brown, G.P., T.R. Madsen & R. Shine. 2017. Resource availability and sexual size dimorphism: differential effects of prey abundance on the growth rates of tropical snakes. *Functional Ecology* 31:1592-1599.
- Bryson, R.W. Jr., C.W. Linkem, M.E. Dorcas, A. Lathrop, J.M. Jones, J. Alvarado-Diaz, C.I. Grünwald & R.W. Murphy. 2014. Multilocus species delimitation in the *Crotalus triseriatus* species group (Serpentes: Viperidae: Crotalinae), with the description of two new species. *Zootaxa* 3826:475-496.
- Calder, W.A. 1996. Size, function, and life history. Courier Corporation.
- Campbell, J.A. & W.W. Lamar. 2004. The venomous reptiles of the Western Hemisphere (Volume. 2). Ithaca [NY]: Comstock Pub. Associates.
- Cowan, D.F. 1968. Diseases of captive reptiles. *Journal of the American Veterinary Medical Association* 153:848-859.
- Cowan, D.F. 1980. Adaptation, maladaptation and disease. 91-6 Pp. In: Murphy, J.B. & J.T. Collins (Eds.), *Reproductive biology and diseases in captive reptiles*, SSAR contributions to Herpetology.
- Crowder, M.J. & D.J. Hand. 1990. Analysis of repeated measures. *Monographs on Statistics and Applied Probability* (Volume 41). CRC Press.
- Davis, C.S. 2003. Statistical methods for the analysis of repeated measurements. Springer.
- Diggle, P.J., K.Y. Liang & S.L. Zeger. 1994. Analysis of Longitudinal Data. Oxford University Press, Oxford.
- Dunham, A.E., D.B. Miles & D.N. Reznick. 1988. Life history patterns in squamate reptiles. Pp. 441-511. In C. Gans & R.B. Huey (Eds.), *Biology of the Reptilia*, Volume 16. Alan R. Liss, New York.



- Ferguson, G.W. & T. Brockman. 1980. Geographic differences of growth rate of *Sceloporus* lizards (Sauria: Iguanidae). *Copeia* 1980:259-264.
- Ford, N.B. & R.A. Seigel. 1989. Phenotypic plasticity in reproductive traits: evidence from a viviparous snake. *Ecology* 70:1768-1774.
- Forsman, A. & L.E. Lindell. 1996. Resource dependent growth and body condition dynamics in juvenile snakes: an experiment. *Oecologia* 4:669-675.
- Gregory, P.T. & K.W. Larsen. 1993. Geographic variation in reproductive characteristics among Canadian populations of the common garter snake (*Thamnophis sirtalis*). *Copeia* 1993:946-958.
- Gregory, P.T. & C.J. Prelypchan. 1994. Analysis of variance of first-year growth in captive garter snakes (*Thamnophis elegans*) by family and sex. *Journal of Zoology* 232:313-322.
- Gregory, P.T. & D.R. Farr. 2018. Factors affecting litter size in Western Gartersnake (*Thamnophis elegans*) in British Columbia: place, time, and size of mother. *The Canadian Field-Naturalist* 1:36-42.
- Hileman, E.T., R.B. King, J.M. Adamski, T.G. Anton, R.L. Bailey, S.J. Baker, N.D. Bieser, T.A. Bell Jr., K.M. Bissell, D.R. Bradke, Henry Campa III, G.S. Casper, K. Cedar, M.D. Cross, B.A. DeGregorio, M.J. Dreslik, L.J. Faust, D.S. Harvey, R.W. Hay, B.C. Jellen, B.D. Johnson, G. Johnson, B.D. Kiel, B.A. Kingsbury, M.J. Kowalski, Y.M. Lee, A.M. Lentini, J.C. Marshall, D. Mauger, J.A. Moore, R.A. Paloski, C.A. Phillips, P.D. Pratt, T. Preney, K.A. Prior, A. Promaine, M. Redmer, H.K. Reinert, J.D. Rouse, K.T. Shoemaker, S. Sutton, T.J. Van De Walle, P.J. Weatherhead, D. Wynn & A. Yagi. 2017. Climatic and geographic predictors of life history variation in Eastern Massasauga (*Sistrurus catenatus*): A range-wide synthesis. *PloS One* 12:e0172011.
- Jaramillo-Alba, J.L., A.H.D. de la Vega, L.E. Bucio-Jiménez, F.R. Méndez-De la Cruz & H.A. Pérez-Mendoza. 2020. Comparative thermal ecology parameters of the mexican dusky rattlesnake (*Crotalus triseriatus*). *Journal of Thermal Biology* 92:102695.
- Krause, M.A. & G.M. Burghardt. 2007. Sexual dimorphism of body and relative head sizes in neonatal common garter snakes. *Journal of Zoology* 272:156-164.
- King, R.B. 1989. Sexual dimorphism in snake tail length: sexual selection, natural selection, or morphological constraint?. *Biological Journal of the Linnean Society* 38:133-154.
- King, R.B., T.D. Bittner, A. Queral-Regil & J.H. Cline. 1999. Sexual dimorphism in neonate and adult snakes. *Journal of Zoology* 247:19-28.
- Luiselli, L. 2005. Snakes don't shrink, but 'shrinkage' is an almost inevitable outcome of measurement error by the experimenters. *Oikos* 110:199-202.
- Luiselli, L., T. Madsen, D. Capizzi, L. Rugiero, Pacini, N. & M. Capula. 2011. Long-term population dynamics in a Mediterranean aquatic snake. *Ecological Research* 4:745-753.
- Macartney, J.M., P.T. Gregory & M.B. Charland. 1990. Growth and sexual maturity of the western rattlesnake, *Crotalus viridis*, in British Columbia. *Copeia* 1990:528-542.
- Madsen, T. & R. Shine. 2000. Silver spoons and snake body sizes: prey availability early in life influences long-term growth rates of free-ranging pythons. *Journal of Animal Ecology* 69:952-958.
- Madsen, T. & R. Shine. 2001a. Do snakes shrink?. *Oikos* 92:187-188.
- Madsen, T. & R. Shine. 2001b. Conflicting conclusions from long-term versus short-term studies on growth and reproduction of a tropical snake. *Herpetologica* 57:147-156.
- Madsen, T., J. Loman, L. Anderberg, H. Anderberg, A. Georges & B. Ujvari. 2020. Genetic rescue restores long-term viability of an isolated population of adders (*Vipera berus*). *Current Biology* 30:R1297-R1299.
- Mani, M.S. & L.E. Giddings. 1980. *Ecology of Highlands*. W. Junk, The Hague.
- Michel, C.L. & X. Bonnet. 2010. Contrasted thermal regimes do not influence digestion and growth rates in a snake from a temperate climate. *Physiological and Biochemical Zoology* 83:924-931.
- Mullin, S.J. & R.A. Seigel. 2011. *Snakes: ecology and conservation*. Cornell University Press.
- Pérez-Mendoza, H.A., S.R. Sanabria-Tobón, J.L. Jaramillo-Alba, I. Solano-Zavaleta, L.F. Vázquez-Vega & A.H. Díaz de la Vega-Pérez. 2018. Reproductive traits of dusky rattlesnakes (*Crotalus triseriatus*) in Central Mexico. *Journal of Herpetology* 52:6-11.
- Plummer, M.V. 1997. Population ecology of green snakes (*Ophedryx aestivus*) revisited. *Herpetological Monographs* 1997:102-123.



- R Core Team. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. 2020. URL <https://www.R-project.org/>.
- Roff, D.A. 2002. Life History Evolution. Sinauer Associates Inc., USA.
- Sasa, M., J.A. Ortega & F. Bonilla-Murillo. 2017. Assessing survival of wild-caught snakes in open venom production systems. *Toxicon* 138:49-52.
- Seigel, R.A., J.T. Collins & S.S. Novak (Eds.). 1987. Snakes: Ecology and Evolutionary Biology. McGraw Hill Publishing Company, USA.
- Shine, R. 1993. Sexual dimorphism in snakes. Pp. 49-86. In Seigel R. & J. Collins (Eds.), Snakes, ecology and behavior. Cornell University Press.
- Shine, R. 2003. Reproductive strategies in snakes. *Proceedings of the Royal Society of London B* 270:995-1004.
- Shine, R. 2005. Life-history evolution in reptiles. *Annual Review of Ecology, Evolution, and Systematics* 36:23-46.
- Stearns, S.C. 1992. The Evolution of Life Histories. Oxford University Press, UK.
- Sunny, A., O. Monroy-Vilchis, M.M. Zarco-González, G.D. Mendoza-Martínez & D. Martínez-Gómez. 2015. Genetic diversity and genetic structure of an endemic Mexican Dusky Rattlesnake (*Crotalus triseriatus*) in a highly modified agricultural landscape: implications for conservation. *Genetica* 143:705-716.
- Sunny, A., O. Monroy-Vilchis & M.M. Zarco-González. 2018. Genetic diversity and structure of *Crotalus triseriatus*, a rattlesnake of central Mexico. *Journal of genetics* 97:1119-1130.
- Sunny, A., F.J. Gandarilla-Aizpuro, O. Monroy-Vilchis & M.M. Zarco-Gonzalez. 2019. Potential distribution and habitat connectivity of *Crotalus triseriatus* in Central Mexico. *Herpetozoa* 32:139.
- Taylor, E.N. & D.F. Denardo. 2005. Sexual size dimorphism and growth plasticity in snakes: an experiment on the Western Diamond-backed Rattlesnake (*Crotalus atrox*). *Journal of Experimental Zoology Part A Comparative Experimental Biology* 303:598-607.
- Tinkle, D.W., A.E. Dunham & J.D. Congdon. 1993. Life history and demographic variation in the lizard *Sceloporus graciosus*: a long-term study. *Ecology* 74:2413-2429.
- Wagler, J. 1830. Natürliches System der Amphibien: mit vorangehender Classification der Säugethiere und Vögel: ein Beitrag zur vergleichenden Zoologie. Cotta'schen, München.
- Wikelski, M. & C. Thom. 2000. Marine iguanas shrink to survive El Niño. *Nature* 403:37-38.
- Wittenberg, R.D. & S.J. Beaupre. 2014. Growth of timber rattlesnakes (*Crotalus horridus*) in an agriculturally fragmented and a contiguously forested habitat. *Herpetologica* 70:171-183.

