



Life stories

Female reproductive cycle and clutch size of *Aspidoscelis costata costata* (Squamata: Teiidae) from Tonatico, Estado de México

Ciclo reproductor de las hembras y tamaño de nidada de Aspidoscelis costata costata (Squamata: Teiidae) en Tonatico, Estado de México

Ana E. López-Moreno^a, Justin L. Rheubert^b, Carlos Pérez-Almazán^a,
Gisela Granados-González^c, Laura E. Hernández-Hernández^a, Kevin M. Gribbins^d,
Oswaldo Hernández-Gallegos^{a,*}

^a Laboratorio de Herpetología, Facultad de Ciencias, Universidad Autónoma del Estado de México, Instituto Literario # 100, Colonia Centro, 50000 Toluca, Estado de México, Mexico

^b College of Sciences, University of Findlay, 1000 N. Main St., Findlay, OH 45840, USA

^c Laboratorio de Morfofisiología de la Reproducción, Facultad de Ciencias, Universidad Autónoma del Estado de México, Instituto Literario # 100, Colonia Centro, 50000 Toluca, Estado de México, Mexico

^d Department of Biology, University of Indianapolis, 1400 E. Hanna Ave, Indianapolis, IN 46227, USA

Received 15 March 2016; accepted 22 August 2016

Available online 4 November 2016

Abstract

Female reproductive cycle and clutch size are important life history traits in lizards that can be influenced by biotic and/or abiotic factors. Here, the ovarian cycle and clutch size of a high-elevation population (1500–1600 m) of *Aspidoscelis costata costata* in Central Mexico are described. Females were collected monthly between 2005 and 2007, and their reproductive condition was evaluated based on appearance and size of ovarian follicles and presence/absence of oviductal eggs. The reproductive cycle was markedly seasonal with asynchrony in reproductive condition among females. Vitellogenic and gravid females were recorded from April (end of the dry season) through July (middle of the rainy season). Although this population inhabits a semi-humid warm climate, the timing of female reproduction in *A. costata costata* is similar to the cycle of temperate-zone species of *Aspidoscelis*. Females produced a single clutch annually with an average clutch size of 7.7 ± 0.44 eggs (median 8 eggs, range 4–14), which is the largest reported to date within the genus *Aspidoscelis*.

© 2016 Universidad Nacional Autónoma de México, Instituto de Biología. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

Keywords: Endemic oviparous lizard; Female life history traits; Oviductal eggs; Whiptail lizard; High-elevation population; High-reproductive output

Resumen

El ciclo reproductor de las hembras y el tamaño de nidada en lagartijas son características importantes de historia de vida que pueden ser influenciadas por factores bióticos y/o abióticos. En este trabajo se describen el ciclo ovárico y el tamaño de nidada de *Aspidoscelis costata costata* en una población de elevación alta (1,500–1,600 m) del centro de México. Las hembras se recolectaron mensualmente entre 2005 y 2007 y se evaluó su condición reproductora con base en la apariencia y tamaño de los folículos ováricos, y la presencia o ausencia de huevos oviductales. El ciclo reproductor fue marcadamente estacional con asincronía ovárica entre las hembras. Hembras vitelogénicas y grávidas se registraron desde abril (final de la estación de sequía) hasta julio (mediados de la estación de lluvias). No obstante que esta población habita en un clima cálido

* Corresponding author.

E-mail address: ohg@uaemex.mx (O. Hernández-Gallegos).

Peer Review under the responsibility of Universidad Nacional Autónoma de México.

sub-húmedo, el ciclo reproductor en las hembras de *A. costata costata* es similar al ciclo de las especies de *Aspidoscelis* de zonas templadas. Las hembras producen una sola nidada anualmente con un tamaño de nidada promedio de 7.7 ± 0.44 huevos (mediana 8 huevos, intervalo 4–14), que es el más alto registrado dentro del género *Aspidoscelis*.

© 2016 Universidad Nacional Autónoma de México, Instituto de Biología. Este es un artículo Open Access bajo la licencia CC BY-NC-ND (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

Palabras clave: Lagartija ovípara endémica; Características de historia de vida en hembras; Huevos oviductales; Lagartija cola de látigo; Población de elevación alta; Esfuerzo reproductor alto

Introduction

The female reproductive cycle often exhibits intra and inter-specific variation in lizards (Fitch, 1970). Temperate species of *Aspidoscelis* show a seasonal female reproductive cycle with increased activity during spring and summer (lasting for 5 or less months, mainly within the rainy season; Vitt & Breitenbach, 1993). In tropical species, both seasonal and continuous patterns have been recorded. In these species, the female reproductive cycle may be extended (lasting for 6–8 months, which includes part of the dry season; Güizado-Rodríguez, 2006; Hernández-Gallegos, Ballesteros-Barrera, Villagrán-Santa Cruz, Alonzo-Parra, & Méndez-de la Cruz, 2003; Manríquez-Morán, Villagrán-Santa Cruz, & Méndez-de la Cruz, 2005; Ramírez-Bautista, Balderas-Valdivia, & Vitt, 2000; Ramírez-Bautista & Pardo-de la Rosa, 2002), or may simply be a continuous reproductive activity throughout the year (Fitch, 1973).

The timing, length, and intensity of each phase of the ovarian cycle are variable (Hernández-Gallegos et al., 2003; Manríquez-Morán et al., 2005), and thus hypothesized to be regulated by characteristics of the habitat and/or environmental cues (photoperiod, temperature, and moisture; Van Dyke, 2015). However, the marked asynchrony in reproductive condition among females of *Aspidoscelis* (Hernández-Gallegos et al., 2003; Manríquez-Morán et al., 2005; Zaldivar-Rae, Drummond, Ancona-Martínez, Manríquez-Morán, & Méndez-de la Cruz, 2008), makes it difficult to evaluate the effects of biotic and/or abiotic factors (Manríquez-Morán et al., 2005). Moreover, some species do not exhibit a correlation between reproductive cycle and microhabitat features or climate, suggesting that the female reproductive cycles represent an “evolutionary baggage” rather than an ecological adaptation (Censky & McCoy, 1988; James & Shine, 1985).

Clutch size is considered one of the most important life history parameters of vertebrates (Stearns, 1989), and has been hypothesized to be correlated with several factors. For instance, clutch size in reptiles can be influenced by ecological (Benabib, 1994; Censky & McCoy, 1988; Dunham, Miles, & Reznick, 1988), evolutionary (Dunham & Miles, 1985; Webb, Brook, & Shine, 2002), anatomical (Du, Ji, & Shine, 2005; Olsson & Shine, 1997a; Olsson, Wapstra, & Olofsson, 2002), and/or physiological factors (Brown & Shine, 2009; Méndez-de la Cruz, Guillelte, & Villagrán-Santa Cruz, 1993; Shine, 1980). In general, Teiid lizards are considered to be active foragers that move about in search of prey. Due to their foraging mode, predator escape tactics, and streamlined body, active foraging

lizards (i.e., *Aspidoscelis*) tend to possess relatively small clutch sizes (Dunham & Miles, 1985; Trauth, 1983; Vitt, 2015; Vitt & Breitenbach, 1993; Vitt & Congdon, 1978). This may be an evolutionary strategy adopted to reduce predation risk of gravid females (Huey & Pianka, 1981; Vitt & Congdon, 1978). However, despite the ecological, morphological, and evolutionary constraints on clutch size within the genus *Aspidoscelis*, and in general for active foragers, we believe that the clutch size could be increased when under strong selection.

The western Mexican whiptail lizard, *Aspidoscelis costata*, is a non-monophyletic species within the *sexlineata* clade and consists of multiple populations that have been recognized as subspecies (Maslin & Secoy, 1986; Reeder, Cole, & Dessauer, 2002). This species is endemic to Mexico (Maslin & Secoy, 1986; Reeder et al., 2002) and inhabits various ecological regions and elevations. The purpose of this study was to assess the reproductive cycle and clutch size in *A. costata costata* from a high-elevation population and compare the data with previous reports from other members of *Aspidoscelis*. This information may help to elucidate the factors that influence reproductive characteristics.

Materials and methods

The study site is located in Tonatico, southeastern Estado de México, north of the Río Balsas basin, at Central Mexico ($18^{\circ}45'17.1''$ N, $99^{\circ}37'20.1''$ W), at an altitude of 1,500–1,600 m asl, which is considered high-elevation for Teiid lizards (Vitt & Breitenbach, 1993). Vegetation at the locality consists of tropical deciduous forest (Rzedowski, 2006), interspersed with agricultural crops. The climate is semi-humid warm with summer rains, which typically occur from mid-June through mid-September with annual variation (Hernández-Gallegos & Domínguez-Vega, 2012).

Aspidoscelis costata costata females were collected monthly (Scientific Collector Permit FAUT 0186, Semarnat) between 2005 and 2007 (with the exception of January and November when no females were observed in the field). Snout-vent length (SVL) and mass were recorded to the nearest 1 mm and 0.1 g, respectively. Females were euthanized via an intraperitoneal injection of sodium pentobarbital (approved by the AVMA Guidelines for Euthanasia of Animals), and ovary and oviducts were removed and placed in 10% neutral buffered formalin. After dissection, females were deposited in the Laboratorio de Herpetología, Facultad de Ciencias, Universidad Autónoma del Estado de México.

Females were categorized into 4 classes based on various gross morphology characteristics as previously described (Licht & Gorman, 1970; Ljubisavljević, Džukić, & Kalezić, 2008; Menezes, Rocha, & Dutra, 2004; Mojica, Rey, Serrano, & Ramírez-Pinilla, 2003): immature (with transparent follicles), previtellogenic (with milky white follicles and no ovarian follicle developing or oviductal eggs), vitellogenic (with at least 1 ovarian follicle developing ≥ 3 mm in diameter) or gravid (with oviductal eggs); vitellogenic and gravid females were considered as reproductive. Snout-vent length at sexual maturity was estimated as the size of the smallest female with vitellogenic follicles or oviductal eggs (Menezes et al., 2004).

As in previous studies in Teiid lizards (Werneck, Giugliano, Collevatti, & Colli, 2009; Zaldivar-Rae et al., 2008), clutch size was estimated by counting enlarged vitellogenic follicles and oviductal eggs. We also calculated the relative clutch mass (RCM) by dividing clutch mass by female total mass (including clutch weight; Tinkle, 1972). Clutch frequency was estimated using the presence/absence of a corpus luteum or oviductal eggs in vitellogenic females (Manríquez-Morán et al., 2005).

A one way Anova was used to examine the differences among SVL for the 3 classes of adult females (previtellogenic, vitellogenic, and gravid), followed by a multiple comparison test (Duncan's test). Reproductive activity was defined by presence of both vitellogenic and gravid females.

Moreover, we evaluated the differences between slopes of regression lines of vitellogenic follicles and number of oviductal eggs against SVL using a modified Student's *t* test (Zar, 1999). The relationship of clutch size and SVL of females was evaluated by Pearson's correlation coefficient. All data were tested for normality via a Kolmogorov–Smirnov test. Analyses were performed using Statgraphics (V 5.0), and results were deemed significant if $p < 0.05$.

Results

Sexual maturity and SVL of adult females

A total of 49 females were collected (43 adults; 6 juveniles), including both dry ($n = 20$), and rainy season ($n = 29$). The smallest reproductive female was 68 mm SVL. The SVL of adult females had a mean $= 89.8 \pm 1.9$ mm SVL (range 68–112 mm, $n = 43$). The SVL among the classes of adult females varied significantly (one way Anova, $F_{2,40} = 4.26$, $p = 0.021$), and multiple comparison test determined 2 significant groups: group A (vitellogenic and gravid females), and group B (previtellogenic females). Vitellogenic (mean $= 91.7 \pm 2.5$ mm SVL, range 68–109, $n = 21$) and gravid (mean $= 95.3 \pm 3.6$ mm SVL, range 78–112, $n = 10$) females were larger than previtellogenic females (mean $= 82.0 \pm 3.3$ mm SVL, range 70–104, $n = 12$).

Female reproductive cycle

Adult females were active from February to September, but were more prevalent during April–July. The female reproductive

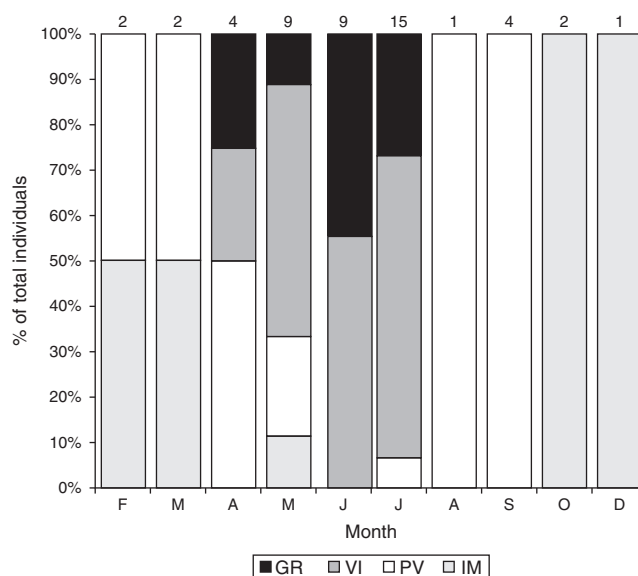


Figure 1. Reproductive classes recorded throughout the year as percent of the total number of females observed in *Aspidoscelis costata costata* from Tonatico, Estado de México, Mexico. Immature = IM; previtellogenic = PV; vitellogenic = VI; and gravid = GR. Numbers above each bar are sample sizes.

cycle of *A. costata costata* was markedly seasonal (Fig. 1), with asynchrony in reproductive condition among females (i.e., multiple reproductive stages were observed in different individuals within the same month). Both vitellogenic and gravid females were only recorded from April to July. During April a few vitellogenic females were observed, but were most abundant during May (55.5%, $n = 5$), June (55.5%, $n = 5$) and July (66.7%, $n = 10$). Though gravid females were present during April and May, they were observed mainly during June (44.4%, $n = 4$) and July (26.7%, $n = 4$). Previtellogenic females were recorded from February to September (with the exception of June). Immature females were collected outside of the breeding season (except 1 individual collected in May).

Clutch frequency, clutch size and egg size

Females of *A. costata costata* produce a single clutch each year as vitellogenic females did not show either corpora lutea or oviductal eggs. We estimated the clutch size by number of vitellogenic follicles (mean $= 7.7 \pm 0.57$ follicles, range 4–14, $n = 21$) and oviductal eggs (mean $= 7.8 \pm 0.70$ eggs, range 4–11, $n = 10$), because the slopes of regression against SVL ($b = 0.212079$, $b = 0.182459$, respectively) did not differ significantly (Student's *t*, $t_{30} = 0.590938$, $p = 0.5595$). The clutch size of *A. costata costata* was mean $= 7.7 \pm 0.44$ eggs (median 8 eggs, range 4–14, $n = 31$), and was correlated with SVL of the females (Pearson's correlation, $R^2 = 0.7178$, $p < 0.0001$, Fig. 2). The RCM was mean $= 0.19 \pm 0.012$ (range 0.14–0.23, $n = 8$). The shelled oviductal eggs had a width mean $= 8.8 \pm 0.08$ mm (range 6.7–9.9, $n = 68$), length mean $= 14.7 \pm 0.16$ mm (range 9.4–17.8, $n = 68$), and mass mean $= 0.61 \pm 0.02$ g (range 0.50–0.69, $n = 68$).

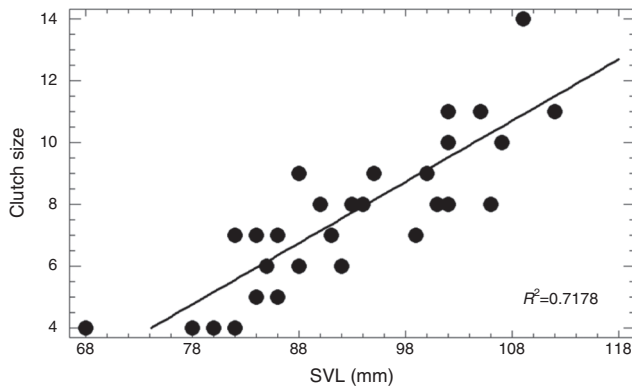


Figure 2. Relationship between clutch size and snout vent length (SVL) in the lizard *Aspidoscelis costata costata* from Tonatico, Estado de México, Mexico.

Discussion

The female reproductive cycle of *A. costata costata* was markedly seasonal, with vitellogenesis and gravidity during spring and summer. Both vitellogenic and gravid females were recorded during 4 months from April (end of the dry season) to July (middle of the rainy season), but with a major peak during June and July. This period was consistent with respect to the maximum testicular activity (Granados-González et al., 2015) and is similar in length (≤ 5 months) to other populations of *A. costata costata* (Reyes-Vaquero, 2013), and temperate species of *Aspidoscelis*: *A. sonora* (Routman & Hulse, 1984), *A. hyperythra* (Bostic, 1966), and *A. sexlineata* (Carpenter, 1960; Clark, 1976; Etheridge, Wit, Sellers, & Trauth, 1986; Fitch, 1970; Hoddenbach, 1966; Trauth, 1983). In tropical populations or species, reproductive season is considered extended (6–8 months) compared to temperate species: *A. costata* (Zaldivar-Rae et al., 2008), *A. rodecki* (Hernández-Gallegos et al., 2003), *A. cozumela* (Hernández-Gallegos et al., 2003; Manríquez-Morán et al., 2005), *A. lineatissima* (Güizado-Rodríguez, 2006; Ramírez-Bautista et al., 2000), *A. communis* (Ramírez-Bautista & Pardo-de la Rosa, 2002), and *A. maslini* (Hernández-Gallegos et al., 2003), or continuous as in *A. deppii* (Fitch, 1973). Although this population of *A. costata costata* is located at a tropical latitude where extended reproductive seasons are observed in other *Aspidoscelis* species, this population is located at a high-elevation where reproductive season is similar to that of temperate species.

Seasonal reproduction has been hypothesized to be correlated with both biotic factors (“evolutionary baggage”: Censky & McCoy, 1988; resource availability: Vitt & Breitenbach, 1993) and abiotic factors (temperature: Censky, 1995; Hernández-Gallegos et al., 2003; cool overcast days “nortes”: Hernández-Gallegos et al., 2003; day length: Manríquez-Morán et al., 2005; incubation conditions: Brown & Shine, 2006). Coinciding with male testicular activity of *A. costata costata* (Granados-González et al., 2015), the presence of both vitellogenic and gravid females correlated with warmest temperatures at the study site. Higher temperatures in adult females (38.8 °C; Rubio-Blanco, 2007) and their presence only during the warmer months of the year suggest that body size in females

may be an important factor in reproductive cycling within this species. Similar patterns of activity within adult individuals related to female reproduction have been recorded in other tropical species of *Aspidoscelis* (Hernández-Gallegos et al., 2003; Manríquez-Morán et al., 2005).

As in other squamates, the female reproductive cycle in *A. costata costata* is correlated with environmental conditions for oviposition (Brown & Shine, 2006). López-Moreno (2011) found that the nesting season in *A. costata costata* occurred during the months with the increased rainfall (between June and September). Moreover, both field and experimental data (López-Moreno, 2011) suggest that optimal embryogenesis occurs exclusively during this period. Therefore, interactions among different abiotic and biotic factors might favor the seasonal reproduction, timing and duration of the reproductive cycle in *A. costata costata*.

Clutch frequency is hypothesized to be associated with the length of reproductive season, which favor multiple clutches at tropical habitats with longer breeding seasons (Vitt & Breitenbach, 1993). According to the data, females of *A. costata costata* (at high elevations in tropical deciduous forest and semi-humid warm climate) produce a single clutch per reproductive season (unusual for the genus *Aspidoscelis*, see Appendix II in Vitt & Breitenbach, 1993). This is most likely a result of a markedly seasonal and short female reproductive activity. During the female reproductive activity gravid females from Tonatico were observed during April and May potentially producing “early” clutches, and gravid females during June and July potentially producing “late” clutches which may result in nesting site variability (López-Moreno, 2011), and in viability of hatchlings (Olsson & Shine, 1997b). The production of early and late clutches may also result in individuals reaching sexual maturity at different times during the year (Rubio-Blanco, 2007).

It is well known that evolutionary and ecological factors may affect the reproductive output in lizards. With the exception of species with fixed clutch sizes (Doughy, 1997), squamates have clutch sizes proportional to female SVL, foraging mode, and/or predator escape tactics (Vitt & Price, 1982). In species of the genus *Aspidoscelis*, small clutches are a general trend (Dunham & Miles, 1985; Vitt & Breitenbach, 1993). The costs associated with carrying a large clutch in active foragers would restrain the clutch size in *Aspidoscelis*, since the ability of a lizard to carry “extra” mass would directly determine the survival through: (1) decreased of the probability of escape by a gravid female when confronted by a predator (Huey & Pianka, 1981; Vitt & Congdon, 1978), and/or (2) a significant change in the thermal profile (typically characterized by high body temperatures; Adolph & Porter, 1993; Güizado-Rodríguez, Reyes-Vaquero, & Casas-Andreu, 2014). Selection on survival may be detrimental to reproduction or vice versa, thus selection must balance both survival and reproduction simultaneously. In this sense, despite the ecological and evolutionary restrictions in clutch size for species with a wide foraging strategy including *Aspidoscelis* (Dunham & Miles, 1985; Huey & Pianka, 1981; Vitt & Breitenbach, 1993; Vitt & Congdon, 1978), the large clutch size in *A. costata costata* may represent a local adaptation to high

predation regimes on their eggs (Pérez-Almazán, 2011), and/or to low survivorship rates (Rubio-Blanco, 2007).

Regardless, the clutch size found in *A. costata costata* (7.7 eggs, range 4–14 eggs) is the largest reported in any *Aspidoscelis* species (including both gonochoristic and parthenogenetic species; see Appendix II in Vitt & Breitenbach, 1993). The females of *A. costata costata* are one of the largest within the genus (mean SVL 89.8 mm) and similar in size to *A. communis* (mean SVL 96.5 mm, clutch size = 6.6 eggs, range 4–11 eggs; Walker, 1982; mean SVL 92.1 mm, clutch size = 4.8 eggs, range 3–9 eggs; Ramírez-Bautista & Pardo-de la Rosa, 2002). *A. costata costata* shows a clutch size even larger than the clutch size of the largest females in the genus, *A. sacki* (SVL 112 mm; clutch size = 5.9 eggs, range 3–10 eggs; Hernández-Gallegos, Pérez-Almazán, López-Moreno, Granados-González, & Walker, 2011; Walker, 1981) and larger than that of *A. costata* from Isabel Island (2.6 and 4.3 eggs, females' SVL range 68–96 mm; Zaldivar-Rae et al., 2008). Furthermore, based on a generalized linear trend (in absence of phylogenetic effects) found within the *Aspidoscelis* genus of clutch size and SVL, individuals that have an average SVL of 89.8 (as seen in this population of *A. costata costata*) are predicted to have a clutch size of 4.4 eggs (Hernández-Gallegos, 2004) which *A. costata costata* from Tonatico surpasses.

Our results also indicate that contrary to life history predictions (Stearns, 1992), by increasing of clutch size, *A. costata costata* does not sacrifice the size of the eggs, because the egg measurements (0.61 g of mass, 14.7 mm of length, and 8.8 mm of width) are similar to the mean values recorded for other species within the genus (0.61 g of mass, 16.12 mm of length and 8.86 mm of width; see Appendix II in Vitt & Breitenbach, 1993). As a result, the RCM of *A. costata costata* is relatively high (0.19) and higher than the RCM average in the genus (0.146; see Appendix II in Vitt & Breitenbach, 1993), which is unusual in widely foraging species.

Females of *A. costata costata* must adopt several strategies to maintain such high-reproductive output. For example, *A. costata costata* produces a single clutch per reproductive season, probably attributable to its large clutch size. Moreover, widening the abdominal area (Aguilar-Moreno et al., 2010), atypical for the elongate and conservative body shape in the family Teiidae (Pianka & Vitt, 2003), seems to be beneficial for harboring a large clutch size. Although widely foraging species should enjoy little advantage associated with camouflage, *A. costata costata* does show a dorsal coloration that varies seasonally and matches background vegetation (Hernández-Gallegos & Domínguez-Vega, 2012). These seasonal coloration differences could be a possible strategy adopted for decreasing predation effects especially to gravid females. Therefore, different morphological and ecological traits seem to be relevant to the persistence and success of a wide forager with a high-reproductive output such as *A. costata costata*.

In conclusion, *A. costata costata* from a high-elevation differs from other populations of *A. costata* and other species within the *Aspidoscelis* genus in multiple life history traits. This population of *A. costata costata* exhibits a reduced breeding season in comparison to other species at tropical latitudes but produces a large

clutch size without reduction in egg size. These data suggest that the variation observed in life history traits are extremely complex, and fully understanding this complexity within a species is invaluable to better understanding interactions not only between various life history traits but between these various traits and the environment.

Acknowledgments

We would like to thank projects UAEM 2620/2008U, UAEM 3740/2014/CID, and PIFI to OH-G and GG-G. We would also like to thank professors and students at Universidad Autónoma del Estado de México for aiding in the collection of lizards.

References

- Adolph, S. C., & Porter, W. P. (1993). Temperature, activity, and lizard life histories. *The American Naturalist*, 142, 273–295.
- Aguilar-Moreno, M., Rodríguez-Romero, F. R., Aragón-Martínez, A., Muñoz-Manzano, J. A., Granados-González, G., & Hernández-Gallegos, O. (2010). Dimorfismo sexual de *Aspidoscelis costata costata* (Squamata: Teiidae) en el sur del Estado de México, México. *Revista Chilena de Historia Natural*, 83, 585–592.
- Benabib, M. (1994). Reproduction and lipid utilization of tropical populations of *Sceloporus variabilis*. *Herpetological Monographs*, 8, 160–180.
- Bostic, D. L. (1966). A preliminary report of reproduction in the teiid lizard, *Cnemidophorus hyperythrus beldingi*. *Herpetologica*, 22, 81–90.
- Brown, G. P., & Shine, R. (2006). Why do most tropical animals reproduce seasonally? Testing alternative hypotheses on the snake *Tropidonophis mairii* (Colubridae). *Ecology*, 87, 133–143.
- Brown, G. P., & Shine, R. (2009). Beyond size-number tradeoffs: clutch size as a maternal effect. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 364, 1097–1106.
- Carpenter, C. C. (1960). Reproduction in Oklahoma *Sceloporus* and *Cnemidophorus*. *Herpetologica*, 16, 175–182.
- Censky, E. J. (1995). Reproduction in two Lesser Antillean populations of *Ameiva plei* (Teiidae). *Journal of Herpetology*, 29, 553–560.
- Censky, E. J., & McCoy, C. J. (1988). Female reproductive cycles in five species of snakes (Reptilia: Colubridae) from the Yucatán Peninsula, Mexico. *Biotropica*, 20, 326–333.
- Clark, D. R. (1976). Ecological observations on a Texas population of six-lined racerunners, *Cnemidophorus sexlineatus* (Reptilia, Lacertilia, Teiidae). *Journal of Herpetology*, 10, 133–138.
- Doughy, P. (1997). The effects of “fixed” clutch sizes on lizard life-histories: reproduction in the Australian Velvet Gecko, *Oedura lesueuri*. *Journal of Herpetology*, 31, 266–272.
- Du, W. G., Ji, X., & Shine, R. (2005). Does body-volume constrain reproductive output in lizards? *Biology Letters*, 1, 98–100.
- Dunham, A. E., & Miles, D. B. (1985). Patterns of covariation in the life history traits of squamate reptiles: the effects of size and phylogeny reconsidered. *The American Naturalist*, 126, 231–257.
- Dunham, A. E., Miles, D. B., & Reznick, D. N. (1988). Life history patterns in squamate reptiles. In C. Gans, & R. B. Huey (Eds.), *Biology of the Reptilia* (pp. 441–522). New York: Wiley.
- Etheridge, K., Wit, L. C., Sellers, J. C., & Trauth, S. E. (1986). Seasonal changes in reproductive condition and energy stores in *Cnemidophorus sexlineatus*. *Journal of Herpetology*, 20, 554–559.
- Fitch, H. S. (1970). *Reproductive cycles of lizards and snakes*. pp. 1–247. Miscellaneous Publication – University of Kansas, Museum of Natural History, No. 52.
- Fitch, H. S. (1973). A field study of Costa Rican lizards. *University of Kansas Science Bulletin*, 50, 39–126.
- Granados-González, G., Rheubert, J. L., Villagrán-SantaCruz, M., González-Herrera, M. E., Dávila-Cedillo, J. V., Gribbins, K. M., et al. (2015). Male

- reproductive cycle in *Aspidoscelis costata costata* (Squamata: Teiidae) from Tonatico, Estado de México, México. *Acta Zoologica*, 96, 108–116.
- Güizado-Rodríguez, M. A. (2006). *Actividad reproductora: efecto del rocío y la alimentación* en *Aspidoscelis lineatissima* (Reptilia: Teiidae), durante las estaciones lluviosa y seca en Chamela, Jalisco M.Sc. thesis. Ciudad de México: Facultad de Ciencias, Universidad Nacional Autónoma de México.
- Güizado-Rodríguez, M. A., Reyes-Vaquero, L., & Casas-Andreu, G. (2014). Thermoregulation by a population of *Aspidoscelis calidipes* from Apatzingán, Michoacán, Mexico. *The Southwestern Naturalist*, 59, 132–135.
- Hernández-Gallegos, O. (2004). *Demografía de los lacertilios del complejo Aspidoscelis (Cnemidophorus) cozumela (Sauria: Teiidae) y sus especies parentales, en la Península de Yucatán, México* Ph.D. thesis. Ciudad de México: Facultad de Ciencias, Universidad Nacional Autónoma de México.
- Hernández-Gallegos, O., Ballesteros-Barrera, C., Villagrán-Santa Cruz, M., Alonzo-Parra, D., & Méndez-de la Cruz, F. R. (2003). Actividad reproductora estacional de las hembras del género *Aspidoscelis* (Reptilia: Teiidae), en la península de Yucatán, México. *Biogeographica*, 79, 1–17.
- Hernández-Gallegos, O., & Domínguez-Vega, H. (2012). Cambio estacional en la coloración dorsal de la lagartija *Aspidoscelis costata costata* (Squamata: Teiidae). *Revista de Biología Tropical*, 60, 405–412.
- Hernández-Gallegos, O., Pérez-Almazán, C., López-Moreno, A. E., Granados-González, G., & Walker, J. M. (2011). *Aspidoscelis sacki* (Sack's Spotted Whiptail). Natural History. *Herpetological Review*, 42, 428.
- Hoddenbach, G. A. (1966). Reproduction in western Texas *Cnemidophorus sexlineatus* (Sauria: Teiidae). *Copeia*, 1966, 110–113.
- Huey, R. B., & Pianka, E. R. (1981). Ecological consequences of foraging mode. *Ecology*, 62, 991–999.
- James, C., & Shine, R. (1985). The seasonal timing of reproduction: a tropical-temperate comparison in Australian lizards. *Oecologia*, 67, 464–474.
- Licht, P., & Gorman, G. C. (1970). Reproductive and fat cycles in Caribbean *Anolis* lizards. *University of California Publications in Zoology*, 95, 1–52.
- Ljubisavljević, K., Džukić, G., & Kalezić, M. L. (2008). Female reproductive life history traits of the meadow lizard, *Darevskia praticola* (Eversmann, 1834) (Squamata: Lacertidae) from the westernmost boundary of the species range. *Polish Journal of Ecology*, 56, 289–297.
- López-Moreno, A. E. (2011). *Efecto de la temperatura de incubación sobre el fenotipo de Aspidoscelis costata costata (Squamata: Teiidae)* M.Sc. thesis. México: Facultad de Ciencias, Universidad Autónoma del Estado de México.
- Manríquez-Morán, N. L., Villagrán-Santa Cruz, M., & Méndez-de la Cruz, F. R. (2005). Reproductive biology of the parthenogenetic lizard, *Aspidoscelis cozumela*. *Herpetologica*, 61, 435–439.
- Maslin, T. P., & Secoy, D. M. (1986). *A checklist of the lizard genus Cnemidophorus (Teiidae)*. Denver: University of Colorado Museum.
- Méndez-de la Cruz, F. R., Guillelte, L. J., Jr., & Villagrán-Santa Cruz, M. (1993). Differential atresia of ovarian follicles and its effect on the clutch size of two populations of the viviparous lizard *Sceloporus mucronatus*. *Functional Ecology*, 7, 535–540.
- Menezes, V. A., Rocha, C. F. D., & Dutra, G. F. (2004). Reproductive ecology of the parthenogenetic whiptail lizard *Cnemidophorus natio* in a Brazilian Restinga Habitat. *Journal of Herpetology*, 38, 280–282.
- Mojica, B. H., Rey, B. H., Serrano, V. H., & Ramírez-Pinilla, M. P. (2003). Annual reproductive activity of a population of *Cnemidophorus lemniscatus* (Squamata: Teiidae). *Journal of Herpetology*, 37, 35–42.
- Olsson, M., & Shine, R. (1997a). Advantages of multiple matings to females: a test of the infertility hypothesis using lizards. *Evolution*, 51, 1684–1688.
- Olsson, M., & Shine, R. (1997b). The seasonal timing of oviposition in sand lizards (*Lacerta agilis*): why early clutches are better. *Journal of Evolutionary Biology*, 10, 369–381.
- Olsson, M., Wapstra, E., & Olofsson, C. (2002). Offspring size-number strategies: experimental manipulation of offspring size in a viviparous lizard (*Lacerta vivipara*). *Functional Ecology*, 16, 135–140.
- Pérez-Almazán, C. (2011). *Éxito de eclosión de Aspidoscelis costata costata (Squamata: Teiidae)* M.Sc. thesis. México: Facultad de Ciencias, Universidad Autónoma del Estado de México.
- Pianka, E. R., & Vitt, L. J. (2003). *Lizards: windows to the evolution of diversity*. Berkeley, CA: University of California Press.
- Ramírez-Bautista, A., Balderas-Valdivia, C., & Vitt, L. J. (2000). Reproductive ecology of whiptail lizard *Cnemidophorus lineatissimus* (Squamata: Teiidae) in a tropical dry forest. *Copeia*, 712–722.
- Ramírez-Bautista, A., & Pardo-de la Rosa, D. (2002). Reproductive cycle and characteristics of the widely-foraging lizard, *Cnemidophorus communis*, from Jalisco, Mexico. *Southwestern Naturalist*, 47, 205–214.
- Reeder, T. W., Cole, C. J., & Dessauer, H. C. (2002). Phylogenetic relationships of whiptail lizards of the genus *Cnemidophorus* (Squamata: Teiidae): a test of monophyly, reevaluation of karyotypic evolution, and review of hybrid origins. *American Museum Novitates*, 3365, 1–61.
- Reyes-Vaquero, L. (2013). *Actividad reproductora de Aspidoscelis costata costata (Reptilia: Teiidae) en tres localidades ubicadas a diferentes altitudes*, Bachelor thesis. Ciudad de México: Facultad de Ciencias, Universidad Nacional Autónoma de México.
- Routman, E. J., & Hulse, A. C. (1984). Ecology and reproduction of a parthenogenetic lizard, *Cnemidophorus sonora*. *Journal Herpetology*, 18, 381–386.
- Rubio-Blanco, T. (2007). *Sobrevivencia, crecimiento y termorregulación de Aspidoscelis costata en Tonatico, Estado de México*, Bachelor thesis. México: Facultad de Ciencias, Universidad Autónoma del Estado de México.
- Rzedowski, J. (2006). *Vegetación de México, 1a. Edición digital*. México: Comisión Nacional para el Conocimiento y Uso de la Biodiversidad. Retrieved from: <http://www.biodiversidad.gob.mx/publicaciones/librosDig/pdf/VegetacionMx.Cont.pdf>
- Shine, R. (1980). Cost of reproduction in reptiles. *Oecologia*, 46, 92–100.
- Stearns, S. C. (1989). Trade offs in the life-history evolution. *Functional Ecology*, 3, 259–268.
- Stearns, S. C. (1992). *The evolution of life histories*. New York: Oxford University Press.
- Tinkle, D. W. (1972). The dynamics of a Utah population of *Sceloporus undulatus*. *Herpetologica*, 28, 351–359.
- Trauth, S. E. (1983). Nesting habitat and reproductive characteristics of the lizard *Cnemidophorus sexlineatus* (Lacertilia: Teiidae). *The American Midland Naturalist*, 109, 289–299.
- Van Dyke, J. U. (2015). Cues for reproduction in squamate reptiles. In J. L. Rheubert, D. S. Siegel, & S. E. Trauth (Eds.), *Reproductive biology of lizards and tuatara* (pp. 109–143). Boca Raton: CRC Press.
- Vitt, L. J. (2015). Lizard reproduction: a history of discovery. In J. L. Rheubert, D. S. Siegel, & S. E. Trauth (Eds.), *Reproductive biology of lizards and tuatara* (pp. 1–26). Boca Raton: CRC Press.
- Vitt, L. J., & Breitenbach, G. L. (1993). Life histories and reproductive tactics among lizards in the genus *Cnemidophorus* (Sauria: Teiidae). In W. Wright, & L. J. Vitt (Eds.), *Biology of whiptail lizards (genus Cnemidophorus)* (pp. 211–244). Oklahoma: Oklahoma Museum of Natural History.
- Vitt, L. J., & Congdon, J. D. (1978). Body shape, reproductive effort and relative clutch mass in lizards: resolution of a paradox. *The American Naturalist*, 112, 595–608.
- Vitt, L. J., & Price, H. J. (1982). Ecological and evolutionary determinants of relative clutch mass in lizards. *Herpetologica*, 38, 237–255.
- Walker, J. M. (1981). Reproductive characteristics of sympatric whiptail lizards (Genus *Cnemidophorus*) in Southern México. *Journal of Herpetology*, 15, 321–328.
- Walker, J. M. (1982). Reproductive characteristics of the Colima Giant Whiptail, *Cnemidophorus communis communis* Cope. *The Southwestern Naturalist*, 27, 241–243.
- Webb, J. K., Brook, B. W., & Shine, R. (2002). What makes a species vulnerable to extinction? Comparative life-history traits of two sympatric snakes. *Ecological Research*, 17, 59–67.
- Werneck, F. P., Giugliano, L. G., Collevatti, R. G., & Colli, G. R. (2009). Phylogeny, biogeography and evolution of clutch size in South American lizards of the genus *Kentropyx* (Squamata: Teiidae). *Molecular Ecology*, 18, 262–278.
- Zaldivar-Rae, J., Drummond, H., Ancona-Martínez, S., Manríquez-Morán, N. L., & Méndez-de la Cruz, F. R. (2008). Seasonal breeding in the western Mexican whiptail lizard *Aspidoscelis costata* on Isla Isabel, Nayarit, Mexico. *Southwestern Naturalist*, 53, 175–184.
- Zar, J. H. (1999). *Biostatistical analysis*. New Jersey: Prentice Hall.