



## Reproductive strategies of a lizard community from an arid environment of Mexico

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### ABSTRACT

The goal of this study is to describe patterns of reproductive activity and associated characteristics in a lizard community from an arid environment in the southern Chihuahuan Desert region of Mexico. Results of this study showed variation in snout–vent length (SVL) in adults female and male among 18 species. A similar pattern occurred in body mass of males and females, which varied mainly among species and not substantially between sexes. Mean clutch/litter size and egg/embryo mass and volume varied among species, and egg/embryo mass and volume were positively correlated with female SVL. Oviparous species were larger in SVL than viviparous species; however, SVL in females, clutch/litter size and egg/embryo volume were similar between oviparous and viviparous species, but the oviductal mass of oviparous species was larger than in viviparous species. Clutch/litter size and oviductal mass were correlated with female SVL in both oviparous and viviparous species. This relationship was similar for egg/embryo volume in oviparous species, but not in viviparous species. Seven species showed a prolonged reproductive period, and five had short reproductive periods. The results of this study provide evidence of high diversity in reproductive strategies that have evolved among organisms that live in this environment.

### 1. Introduction

Arid environments are often characterized by high spatial and temporal variation in the occurrence of rainfall (Dickman et al., 1999). Additionally, water is the basic component for animal life in such environments (Hadley and Szarek, 1981; Zani and Stein, 2018), therefore, the activity of animals living there can in turn be expected to be spatially and temporally variable (Schmidt-Nielsen, 1979). Consequently, during extreme weather events in an ecosystem, such as a severe drought, a

suite of food-web responses amongst species can be expected (Zani and Stein, 2018). Water limitations cause a strong decrease in food (Pianka, 1986; Costa et al., 2008) and increased competition, leading to diseases, population declines, and short reproductive periods (Torres-Cervantes et al., 2019). Therefore, the challenge for survival and reproduction in animals inhabiting these environments is strong, which means that they must be adapted to these changing regimes (Pianka, 1986; Torres-Cervantes et al., 2019).

Vertebrates' adaptations in arid and semiarid environments have

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evolved through their biology, such as morphology, physiology, behavior, and ecology (Louv and Seely, 1982; Zani and Stein, 2018; Torres-Cervantes et al., 2019). In these environments, the reproduction of most animals and plants is seasonal, synchronized, and controlled by both environmental (temperature, food, precipitation) and endogenous factors (hormone production), with the latter being predominantly important in amphibians (Torres-Cervantes et al., 2019). In this landscape, the period of optimum conditions for primary production (flowering and insects) is noticeably short, and dependent on the rains (Pianka, 1986; Dickman et al., 1999). At the beginning of this period (spring), primary production starts (e.g., phenology of plant communities with production of leaves, flowers, fruits, and seeds), which supports a high diversity of arthropods and at the same time enables an increase in the density of vertebrate populations (Williams and Tieleman, 2005), which is reflected by recruitment of the offspring of different species (Schmidt-Nielsen, 1979; Williams and Tieleman, 2005).

Lizard species are one of the groups particularly well adapted to arid environments due to their low water requirements (Dickman et al., 1999), ability to aestivate during periods of severe drought (Dickman et al., 1999), opportunistic food habits (Puga y Colmenares et al., 2019), ability to store fat bodies (Ramírez-Bautista et al., 2008), and high growth rates (Ramírez-Bautista et al., 2016). In these environments, most species studied to date appear to be seasonal breeders, with some exceptions in small-body-sized species (Ramírez-Bautista et al., 2017).

Lizard species from arid environments display a diverse set of phylogenetically conserved life history traits that encompass the range of predictions of r/K selection models (Pianka, 1970), and supported by the fast-slow continuum hypothesis (Pérez-Mendoza and Zúñiga-Vega, 2014; Schwarz and Meiri, 2017). According to Tinkle et al. (1970), small-body-sized lizard species show annual life cycles, and are characterized by fast growth rates, early maturity, production of multiple clutches, and low numbers of eggs per clutch; therefore, this group is r-selected (Pianka, 1970) and falls within the fast-slow continuum (Schwarz and Meiri, 2017). In contrast, a second group of lizards are large-body-sized, exhibit low growth rate, late maturity, and a single clutch size of many eggs; such species are regarded as K-selected (Pianka, 1986).

The Chihuahuan Desert region (CDR) is the largest in North America, and is considered one of the arid zones with the greatest species richness in the world (Hoyt, 2002). The municipality of Guadalcázar, San Luis Potosí, Mexico, is located at the southernmost end of the CDR (Hernández-Ibarra, 2005). In this arid environment, theoretically, all vertebrate groups have evolved not only under the ecological rules of r/K selection, fast-slow continuum, and the bet-hedging hypotheses (Ramírez-Bautista et al., 2017), but also under constraints imposed by physiological conditions of the animals (Guillette, 1981, 1982).

The lizard community from Guadalcázar is composed of 20 species in six families (Anguidae, Crotophytidae, Phrynosomatidae, Scincidae, Teiidae, and Dibamidae), with Phrynosomatidae being the most diverse with 11 species (Hernández-Ibarra, 2005; Cruz-Elizalde et al., 2014). Representative species of these families exhibit different reproductive patterns, life histories, and morphological characteristics (Hernández-Ibarra, 2005), which are associated with the environmental conditions of the CDR (e.g., temperature and precipitation), as well as resource availability (e.g., food and microhabitats; Hernández-Ibarra, 2005). For example, according to the levels of intensity and extent of rain, primary production would allow for higher frequency of clutches per season in small-sized lizard species, and/or a larger clutch size in species with variable clutch size (Tinkle et al., 1970; Ramírez-Bautista et al., 2017). The lizard community that inhabits this arid environment, however, could reflect phylogenetic inertia instead of an ecological response (Losos, 1994; De Pinho Werneck et al., 2009). This can also be supported by limitation of resources such as food and water, where in many cases the lizards withstand severe periods of drought. This reflects that the behavior and variables associated with reproduction or morphology can

remain fixed, regardless of variation in environmental factors, substantiating this phylogenetic inertia (Zani and Stein, 2018).

Currently, there are few studies regarding reproductive patterns and strategies of lizard assemblages in arid and semiarid environments (Hernández-Ibarra, 2005; Pianka, 2010, 2011; Cruz-Elizalde et al., 2014). Therefore, considering the context of an arid environment and how lizard species have evolved to reproduce in this kind of challenging environment, the goal of this study was to describe the patterns of reproductive activity and associated characteristics in the community of lizards from an arid environment in the southern Chihuahuan Desert region (as defined by Cruz-Elizalde et al., 2014). More specifically, we describe the reproductive activity (reproductive period of females and males, clutch/litter sizes, clutch/litter frequency, egg/embryo volume), snout-vent length (SVL) at sexual maturity (females and males), size classes (SVL), and reproductive strategies (14 oviparous and four viviparous species, single vs. multiple clutches). We expected a marked temporality in the reproductive characteristics of the species, associated with the environment where they occur, as well as a similarity among species according to reproductive mode (oviparous vs. viviparous).

## 2. Materials and methods

### 2.1. Study area

The study was carried out from May 1996 to June 1997, and from October 1998 to April 2001 at the southern end of the Chihuahuan Desert region (CDR) in the municipality of Guadalcázar (23° 7' 35", 22° 53' 41" N and 100° 24' 18", 100° 29' 3" W), San Luis Potosí, Mexico, at sites ranging in elevation from 1100 to 2700 m. The vegetation community at these sites is composed of different areas with arid and semiarid vegetation types, such as microphyll xeric scrub, rosette xeric shrub, mesquite, submontane scrub, chaparral, and pasture. In addition, there are areas associated to temperate environments, such as oak forest, juniper forest, and transformed environments such as farmland (Rzedowski, 1994; Hernández-Ibarra, 2005). The area is dominated by extensive lowlands interrupted by numerous mountain ranges of variable elevation. The area experiences different local climates, but the dominant type is dry semi-warm (BSh; García, 1981). Mean annual precipitation in this area is 330.3 mm (range: 22.4–497.7 mm). Temperatures in the region range from 5 °C (coldest months, December to March; winter) to 45 °C (warmest months, April to September; spring–summer) (García, 1981).

### 2.2. Lizard sampling

Sampling was conducted during two-week periods every two months. In the present study, the environment in which the specimens were collected was not differentiated, since in previous studies of the lizard community, a high exchange of species among environments in the region was reported (see Cruz-Elizalde et al., 2014). All specimens of lizard species were caught and collected in a variety of microhabitats (on rock, logs, ground, holes, among others; Cruz-Elizalde et al., 2014) present at the site. Lizards were caught by hand or with rubber bands during their activity periods (0900–1800 h).

The lizard community of the region is composed of 20 species (Hernández-Ibarra, 2005; Cruz-Elizalde et al., 2014), however, for this study we analyzed 18 species (excluding *Anelytropsis papillosus* and *Holbrookia approximans*, due to lack of reproductive information) for certain reproductive characteristics, such as SVL of mature females and males, reproductive activity (extension in months), clutch/litter size, egg/embryo volume, clutch frequency, size class, and body mass (g). We analyzed a total of 723 adult lizards, 341 females and 382 males. Females were used to analyze most of the reproductive traits listed above. The SVL at sexual maturity and reproductive season or reproductive extension (short or long) were based for most species on adult females with the presence of vitellogenic follicles in the ovary or eggs/embryos

in the oviduct (Lozano et al., 2014), and males with enlarged testes and convoluted epididymides consistent with sperm production (Lozano et al., 2015; Cruz-Elizalde and Ramírez-Bautista, 2016). For the species in which this information was not obtained in the field, information was taken from the literature (i.e., *S. variabilis*; Cruz-Elizalde and Ramírez-Bautista, 2016). Archived work was conducted according to the standards of the Herpetological Animal Care and Use Committee (2004), and the Mexican federal laws CT-CERN-001-19 (DOF, 1991) and NOM-PA-CRN-001/93 (DOF, 1993). Specimens were collected under scientific permit SGPA/DGPA/01902/11 issued by SEMARNAT. All specimens were deposited in the amphibian and reptile collection of the Centro de Investigaciones Biológicas of the Universidad Autónoma del Estado de Hidalgo.

### 2.3. Morphological and reproductive characteristics

After lizard collection, we measured the following morphological characteristics: snout-vent length (SVL;  $\pm 0.01$  mm; using a digital caliper), body and oviductal mass (g; on an analytical balance), and egg/embryo volume ( $\text{mm}^3$ ). To assess reproductive traits, eggs/embryos (females) and testes (males) were removed and weighed ( $\pm 0.0001$  g). For females, clutch size (oviparous; Cruz-Elizalde and Ramírez-Bautista, 2016; Ramírez-Bautista et al., 2017), litter size (viviparous; Ramírez-Bautista et al., 2008; Lozano et al., 2014; Cruz-Elizalde and Ramírez-Bautista, 2016) and oviductal mass ( $\pm 0.0001$  g) were recorded. Female reproductive activity was classified according to the follicles contained in the ovary (non-vitellogenic follicles, NVF; or vitellogenic follicles, VFs), or eggs/embryos in the oviduct (Lozano et al., 2014; Cruz-Elizalde and Ramírez-Bautista, 2016). The largest egg/embryo (in each oviduct) was removed, weighed to the nearest 0.0001 g, and multiplied by the total number of eggs/embryos on that side to estimate total oviductal mass on each side of the body (Lozano et al., 2014; Ramírez-Bautista et al., 2017).

We determined total mean clutch/litter size by counting VFs or eggs/embryos during the reproductive season (Lozano et al., 2014; Ramírez-Bautista et al., 2017); however, if the mean of VFs and the mean of eggs/embryos were not statistically different, they were added together to obtain the total mean clutch/litter size (Ramírez-Bautista et al., 2017). In addition, we calculated Pearson's correlation coefficient to test for a significant relationship between clutch/litter size and SVL of females (Ramírez-Bautista et al., 2017). Egg/embryo volume was calculated with the formula  $V = (4/3) \pi a^2 b$ , where  $a$  is one-half the shortest diameter and  $b$  is one-half the longest diameter. We calculated correlations between female SVL and oviductal mass and egg/embryo volume for each species, considering only species with a female sample size  $\geq 3$ . Clutch frequency (oviparous) was recorded for females that contained VFs (in the ovaries) and eggs (in the oviducts) simultaneously (Ramírez-Bautista et al., 2016, 2017) or that had VFs and corpora lutea (Cruz-Elizalde and Ramírez-Bautista, 2016). To analyze differences in body size between females that had VF and eggs/embryos, non-parametric Mann-Whitney  $U$ -tests were used.

The species size classes were determined based on the intervals for oviparous and viviparous species according to Tinkle et al. (1970). ANOVAs were used to compare SVL (female/male), egg/embryo volume, clutch/litter size among species and among classes. Fisher's post hoc comparison test was used to identify differences among groups. Phylogenetic ANOVAs were carried out using the *phytools* R package (Revell, 2012) to compare female SVL and clutch/litter size between reproductive modes (oviparous vs. viviparous). Phylogenetic generalized least squares regressions were carried out using the *caper* R package (Orme et al., 2018) to test for a relationship between clutch/litter size and female SVL. For these phylogenetic analyses, we used the topology of Pyron et al. (2013) with original branch lengths, pruning the tree to contain only the species considered in this study. Results were considered significant if  $P \leq 0.05$ . All statistical analyses were carried out using Statistica 7.0 (StatSoft, Inc., Tulsa, OK, USA) and R 4.0.3 (R Core Team,

2020). Means are presented as  $\pm 1$  SE (Zar, 2010).

## 3. Results

### 3.1. Morphology

In the lizard community, SVL varied among species for both adult males ( $F_{11, 370} = 46.979$ ,  $P < 0.0001$ ; Table 1) and females ( $F_{17, 323} = 47.468$ ,  $P < 0.0001$ ; Table 1). Females and males did not differ in SVL in *Aspidoscelis gularis*, *A. inornata*, *Phrynosoma modestum*, *P. orbiculare*, *Sceloporus parvus*, *S. scalaris*, *S. spinosus*, *S. grammicus*, or *S. olivaceus* (Table 1), but males were larger than females in *Cophosaurus texanus*, *S. minor*, and *S. variabilis* (Table 1). A similar pattern was observed in body mass of males and females, which varied among species (Table 1), and between sexes in *C. texanus* and *S. minor* ( $P < 0.0001$ ; Table 1), while males and females did not differ in body mass in the remaining species (Table 1).

For adult females, three size classes were identified; small ( $44.2 \pm 1.2$  mm, range = 30.5–58.0 mm,  $n = 32$ ), medium ( $60.9 \pm 0.71$ , range = 41.1–82.0 mm,  $n = 162$ ), and large ( $88.8 \pm 1.7$ , range = 55.9–204 mm,  $n = 140$ ), which were statistically different ( $F_{2, 331} = 191.737$ ,  $P < 0.0001$ ).

### 3.2. Reproductive analyses

Reproductive characteristics were determined in 14 (77.8%) oviparous and four (22.2%) viviparous lizard species (Tables 2 and 3). The minimum female SVL at sexual maturity for all oviparous species was found in *P. modestum* (35.8 mm) and the maximum (124.1 mm) in *S. spinosus*, while in males the minimum was 31.1 mm in *P. modestum* and the maximum 158.1 mm in *S. spinosus* (Tables 2 and 3). The minimum female SVL at sexual maturity for viviparous species was found in *S. grammicus* (41.1 mm), and the maximum (76.0 mm) was for females of *S. minor*, and for males the minimum was 40.0 mm in *S. grammicus* and the maximum 105.1 mm in *P. orbiculare* (Tables 2 and 3). Snout-vent length of adult females with VF and eggs differed in *A. gularis*, *A. inornata*, *C. texanus*, and *S. minor* ( $P < 0.05$  in all cases; Table 2), as well as body mass in *A. gularis*, *C. texanus*, and *S. spinosus* ( $P < 0.05$  in all cases; Table 2).

The results showed differences in female SVL among species ( $F_{17, 323} = 47.468$ ,  $P < 0.0001$ ; Table 1). Fisher's pairwise comparison tests showed that SVL was larger in *Crotaphytus collaris* than in the other species ( $P < 0.005$ ). Because mean clutch/litter size based on the number of VFs did not differ from that of egg/embryos in all species ( $P > 0.05$ , in all cases), the two data sets were pooled to find the mean clutch/litter size among species (Table 3). Mean clutch/litter size varied among species ( $F_{16, 165} = 42.645$ ,  $P < 0.0001$ ), being largest in *Gerhonotus ophiurus* and smallest in *S. parvus* (Fisher tests:  $P < 0.001$ ). Oviductal mass ( $F_{6, 65} = 23.187$ ,  $P < 0.0001$ ) and egg/embryo volume ( $F_{12, 73} = 14.47$ ,  $P < 0.003$ ) varied among species and were positively correlated with female SVL ( $r = 0.756$ ,  $P < 0.0001$ ;  $r = 0.445$ ,  $P < 0.0001$ , respectively). Six oviparous species showed at least two clutches per season; for example, *P. modestum*, *S. parvus*, and *S. variabilis* showed VFs in the ovary and eggs in the oviduct simultaneously, whereas 12 species presented a single clutch/litter during reproductive season (Table 3).

### 3.3. Reproductive traits among species of different size classes

Reproductive adult females of the species with NVF, VF, and eggs varied in SVL, classified into small ( $44.1 \pm 1.2$  mm, range = 30.5–58.0,  $n = 32$ ), medium ( $60.9 \pm 0.71$  mm, range = 41.1–82.0,  $n = 162$ ), and large species ( $88.8 \pm 1.7$  mm, range = 55.9–204,  $n = 140$ ). A similar pattern was observed in clutch/litter size for small ( $7.2 \pm 1.6$ , range = 4.0–18.0,  $n = 9$ ), medium ( $6.5 \pm 0.54$ , range = 2.0–16.0,  $n = 38$ ), and large-body-sized species ( $10.0 \pm 1.3$ , range = 2.0–38,  $n = 39$ ;  $F_{2, 83} =$