

POPULATION DYNAMICS OF THE MEXICAN HORNED LIZARD (*PHRYNOSOMA ORBICULARE*) IN THE PARQUE DE LA CIENCIA SIERRA MORELOS, STATE OF MEXICO, MEXICO

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Abstract.—Population dynamics studies provide evidence for understanding the fluctuation of vital variables with respect to habitat characteristics, are becoming a valuable tool for the management of conservation programs in synergy with ecological and evolutionary research. In this study we describe the dynamics of the size classes, population size, and survival rate of a population of the Mexican Horned Lizard (*Phrynosoma orbiculare*) during 4 y in a protected natural area in central Mexico. Sex ratio was not significantly different from 1:1. Average snout-vent length (SVL) of adult females was significantly larger than SVL of adult males. Subadults and adult lizards were present in every month and were most abundant from June to October (subadults) and May to October (adults). Neonates were present from April to August and were most abundant from April to May. Population size did not differ between study months, but tended to be larger in April and was positively correlated with temperature. The estimated density (154.7 lizards/ha), to the best of our knowledge, is the highest for the genus; however, the density decreases by 32.7% (104 lizards/ha) when the home range is considered. The survival rate did not differ over the duration of the study and was positively correlated with higher levels of precipitation. These data suggest that the population dynamics of *P. orbiculare* are influenced by both habitat characteristics and biological characteristics of this lizard. This is a first overview of the dynamics of *P. orbiculare* and the influence of the environment in which it inhabits.

Key Words.—Jolly model; natural protected area; population ecology; population size; precipitation; survival rate; temperature

Resumen.—Los estudios de dinámica de poblaciones proporcionan evidencia para comprender la fluctuación de variables vitales con respecto a las características del hábitat y se están convirtiendo en una herramienta valiosa para la gestión de programas de conservación en sinergia con la investigación ecológica y evolutiva. En este estudio describimos la dinámica de las clases de tamaño, el tamaño poblacional y la tasa de supervivencia de una población del Lagarto Cornudo Mexicano (*Phrynosoma orbiculare*) durante 4 años en una área natural protegida en el centro de México. La proporción sexual no fue significativamente diferente de 1:1. La longitud promedio hocico-cloaca (LHC) de las hembras adultas fue significativamente mayor que la LHC de los machos adultos. Las lagartijas subadultas y adultas estuvieron presentes todos los meses y fueron más abundantes de junio a octubre (subadultas) y de mayo a octubre (adultas). Los neonatos estuvieron presentes de abril a agosto y fueron más abundantes de abril a mayo. El tamaño de la población no difirió entre los meses de estudio, pero tendió a ser mayor en abril y se correlacionó positivamente con la temperatura. La densidad estimada (154,7 lagartijas/ha), hasta donde sabemos, es la más alta para el género; sin embargo, la densidad decrece un 32.7% (104 lagartijas/ha) cuando el ámbito hogareño es considerado. La tasa de supervivencia no difirió entre el tiempo que duró el estudio y se correlacionó positivamente con los mayores niveles de precipitación. Estos datos sugieren que la dinámica poblacional de *P. orbiculare* está influenciada tanto por las características del hábitat como por las características biológicas de esta lagartija. Esta es una primera visión general de la dinámica de *P. orbiculare* y la influencia del ambiente en el que habita.

Palabras Clave.—área natural protegida; ecología poblacional; modelo de Jolly; precipitación; tamaño poblacional; tasa de supervivencia; temperatura

INTRODUCTION

Variations in population dynamics have been considered as the result of fluctuations in the vital rates of wild populations (i.e., survival rates, mortality, birth rates, migrations, among others). Studying these characteristics provides insights into how the variations in number or density of a species fluctuate through time and space (Gadsden 2006; Zani 2008; Leavitt et al. 2015; Vargas-García et al. 2019). Previous studies have suggested that these vital rates can be closely related to specific biotic and abiotic conditions of the habitat (Adolph and Porter 1996; Barrows and Allen 2009; Zamora-Abrego et al. 2010), including, but not limited to: availability of food, the presence or absence of competitor and/or predatory species, temperature, precipitation, elevation, and latitude (Wone and Beauchamp 2003; Hernández-Gallegos 2004; Barrows and Allen 2009; Wolf et al. 2014; Torres-Barragán et al. 2020). These relationships have been considered as the result of different responses to selective pressures, which can differ mainly between populations, species, ages, sexes, and reproductive and social status (Rojas-González et al. 2008; Mesquita et al. 2016; Torres-Barragán et al. 2020).

Historical ecological data from lizards suggests that population dynamics are the result of selective pressures that have had a direct impact on abundance, population size (Leavitt et al. 2015), population structure (Pianka and Parker 1975; Hult and Germano 2015), as well as survival and mortality rates (Fair and Henke 1999; Zani 2008; Torres-Barragán et al. 2020). Understanding the dynamics of a population is key to the full comprehension of variables related to the ecology, evolution, and conservation of species, as well as aiding in the establishment of

specific management plans for wild populations (Hult and Germano 2015; Vesý et al. 2021). The ability to better understand these dynamics is especially important for species that, due to their biology and life-history traits, are under some category of risk from the effects of humanity (Zúñiga-Vega et al. 2007; Wolf et al. 2014; Vesý et al. 2021; González-Fernández et al. 2024).

The Mexican Horned Lizard, *Phrynosoma orbiculare* (Fig. 1), is a high mountain viviparous lizard with a sit-and-wait foraging behavior. This species is endemic to Mexico with a wide geographical distribution; however, its distribution to the center of the country is limited to the states of Puebla, Morelos, Hidalgo, Mexico City, and the State of Mexico (Méndez-de la Cruz et al. 2003; Sherbrooke 2003; Bryson et al. 2012). *Phrynosoma orbiculare* is found at elevations ranging from 1,500 to 3,352 m above sea level, in semi-desert areas with semi-arid vegetation and a temperate climate in Pine-Oak forests (Méndez-de la Cruz et al. 2003; Sherbrooke 2003). According to the International Union for Conservation of Nature Red List, *P. orbiculare* is classified as a Species of Least Concern (LC), while in the list NOM-059-SEMARNAT-2010 from Secretaria del Medio Ambiente y Recursos Naturales (SEMARNAT) it is considered as a Threatened species and according to Wilson et al. (2013), it has a value of 12 on the scale of Environmental Vulnerability Score (EVS; which range from 3–19), thus it is classified as a species with medium vulnerability.

Numerous investigation have been carried out in Parque de la Ciencia Sierra Morelos (PCSM), Mexico, related to the natural history of *P. orbiculare*, such as population structure (Pérez-Arriaga et al. 2016), age and growth (Hernández-Navarrete 2018), diet (Rojas-Hernández 2018), litter size (Suárez-Rodríguez et al. 2018), home range (Martínez-Nova 2019), breeding season (Gómez-Benitez 2020; Hernández-Hernández 2020) and activity patterns and space-temporary movements (Gómez-Benitez et al. 2021; Rojas-Hernández 2022). There are no studies, however, that provide quantitative evidence of the dynamics of the vital rates of this lizard at this locale. Despite its wide range of distribution in Mexico, there are few studies focused on the population dynamics of the species (Luna-Kamishev 2012). Most of the studies that provide data on population dynamics in the genus *Phrynosoma* are biased towards species with populations in the U.S., such as the Texas Horned Lizard (*P. cornutum*; Fair and Henke 1999; Endriss



FIGURE 1. A Mexican Horned Lizard (*Phrynosoma orbiculare*) photographed 21 March 2023 in the Parque de la Ciencia Sierra Morelos, State of Mexico, Mexico. (Photographed by Edgar Oviedo-Hernández).

et al. 2007; Wolf et al. 2014; Vesý et al. 2021), Flat-tailed Horned Lizard (*P. mcallii*; Barrows and Allen 2009; Grant and Doherty 2009), and Desert Horned Lizard (*P. platyrhinos*; Pianka and Parker 1975). We present demographic information as well as the characterization of the population dynamics of *P. orbiculare* in the PCSM and its relationship with environmental factors of its high mountain habitat.

MATERIALS AND METHODS

Study site.—The PCSM is a protected natural area at an average elevation of 2,700 m located between the municipalities of Toluca and Zinacantepec in the State of Mexico. Both municipalities are considered urban areas because the landscape is dominated by human settlements. The study site is a recreational area that may be considered disturbed due to activities such as cycling and with walking and hiking areas. The site is dominated by a temperate sub-humid climate where the highest levels of precipitation are recorded in summer with an average range of 153 mm to 217 mm, and the highest temperatures in spring with an average range of 17.4° C to 19.3° C. Conversely the driest and coolest season are at the end and beginning of the calendar year with an average range of 4.1 mm to 72 mm, 15.9° C to 16.2° C, and 7.7 mm to 27 mm, 15.6° C to 18° C, respectively (<https://smn.conagua.gob.mx/es/climatologia/informacion-climatologica/informacion-estadistica-climatologica>; Fig. 2). The arboreal stratum consists of oaks (*Quercus* sp.), while the bushy stratum consists of minor species of brushes, agaves, asters, and cactus, and the herbaceous layer is made up of species from the families Asteraceae, Amaranthaceae, Burseraceae, among others (Gobierno del Estado de México 2013; 2015). In this natural area, reforestation programs have been carried out that have introduced non-native vegetation (i.e., Eucalyptus trees, *Eucalyptus* sp.). The site has a total area of 1,255 ha (Gobierno del Estado de México 2013; 2015), while our study area was 1.48 ha.

Field data collection.—We searched for lizards each month for 7 h (0900–1600) per sampling period from January 2016 to December 2019 (with the exception of December 2017 and from January to March 2018) for a total of 44 mo of sampling. We performed exhaustive searches in the microhabitats where *P. orbiculare* has been previously observed. We hand-captured all individuals. After their capture, we recorded snout-vent length (SVL; in millimeters)

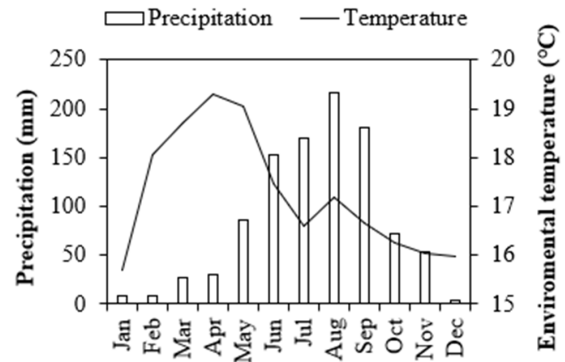


FIGURE 2. Environmental temperature (°C) and accumulated precipitation (mm) in the Parque de la Ciencia Sierra Morelos, State of Mexico, Mexico. The data correspond to the average of the four years of study (2016–2019) from <https://smn.conagua.gob.mx/es/climatologia/informacion-climatologica/informacion-estadistica-climatologica>.

using a transparent plastic ruler, sex (males have two enlarged post-anal scales; Sherbrooke 2003), and size class (following Pérez-Arriaga et al. 2016). We classified lizards as neonates if individuals were ≤ 33 mm SVL, as sub-adult males for lizards $\geq 34 \leq 64$ mm SVL and sub-adult females $\geq 34 \leq 65$ mm SVL. We considered males as adults that were ≥ 65 (minimum size in which there is secretion in the femoral pores; Hernández-Gallegos et al. 2002; Pérez-Arriaga et al. 2016) and ≥ 66 mm SVL for females (the minimum size in which pregnant females have been recorded; Pérez-Arriaga et al. 2016). We also recorded the year and month of capture or recapture. We permanently marked lizards by toe-clipping (Tinkle 1967). We released all the lizards at the capture site and marked them with a small temporary paint dot at the base of their tails to avoid repeated capture on the same day. We obtained temperature (°C) and precipitation (mm) data for each year and month of sampling, from which we determined the monthly average and annual average. Weather data were from the Coordinación General del Servicio Meteorológico Nacional de la Comisión Nacional del Agua, obtained through the Observatorio Meteorológico de Toluca (weather station key: 15126), in the State of Mexico, Mexico, located approximately 3.5 km southwest of the study site.

Parameter estimation.—We used data from the first recapture of individuals for parameter estimates. Additionally, we used the model by Jolly (1965) to obtain the population size and the survival rate. This model is a stochastic tool, which considers the variations that the populations present under natural conditions in each of the samplings. Therefore,

values of parameters of interest can be obtained for each sampling, resulting in a more realistic dynamic model. This model offers reliable estimates of survival if there is a minimum of 20% recaptures per sampling (Hernández-Gallegos 2004). In our study, 77% of samplings had recapture rates > 20%, so we assumed that our data fit the model adequately.

Number of live and marked lizards.—The Jolly model (1965) assumes that to obtain the number of marked lizards that are alive (M_i) the probability of recapture is the same for both marked and unmarked individuals. We estimated M_i using the equation:

$$M_i = \frac{z_i r_i}{y_i} + m_i$$

(for details for solving see Lemos-Espinal et al. 2005), where z_i = lizards recaptured after sampling, r_i = lizards that were released on the day of sampling, y_i = lizard from the group r_i that will be recaptured in days after the sampling, and m_i = total number of lizards recaptured on the day of sampling.

Population size.—Using the values of (M_i), we estimated the population size (N_i) for each sample period according to the Petersen's modified equation (Lemos-Espinal et al. 2005):

$$N_i = \frac{M_i(n_i + 1)}{m_i + 1}$$

where n_i = number of lizards captured on the day of sampling and M_i and m_i are the same as above. We calculated standard errors (SE) of population size using the equation (Lemos-Espinal et al. 2005):

$$SE_{N_i} = \sqrt{N_i(N_i - n_i) \left\{ \frac{M_i + r_i - m_i}{M_i} \left(\frac{1}{y_i} - \frac{1}{r_i} \right) + \frac{1}{m_i} - \frac{1}{n_i} \right\}}$$

where variables are as defined in the above two equations.

Survival rate.—We estimated survival rate (S_i) between the time elapsed from one sampling to another using the equation (Lemos-Espinal et al. 2005):

$$S_i = \frac{M_{i+1}}{M_i + r_i - m_i}$$

that estimates a survival rate for each month, where M_{i+1} = number of lizards marked alive in

the subsequent sampling. Values close to zero are indicative of low survival rates, values close to one are indicative of high survival rates. We also calculated standard errors (SE) of the survival rate (See Appendix).

Statistical analysis.—We used a Yates Chi-Square to compare the sex ratio for size classes of the lizards that we captured. Data were normally distributed and variances were not significantly different. We used a *t*-test to compare SVL of adult males and females. Additionally, we calculated the size dimorphism index (SDI) using the Compressed SDI formula (see below), which makes use of the average values of females and males of the variable to be compared, in this case the SVL (for details, see Lovich and Gibbons 1992). We multiplied the SDI value by 100 to get the percentage.

$$SDI = \left[\left(\frac{\text{size of largest sex}}{\text{size of smallest sex}} \right) - 1 \right] \times 100$$

We applied the SDI adjustment with the Delta method (see below), which estimates a linear function that can be used for statistical inference and as a measure of standard deviation (see Nemes and Hartel 2010).

$$\sigma_{SDI}^2 = \frac{\theta_y^2 \sigma_x^2 + \theta_x^2 \sigma_y^2}{\theta_y^4}$$

In this context, θ_x represents the average of the character of the larger sex, θ_y smaller sex, and σ_x^2 and σ_y^2 the variance of θ_x and θ_y , respectively, and we performed a Two-sample Hypothesis test to test H_0 : SDI = 0 between the sexes. We used a Spearman's Correlation analysis to evaluate the association of temperature and precipitation with fluctuations in the population size and survival rate. Finally, we used a Kruskal-Wallis test to compare the medians population sizes and survival rates among study months. We performed all statistical analyses in Statgraphics Centurion ver. XVII.I, and in PAST (PAleontological STatistics) ver. 1.0.0.0. In all cases, we used $\alpha = 0.05$.

RESULTS

During the 4 y of study in the PCSM, we made 1,186 captures of *P. orbiculare* of 592 individuals (49.9% recaptures), of which 318 were females and 274 were males. Sex ratios did not differ significantly from 1:1 ($X^2 = 3.123$, $df = 1$, $P = 0.077$). Of the 592 individuals we captured, 252 lizards were neonates, 191 were subadults, and 149 were adults (Table 1).

TABLE 1. Snout-vent length (SVL) of the Mexican Horned Lizard (*Phrynosoma orbiculare*) by size class, sex, and the number captured (n) from 2016–2019 in the Parque de la Ciencia Sierra Morelos, State of Mexico, Mexico. F = females and M = males.

Size class	Sex	n	SVL (mm)			F + M
			Mean	SE	Range	
Neonate	F	130	29	0.20	20–33	252
Neonate	M	122	29.21	0.18	25–33	
Subadult	F	100	44.23	0.92	34–65	191
Subadult	M	91	44.6	1.02	34–64	
Adult	F	88	79.34	0.64	66–98	149
Adult	M	61	74.60	0.62	65–85	

Female SVL ranged from 20–98 mm. Male SVL ranged from 25 mm to 85 mm (Fig. 3; Table 1). The average (\pm standard error) adult female SVL was 79.34 ± 0.64 mm, while the average adult male SVL was 74.60 ± 0.62 mm (Table 1). The SVL of adult females was significantly larger than SVL of adult males ($t = 5.04$, $df = 147$, $P < 0.001$) and SDI value estimated were 0.635 ± 0.01 female biased, meaning that adult females were 6.35% larger than adult males, which was significant ($z = 5.04$, $P < 0.001$).

Size class dynamics.—We found variation between the size classes in relation to sampling months. We found neonates (average SVL = 29.1 ± 0.14 mm) between the months of April and August, which were most numerous during April and May and less numerous during June to August (Fig. 3). We found subadults (average SVL = 44.41 ± 0.68 mm) and adults (average SVL = 77.4 ± 0.49 mm) in all sampling months (Fig. 3), although we found

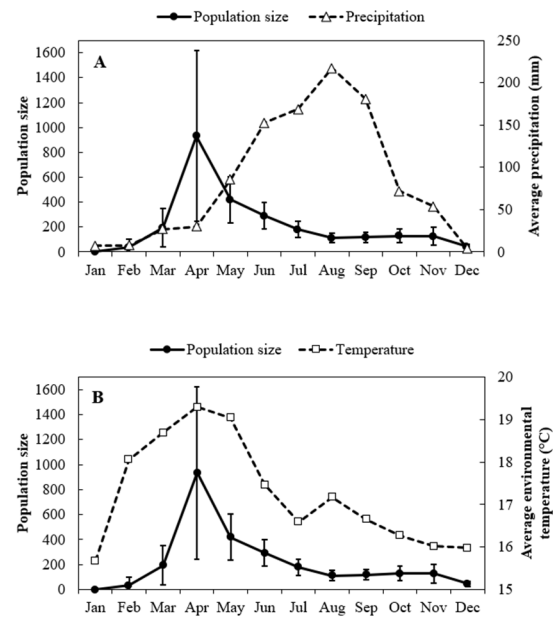


FIGURE 4. Monthly temporal pattern of (A) precipitation and (B) temperature with population size of Mexican Horned Lizards (*Phrynosoma orbiculare*) from 2016–2019 in the Parque de la Ciencia Sierra Morelos, State of Mexico, Mexico. Means \pm 1 standard error are shown.

subadults most often from June to October and adults from May to October (Fig. 3).

Population size dynamics.—We observed marked fluctuations in the population size and a repetitive pattern for all the years of the study, so we present these data as averages (Fig. 4). April was the peak of the population size in which we recorded a mean number of 933 lizards (± 687). April also corresponds

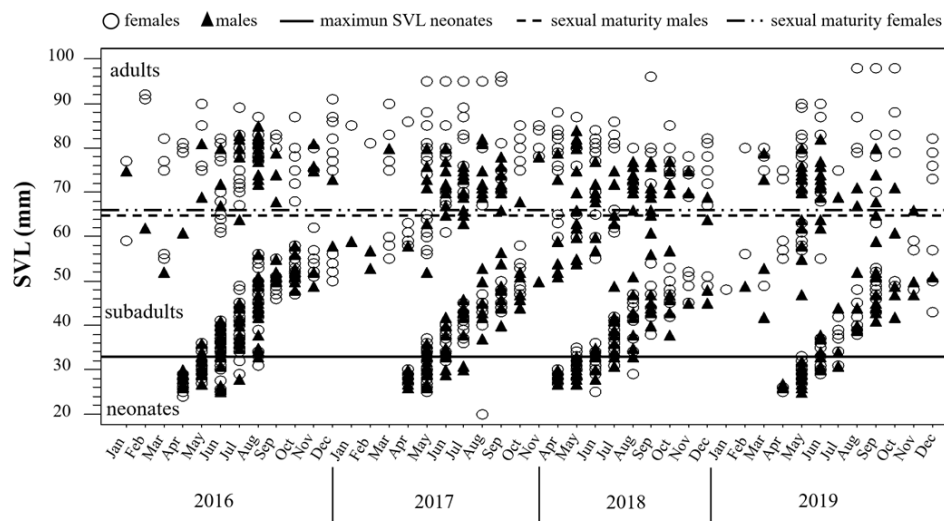


FIGURE 3. Annual and monthly variation of the snout-vent length (SVL) of Mexican Horned Lizards (*Phrynosoma orbiculare*) from 2016–2019 in the Parque de la Ciencia Sierra Morelos, State of Mexico, Mexico. The SVL intervals of the size classes are shown.

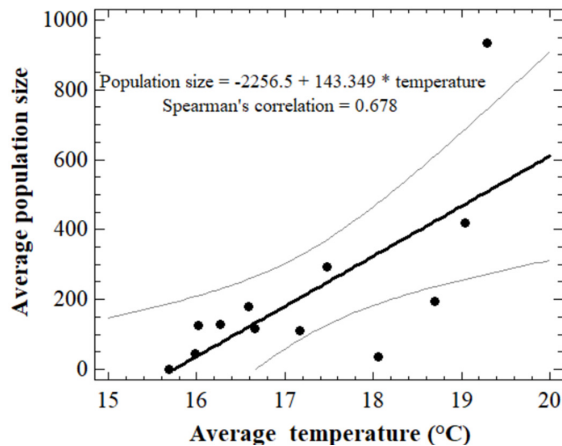


FIGURE 5. Monthly population size of Mexican Horned Lizards (*Phrynosoma orbiculare*) from 2016–2019 in the Parque de la Ciencia Sierra Morelos, State of Mexico, Mexico in relationship to temperatures. 95% confidence limits are shown in grey.

to the warmest month (average temperature of 19° C) and when the first rainfall begins (Fig. 4). We found the fewest lizards from December to February, which is also the coldest (except for February) and driest period. Population size was significantly correlated with temperature ($r_s = 0.67$, $P = 0.024$; Fig. 5), but not with precipitation ($r_s = 0.32$, $P = 0.286$). Population size, however, did not differ significantly among months ($H = 10.67$, $df = 11$, $P = 0.470$). During the 4 y of study, we estimated a mean population size of $229 (\pm 43.4)$ lizards. The mark-recapture study area was 1.48 ha, from which we estimate an uncorrected population density of $154.7 (\pm 29.3)$ lizards/ha. If we consider that the average home range for lizards in this population is 0.035 ha and that the overlap is close to 46.3% (Martínez-Nova 2019), the actual area used by lizards was 2.202 ha, which gives an estimated density of $104.0 (\pm 19.7)$ lizards/ha.

Survival rate dynamics.—We found that average survival rate was highest from April to November (Fig. 6). This period corresponds to the rainy season with average temperature fluctuations ranging between 19° C to 16.6° C (Fig. 6). From December to March, we registered survival rates equal to zero, which were periods of the lowest air temperatures, though temperatures increased in February and March, and precipitation was lowest (Fig. 6). Survival rates were significantly correlated with precipitation ($r_s = 0.89$, $P < 0.001$; Fig. 7), but not with temperature ($r_s = 0.08$, $P = 0.776$). We did not find significant differences in survival rates among study months ($H = 11.92$, $df = 11$, $P = 0.369$).

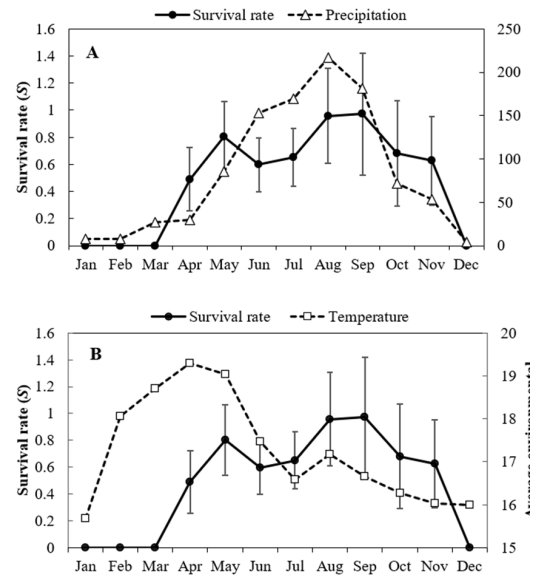


FIGURE 6. Monthly temporal pattern of (A) precipitation and (B) temperature with survival rate of Mexican Horned Lizards (*Phrynosoma orbiculare*) from 2016–2019 in the Parque de la Ciencia Sierra Morelos, State of Mexico, Mexico. Means \pm 1 standard error are shown.

DISCUSSION

Ecological studies based on demographic data have been effective in evaluating the variation of vital rates of species with respect to the environmental regimes present in each habitat (Fair and Henke 1999; Leavit et al. 2015; Mesquita et al. 2016). In the case of the Parque de la Ciencia Sierra Morelos, the conditions and fluctuations of precipitation (with its effect on survival rates) and temperature (with its

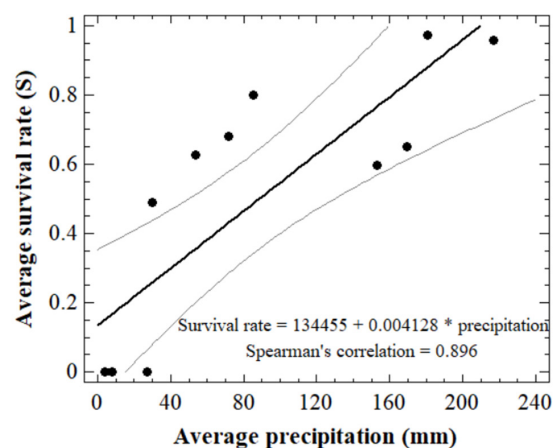


FIGURE 7. Monthly survival rate of Mexican Horned Lizards (*Phrynosoma orbiculare*) from 2016–2019 in the Parque de la Ciencia Sierra Morelos, State of Mexico, Mexico in relationship to precipitation. 95% confidence limits are shown in grey. We present only eleven points because the intervals of two survival rates are short (7.7, 0 and 7.9, 0).

effect on population size) seem to suggest that they are the main mediators of the population dynamics of *P. orbiculare*, which is a pattern often seen in lizards (Zani 2008; Mesquita et al. 2016; Vargas-García et al. 2019; Torres-Barragan et al. 2020).

The sex ratio of *P. orbiculare* did not differ from 1:1 in 4 y of study, which is consistent with previous studies on this population (Suárez-Rodríguez et al. 2018), although this study only considered the sex ratio of neonates born in captivity. These combined results suggest a stabilizing life-history trait to maximize fitness (Suárez-Rodríguez et al. 2018). Sex ratios can be skewed because of environmental effects (i.e., seasonally, predation) or intrinsic characteristics (i.e., activity) that exert greater pressure on one sex (Hult and Germano 2015). For example, in *P. blainvillii* the sex ratio was biased in favor of females in a one year but was not significantly different a year later (Hult and Germano 2015). The bias in sex ratio recorded in *P. blainvillii* was related to sample size, however, and the authors could not identify an environmental reason for the differences.

Our results suggest that the onset of parturition is in April and ends in June. This corresponds to the spring season, which has the highest ambient temperature, and a previous study at the site found significant effects of high temperatures on reproductive hormones that cause parturition phenology in *P. orbiculare* (Hernández-Hernández 2020). We also found that spring is the beginning of the increase in average precipitation. The increase in rain in the spring seems to cause a greater abundance of ants, the main diet of *P. orbiculare* in the PCSM (Rojas-Hernández 2018). Higher ant abundance may result in less competition for food between neonates (Vitt and Cadwell 2014).

Subadult and adult lizards became more abundant in May and June in response to accelerated neonate growth (Hernández-Navarrete 2018), which boosted recruitment. In the case of adults, their activity increases due to the search for food to recover the energy invested in births and meet physiological requirements after 6 mo of adverse conditions in which they remained in dormancy (Gómez-Benitez 2020). We found that subadult and adult individuals remained active during the cold and dry season. Three possible causes for the above changes in activity levels have been proposed: (1) Individuals did not accumulate enough reserve energy, so they remained active to meet this requirement (Grant and Doherty 2006; 2009); (2) Sightings coincided with the time when they change burrows (Grant and Doherty

2009), or (3) Lizards experienced early awakening due to an increased temperature (Bülbül et al. 2019). We also think that these sightings may be due to individuals that take advantage of the inactivity of other individuals to establish territories with better thermal sites, greater trophic resources, and with low human disturbance, due to low competition.

Sexual size dimorphism occurs in many species of lizards. Within the genus *Phrynosoma*, females are larger than males (Pianka and Parker 1975; Endriss et al. 2007; Hult and Germano 2015; Vesey et al. 2021) and this is what we found for *P. orbiculare*. The hypothesis that best explains the female-oriented sexual size dimorphism is the fecundity hypothesis (Aguilar-Moreno et al. 2010; Suárez-Rodríguez et al. 2018), which suggests that the greater the size, the greater the number of progeny, so selection pressures favor large females.

We also found a positive correlation between temperature and population size and a higher number of neonates in the warmer season. In this context, in vertebrates, births can be one of the main factors that have more influence in the growth and stability of populations than what immigration contributes (Rodríguez-Romero 2004). Additionally, environmental factors, such as temperature, have a great impact on the number of individuals in reptiles due to their ectothermic biology, which involves achieving optimal body temperatures for digestion, spatiotemporal movements, performance, physiological processes involved in reproduction, among others (Suárez-Rodríguez 2014; Vitt and Cadwell 2014; Gómez-Benitez 2020; Hernández-Hernández 2020; Gómez-Benitez et al. 2021). In other words, high or low thermal fluctuations in different seasons are good predictors of lizard population size. For example, in the Largescale Spiny Lizard (*Sceloporus megalepidurus*), the warm-dry season had a positive impact on population growth (Vargas-García et al. 2019). Higher than average environmental temperatures have been shown to cause a decrease in the number of individuals and thus population growth rate (Zúñiga-Vega et al. 2007; Zamora-Abrego et al. 2010) in crevice lizards (*Xenosaurus* spp.). Conversely, the estimated population numbers decrease at low temperatures because the lizards enter a period of dormancy (Gómez-Benitez 2020) and fewer lizards are seen above ground.

We found that population size of *P. orbiculare* was not related to precipitation. This is contrary to what has been found for other lizards. For example, in *P.*

mcallii the relative density of individuals decreased in years with high rainfall (Barrows and Allen 2009), and in Torquate Lizard (*S. torquatus*) and Mesquite Lizard (*S. grammicus*) population abundances were higher in the rainy season (Vargas-García et al. 2019). We believe that the lack of relationship between population size of *P. orbiculare* and rainfall, could be due to the fact that this lizard lives in an more equitable climate compared to that of *P. mcallii*, *S. torquatus*, and *S. grammicus*. The high variation in the number of lizard we found in April could be linked to the low values that we obtained in the parameters: lizards released (r_i), lizards released that will be recaptured (y_i), and total number of lizards recaptured (m_i), which may be reflected in birth, mortality, an/or migration changes (Tinkle 1967; Gadsden 2006).

The density that we obtained in *P. orbiculare* is higher than that registered in the desert congeners, such as: *P. mcallii* (4.99–16.71 lizards/ha; Barrows and Allen 2009), Pigmy Short-horned Lizard (*P. douglasii*; fewer than 2 lizards/ha; Lahti et al. 2010), and *P. cornutum* (5 lizards/ha; Endriss et al. 2007) and 7.96 lizards/ha (Vesý et al. 2021). Perhaps the biotic and abiotic characteristics of a forest habitat (i.e., tree canopy, access to different trophic resources, greater availability of microhabitats, elevation, precipitation, etc.), as in the case of the PCSM, can explain (at least partially) the difference of densities of the congeners. The estimated density of 149 lizards/ha in the Eastern Spiny Lizard (*S. spinosus*; Torres-Barragán et al. 2020), a lizard that also lives in forests, is similar to our estimated density for *P. orbiculare*, although our adjusted density estimate is 32% lower, so the density of *S. spinosus* was not adjusted for home range size and could be lower.

We found that survival rate was positively related to precipitation. Perhaps rain shortens the activity hours of lizards and their predators, resulting in less predation, as has been reported for other lizards in temperate environments (Adolph and Porter 1996; Rojas-González et al. 2008). Precipitation has also been shown to have a positive relationship with the availability of trophic resources (Zúñiga-Vega 2005), which suggests that during the rainy season, individuals have greater access to food to meet the necessary energy and physiological requirements, increasing the probability of survival. Accumulated precipitation also promotes plant growth, favoring the growth of herbaceous substrate (main refuge of *P. orbiculare*; Martínez-Nova 2019), which individuals can take advantage of and be less susceptible to their predators. In the dry season, fires are more likely to

occur that negatively affect survival, and although the fires that have occurred in the PCSM have not occurred exactly in the place where we studied this population of *P. orbiculare*, other metapopulations have been affected (González-Fernández et al. 2024). According to Endriss et al. (2007), metapopulations are key to population stability in human-altered environments. More people visit the PCSM when rainfall is scarce, which could negatively affect *P. orbiculare*. We also think that the survival rate could be underestimated when rainfall is scarce because lizards are inside their shelters to lessen environmental adversities (Martínez-Nova 2019; Gómez-Benítez 2020) and to save energy due to the low density of trophic resources (Rojas-Hernández 2018). Survival rate was not related to the temperature, which suggests that *P. orbiculare* probably uses behavioral strategies and active thermoregulation (evidence in Suárez-Rodríguez 2014) to survive to low and high temperatures.

According to the staff of PCSM, various activities such as cycling, hiking, as well as the free walk with pets are common in this study area. These activities could negatively impact *P. orbiculare* populations. We consider that these actions, and others that could come from people, are key factors that interfere with survival of *P. orbiculare* in the PCSM. Our data on the biology of this horned lizard should be communicated to site managers for use in environmental presentations to the public to educate them about ways to lessen their impact on this threatened species.

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APPENDIX: Standard errors (SE) of the survival rate (Lemos-Espinal et al. 2005).

$$SE_{S_i} = S_i \left\{ \frac{(M_{i+1} - m_{i+1})(M_{i+1} - m_{i+1} + r_{i+1})}{M_{i+1}^2} \left(\frac{1}{y_{i+1}} - \frac{1}{r_{i+1}} \right) + \frac{M_i - m_i}{M_i + r_i - m_i} \left(\frac{1}{y_i} - \frac{1}{r_i} \right) \right\}^{1/2}$$

where variables are: S_i = survival rate, M_i = number of marked lizards that are alive, m_i = total number of lizards recaptured on the day of sampling, r_i = lizards that were released on the day of sampling, and y_i = lizard from the group r_i that will be recaptured in days after the sampling.



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