

# Reproductive effort of *Plestiodon copei* (Squamata, Scincidae), a highland viviparous lizard from Central Mexico

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## Abstract

Female reproductive effort is defined as the proportion of total energy or resources devoted to reproduction. In reptiles, there is frequently high inter- and intra-population variation related to several factors, such as food availability, climatic conditions, age and size, all of which, in turn, also influence survival and future reproduction. The present study is the first reproductive effort analysis of a population of the high-mountain scincid lizard *Plestiodon copei* in central Mexico, focusing on relative litter mass (RLM), investment per capita (INV) and productivity (PROD). We also compared the reproductive efficacy of *P. copei* to those of other Mexican congeners. We collected 24 gravid females of *P. copei* over a 4-year period and recorded a total of 90 neonates born in captivity. We found significant variation in neonatal mass amongst individual females and across years. We recorded an average litter size of 3.75 and an average litter mass of 1.25 g, which were positively correlated with both the size and total mass of the reproductive females. The RLM, INV and PROD values (0.301, 0.428 g and  $1.236 \text{ g} \times \text{year}^{-1}$ , respectively) for *P. copei* were greater than those for other Mexican species in the *P. brevirostris* group (0.290, 0.412 g and  $1.135 \text{ g} \times \text{year}^{-1}$ ), revealing that females of *P. copei* from Tenango invest a comparatively high amount of their resources in reproduction.

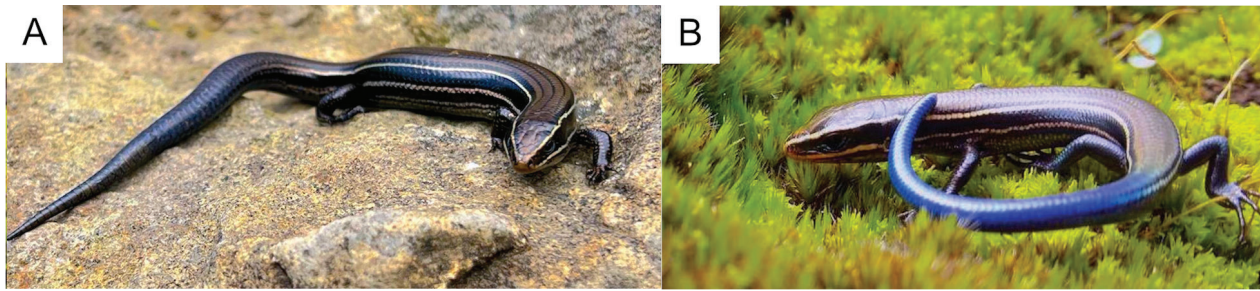
## Key Words

life history, litter mass, litter size, reproductive investment, skink lizard, Trans-Mexican Volcanic Belt

## Introduction

Reproductive investment is a central aspect of the theory of life history evolution, which states that an individual must allocate an optimal proportion of its available energy to reproduction which, in turn, will be reflected in statistics, such as in neonate/egg size and mass, litter/clutch size and mass and reproductive effort (Stearns 1992; Schwarzkopf 1993; Shine 2005). In ectothermic organisms, repro-

ductive investment is strongly affected by both physiological and ecological constraints. In reptiles, the reproductive investment of females is strongly influenced by body size and pelvic opening (Congdon and Gibbons 1987; Sinerovo and Licht 1991; Rodríguez-Romero et al. 2002, 2004, 2005; Ramírez-Bautista et al. 2016, 2017; Suárez et al. 2018). However, local environmental conditions also affect the reproductive investment of females and can lead to significant variations in the number and mass of eggs or



**Figure 1.** A) Adult female and B) neonate of *Plestiodon copei*. Photo Credits A: H. Sánchez-Sánchez; B: JC. Alvarado-Avilés.

neonates (Stearns 1992; Roitberg et al. 2013; Muñoz 2015; Suárez et al. 2018). The metabolic rate, food intake and environmental temperature are also related to reproductive investment, whereby lizard species inhabiting temperate environments may accelerate their sexual maturation and reproduce at smaller sizes, leading to smaller clutches/litters (Warne and Charnov 2008; Meiri et al. 2012).

Female lizards can also exhibit remarkable inter- and intraspecific variations in their reproductive life history traits (Cruz-Elizalde and Ramírez-Bautista 1998; López-Alcaide et al. 2020) due to environmental factors associated with temperature and precipitation regimes, as well as evolutionary history factors, such as phylogenetic constraints and adaptations to adverse environmental conditions, such as cold temperatures in high-elevation forests (Vitt and Price 1982; De Marco 1989; Rohr 1997; Abell 1999; Shine 2005; Castro-Franco et al. 2011).

In the mountainous regions of Mexico, several studies have analysed the reproductive strategies utilised in different genera of lizards, such as *Barisia* (Guillette and Casas-Andreu 1987), *Phrynosoma* (Zamudio and Parra-Olea 2000; Suárez et al. 2018), *Sceloporus* (Feria-Ortiz et al. 2001; Rodríguez-Romero et al. 2002, 2004, 2005; Bastiaans et al. 2013; Ramírez-Bautista et al. 2016; Maciel-Mata 2017; López-Alcaide et al. 2020) and *Plestiodon* (Guillette 1983; Vitt and Cooper 1986; Ramírez-Bautista et al. 1996, 1998; Ramírez-Bautista and Arizmendi 2004; Feria-Ortiz et al. 2007; López et al. 2008; García 2009; Chávez 2012; Laguna 2014; Morales 2014; Muñoz 2015; Bañuelos et al. 2016), in which both the characteristics of females and their progeny were evaluated. Some studies on the reproduction of sympatric or phylogenetically related species of the genus *Plestiodon* indicate that inter- and intra-population variations in reproductive patterns are related to environmental heterogeneity and can lead to local adaptations (Mathies and Andrews 1995; Wapstra and O'Reilly 2001; Rodríguez-Romero et al. 2002, 2004, 2005; Shine 2005; Chávez 2012; Ramírez-Bautista et al. 2016; Maciel-Mata 2017).

To estimate the reproductive investment of female reptiles, several indices have been developed that take into consideration the characteristics of both females and their progeny. Relative clutch mass/relative litter mass (RCM/RLM = fraction of female body mass devoted to reproduction) is the most frequently used index for estimating reproductive effort in lizards for both oviparous and

viviparous species (Tinkle and Hadley 1975; Vitt and Congdon 1978; Vitt and Price 1982; Shine and Schwarzkopf 1992; Suárez et al. 2018; Padilla-Pérez et al. 2022). Other indices that have been estimated for several lizard species include the productivity index (PROD = total mass of offspring produced in one year) and the per capita reproductive investment index (INV = investment per capita in the offspring) (Meiri et al. 2012; Rutschmann et al. 2016).

*Plestiodon copei* (Fig. 1) is an endemic and high-elevation specialist skink lizard distributed in temperate pine and pine-oak forests (i.e. elevation range ca. 2466–3966 m) in the Trans-Mexican Volcanic Belt (TMVB) (Alvarado-Avilés et al. 2020). *Plestiodon copei* is a species with asynchronous gonadal activity and an autumn reproductive period (Guillette 1983; Ramírez-Bautista et al. 1996). This species produces one litter per year and apparently displays parental care, but little is known about the reproductive investment of the females of the species. The present study aimed to characterise the reproductive strategies adopted by females of *P. copei* in a mountainous region of Central Mexico by estimating the reproductive effort under extreme environmental conditions that can lead to different adaptive responses relative to those of other species of the same genus.

## Materials and methods

We collected 24 late-pregnant females of *P. copei* from March–early April 2014 to 2017 near Tenango del Valle (19°05'54.74"N, 99°38'26.43"W) at an elevation of ca. 3030 m in the TMVB of central Mexico. Gravid females of *P. copei* were identified *in situ* by their greater abdominal volume. All females were captured in a landscape dominated by pine forests (*Pinus teocote*, *P. montezumae* and *P. rudis*) and grasslands (*Muhlenbergia macroura*) and surrounded by agricultural fields (Alvarado-Avilés et al. 2020).

We transported the collected females to the Laboratory of Genetic and Molecular Evolution (Universidad Autónoma del Estado de México) and individually housed them in plastic boxes (400 × 220 × 180 mm) with natural substrate (e.g. soil, gravel, mulch) and refuge objects (e.g. rocks and bark) obtained from the capture site. All females were maintained according to the thermal conditions described by García (2009), were fed live

food every two days (crickets and mealworms) and were supplied with water *ad libitum*.

## Reproductive effort estimation

We recorded the snout–vent length (SVL) and the total mass (TM = female body mass before birth) of each gravid female after capture. Females were checked at least once per day for 2 to 3 weeks and weighed daily until parturition. After birth, the following data were immediately recorded: absolute mass (AM = female body mass after birth), litter size (LS = number of neonates produced by a female), litter mass (LM = sum of the masses of all neonates produced by a female) and mean litter mass (MLM = average mass of the neonates of each litter).

The reproductive effort of *P. copei* females was estimated as follows: (a) relative litter mass;  $RLM = LM/AM$ ; (b) reproductive investment per capita;  $INV = (TM - AM)/LS$ ; and (c) estimated productivity;  $PROD = (MLM \times LS) \times \text{year}^{-1}$  (Tinkle and Hadley 1975; Vitt and Congdon 1978; Vitt and Price 1982; Rodríguez-Romero et al. 2002, 2004, 2005; Castro et al. 2011; Meiri et al. 2012; Bastiaans et al. 2013; Muñoz 2015; Rutschmann et al. 2016; Suárez et al. 2018). After all the measurements were made, both the females and neonates were released at the place where the female was captured. We also estimated the reproductive effort of other Mexican *Plestiodon* species by examining published data. Recently, taxonomic changes were considered for undescribed species (Pavón-Vázquez et al. 2018).

## Data analysis

We checked all variables for normality using the Shapiro–Wilk test and for the presence of outliers with box plots in SPSS ver. 24 (IBM Corporation 2016). To estimate whether the variations in litter characteristics could be explained by female traits, we performed linear regression analysis on the LS, LM, RLM, INV and PROD variables, using the SVL, TM and AM of the females as independent variables. To evaluate whether female mass affects reproductive characteristics, we conducted two regression analyses using LS and MLM as dependent variables and the residuals of the regression of AM on SVL (a measure of robustness) as independent variables (Castro-Franco et al. 2011). We estimated the coefficient of variation ( $CV = \text{standard deviation}/\text{mean} \times 100\%$ ), a standardised measure of the dispersion of a frequency distribution (Sokal and Rohlf 2012; Hutchings 2021) of SVL, LS, LM, MLM and the three reproductive effort indices; values whose CVs were  $\leq 5\%$  were considered invariant and those whose CVs were  $> 5\%$  were considered variable, as described by Castro-Franco et al. (2011) and Suárez et al. (2018) in studies on reproductive effort in Mexican lizard species. Finally, after checking the homogeneity of the variances with Levene's tests and not assuming the same variances, we analysed whether the

mass of neonates at birth differed between litters and the annual variation in mean litter mass using Welch's ANOVA and Games–Howell post hoc tests in SPSS ver. 24.

## Results

### Births

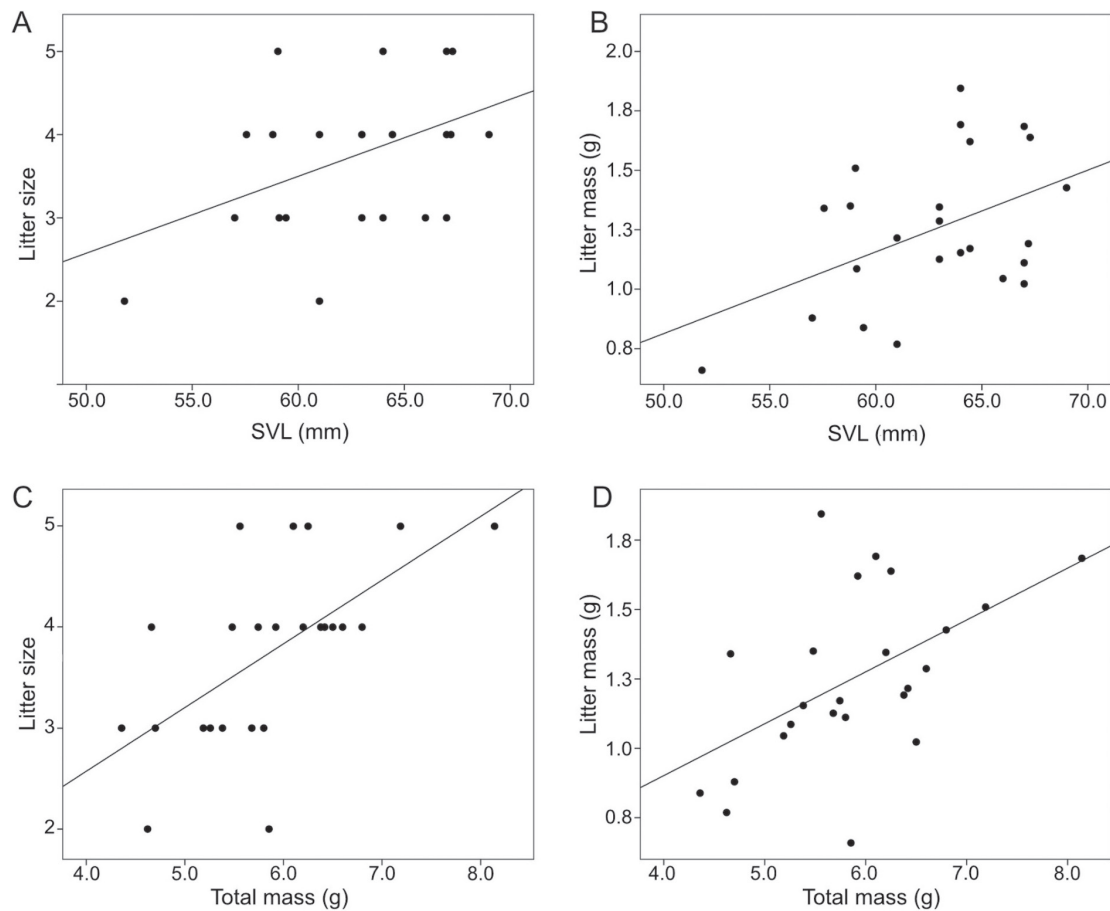
Twenty-four gravid females were captured over a 4-yr period. The SVL ranged from 51.8 mm to 69.0 mm and the mean size was 62.711 mm ( $SD = 4.141$  mm,  $CV = 6.6\%$ ,  $n = 24$ ). In captivity, the females gave birth to a total of 90 neonates (range = 2–5 neonates per litter, mean = 3.750,  $SD = 0.897$ ,  $CV = 23.9\%$ ) from mid-April to the last week of June. LMs ranged from 0.659 g to 1.844 g (mean = 1.250 g,  $SD = 0.310$ ,  $CV = 31.2\%$ ,  $n = 24$ ), while MLMs ranged from 0.256 g to 0.405 g (mean = 0.330 g,  $SD = 0.033$ ,  $CV = 10.0\%$ ,  $n = 24$ ).

### Reproductive effort

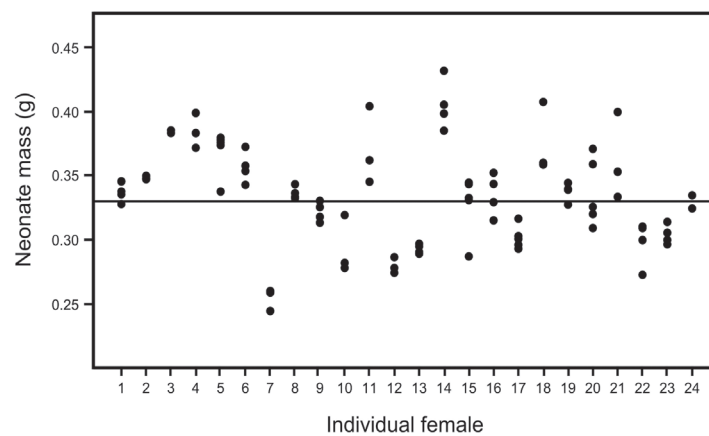
For *P. copei*, the estimated range for RLM was 0.129–0.530 (mean = 0.301,  $SD = 0.094$ ,  $CV = 31.2\%$ ,  $n = 24$ ), the range for INV was 0.190–0.694 g (mean = 0.428 g,  $SD = 0.103$ ,  $CV = 24.1\%$ ,  $n = 24$ ) and the range for PROD was 0.659–1.844 g  $\times \text{year}^{-1}$  (mean = 1.236 g  $\times \text{year}^{-1}$ ,  $SD = 0.326$ ,  $CV = 26.4\%$ ,  $n = 24$ ).

### Female characteristics and their effects on reproductive output

Correlation analyses revealed significant positive correlations between female SVL and LS ( $r = 0.427$ ,  $R^2 = 0.182$ ,  $F_{1,23} = 4.903$ ,  $p = 0.037$ ) and LM ( $r = 0.458$ ,  $R^2 = 0.210$ ,  $F_{1,23} = 5.851$ ,  $p = 0.024$ ) (Fig. 2A, B). Similarly, we found significant positive correlations between female TM and both litter traits (LS:  $r = 0.616$ ,  $R^2 = 0.379$ ,  $F_{1,23} = 13.451$ ,  $p = 0.001$ ; LM:  $r = 0.527$ ,  $R^2 = 0.278$ ,  $F_{1,23} = 8.455$ ,  $p = 0.008$ ) (Fig. 2C, D). Analyses between the SVL of females and the three estimated reproductive investment indices revealed a significant correlation only for PROD ( $r = 0.433$ ,  $R^2 = 0.188$ ,  $F_{1,23} = 5.082$ ,  $p = 0.034$ ), but not for INV ( $r = 0.386$ ,  $R^2 = 0.149$ ,  $F_{1,23} = 3.885$ ,  $p = 0.062$ ) or RLM ( $r = 0.253$ ,  $R^2 = 0.064$ ,  $F_{1,23} = 1.502$ ,  $p = 0.233$ ). Additionally, a negative correlation between female AM and RLM was observed ( $r = -0.291$ ,  $R^2 = 0.540$ ,  $F_{1,23} = 9.041$ ,  $p = 0.006$ ). We also observed no significant relationships between LS ( $r = 0.206$ ,  $R^2 = 0.042$ ,  $F_{1,23} = 0.976$ ,  $p = 0.334$ ) or LM ( $r = 0.024$ ,  $R^2 = 0.001$ ,  $F_{1,23} = 0.013$ ,  $p = 0.912$ ) and the TM length of females. Finally, when comparing the masses of the neonates, we observed significant variations amongst both litters (Fig. 3) ( $F_{23,20.871} = 5.765$ ,  $p < 0.001$ ) (Suppl. material 1), and years ( $F_{3,44.102} = 6.530$ ,  $p < 0.001$ ). The MLM varied amongst years and was greater in 2014 (mean = 0.3604 g) than in other years (2015 = 0.3136 g; 2016 = 0.3301 g and 2017 = 0.3266 g) (Fig. 4).



**Figure 2.** Relationships between individual *Plestiodon copei* female size (SVL) and (A) litter size, (B) litter mass. Additionally, relationships between individual female total mass and (C) litter size and (D) litter mass.



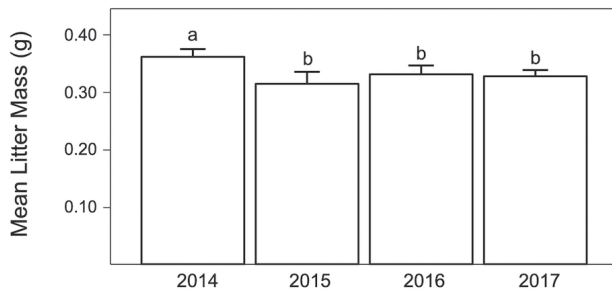
**Figure 3.** Within-litter variation in neonate mass (g) of *Plestiodon copei*. The horizontal line shows estimated mean litter mass (MLM) for the species.

## Discussion

In several lizard species, reproductive investment has been shown to be associated with phenotypic and physiological traits, both of which are optimised by natural selection (Tinkle and Handley 1973; Vitt 1974; Rodríguez-Romero et al. 2002). The reproductive effort indices estimated in this study for *Plestiodon copei* showed that females invest

a high amount of their resources in the development of their offspring and that the size of the female correlates with the size and aggregate weight of the offspring. In addition, Castro-Franco et al. (2011) discussed the pattern between the estimated values of RCM/RLM and their coefficients of variation (CVs) in several lizard species. They concluded that high RCM/RLM values and CV values above 20% could indicate a recurrent pattern for lizard species inhabiting extreme environments. In the case of *P. copei*, this





**Figure 4.** Annual variation in mean litter mass (g) of *Plestiodon copei*. Values are means  $\pm$  SE. Letters denote differences between years, based on Games-Howell post-hoc test.

reproductive effort is associated with its habitat at high elevations within the TMVB. This condition has also been documented for other viviparous high-mountain lizard species within the TMVB, such as *Sceloporus bicanthalis* (Rodríguez-Romero et al. 2002), *Phrynosoma orbiculare* (Suárez et al. 2018) and Mexican skink lizards, such as *Plestiodon* sp. from Tlaxcala and *P. dugessi* (Muñoz 2015), all of which have high RLM values and  $> 20\%$  variation. In the specific case of *P. copei*, the CVs of the three indices used to estimate reproductive effort were  $> 26\%$ , also indicating high reproductive investment for the population studied.

The gravid females varied in both SVL and TM; these variables, in turn, showed significant correlations with litter size and litter mass. Ford and Siegel (1989) showed that several phenotypic traits can vary within reptile populations in response to different biotic and abiotic factors and that phenotypic plasticity can be expected in life-history traits, as might be the case in *P. copei*. The reproductive investment of *P. copei* females is strongly influenced by maternal size; specifically, in *P. copei*, litter size increases with increasing maternal body size. Similar results were reported by Guillelte (1983) and Ramírez-Bautista et al. (1996) for viviparous or oviparous lizard species sympatric with *P. copei* within the TMVB (Rodríguez-Romero et al. 2002, 2004, 2005; Suárez et al. 2018).

The timing of birth in captivity for these study animals was consistent with the birth period reported by García (2009) for *P. copei*. Similarly, the birth months of *P. copei* were the same as those of other *Plestiodon* species inhabiting the TMVB (e.g. *P. dugessi*, *P. indubitus*, *P. lynxe* and *Plestiodon* sp. PT) (López et al. 2008; Chávez 2012; Lagunas 2014; Muñoz 2015). The date of parturition of lizards is typically associated with an abundance of food resources, which favours the growth and survival of neonates (Olsson and Shine 1998; Ramírez-Bautista et al. 1998, 2004; Chávez 2012; Lagunas 2014; Muñoz 2015), increasing their probability of reaching sexual maturity earlier (Chávez 2012).

The minimum gravid female sizes reported here indicate that Tenango females can reach sexual maturity at relatively small body sizes (SVL = 51.8 mm), as the SVL of the smallest pregnant female previously reported was 56.0 mm (Ramírez-Bautista et al. 1996); this finding indicates a relatively fast life history for the Tenango population. Ramírez-Bautista et al. (1996) also reported the growth rates of *P. copei* in the first year of life; by comparing the SVL of

the smallest gravid female from Tenango, we can confirm that at least some *P. copei* females from Tenango become sexually mature in the year after birth. Variation in the body size of sexually mature females has been associated with the specific climatic conditions (temperature and precipitation) to which a population is exposed (Wapstra and O'Reilly 2001; Arribas and Galán 2005; Gutiérrez et al. 2010), as well as a combination of biotic (predation, foraging capacity, food availability and quality) and abiotic factors (climatic conditions) (Du et al. 2005, 2014; Roitberg et al. 2013; Hosseinian et al. 2014; Cruz-Elizalde and Ramírez-Bautista 2016; Maciel-Mata 2017; Wang et al. 2017; López-Alcaide et al. 2020). Based on the records collected for 59 years from meteorological stations near each population, the mean annual temperature in our study area was greater (Tenango =  $13.4^{\circ}\text{C}$ ) than those in other *P. copei* population sites reported by other authors (Cuajimalpa:  $10.1^{\circ}\text{C}$ ; Zoquiapan =  $11.6^{\circ}\text{C}$ ; Ajusco =  $10.0^{\circ}\text{C}$ ) (Suppl. material 2), suggesting that warmer temperatures in Tenango may favour *P. copei* females reaching sexual maturity at a smaller size (Kubisch et al. 2012; Cabezas-Cartes et al. 2018).

It has been shown that, particularly for ectothermic species living at high elevations, temperature is an important factor shaping life history strategies, as well as determining growth rate and age and size at sexual maturity (Atkinson and Sibly 1997; Angilletta et al. 2006; Amat and Meiri 2018; Padilla-Pérez and Angilletta Jr. 2022). For example, populations living in relatively warmer environments, such as the Tenango population compared to those of Cuajimalpa, Zoquiapan and Ajusco, are expected to have faster gonadal maturation. This would allow sexual maturity to be reached at a smaller size relative to populations living in colder regions, where sexual maturity is delayed and, in turn, reflected in the larger average body size of the gravid females (Wapstra et al. 2001; Morrison and Hero 2003; Angilletta Jr. et al. 2006; Meiri et al. 2013; Padilla-Pérez and Angilletta Jr. 2022).

The effects of temperature on determining the size of females of *P. copei* at sexual maturity are similar to those of other high-mountain lizards, such as *Mediodactylus heterocercus* and *Darevskia derjugini*. In all three lizard species, sexually mature females with smaller minimum body sizes were encountered under relatively warm temperature conditions, while sexually mature females with larger minimum sizes were found in comparatively cooler environments. (Altunışık and Eksilmez 2020; Altunışık et al. 2022). This variation in reproductive strategy amongst and within lizard species (i.e. the existence of females with early reproduction and small body size versus females with later reproduction at larger sizes) has already been recognised by earlier herpetologists within the fast-slow continuum hypothesis of life history theory (Adolph and Porter 1996; Shine 2005; Rojas-González et al. 2008; Pérez-Mendoza and Zúñiga-Vega 2014; Cruz-Elizalde and Ramírez-Bautista 2016; Boretto et al. 2018). The fast-slow continuum hypothesis proposes that organisms inhabiting colder environments and higher altitudes adopt a slow reproductive strategy, resulting

in delayed maturation, as well as comparatively smaller litters. Conversely, in warmer climates and at lower altitudes, a rapid reproductive strategy is observed, marked by early maturation and larger litters (Promilsoy and Harvey 1990; Shine 2005; Li et al. 2014; Pérez-Mendoza and Zúñiga-Vega 2014). Comparing these conditions between the populations of *P. copei* in Tenango and San Lorenzo Acopilco, we observe that the Tenango population follows a faster strategy, while the San Lorenzo Acopilco population follows a slower strategy. Thus, in Tenango, which is a population living at relatively warm temperatures at lower elevations, natural selection favours sexually mature females with smaller body sizes and larger litters. Conversely, in San Lorenzo Acopilco, which has higher elevations and colder temperatures, natural selection favours larger gravid females, but smaller litters (García 2009). Moreover, the possibility that a fast life history strategy may lead to a decrease in adult female survival has also been documented (Tinkle et al. 1970; Stearns 1992; Rohr 1997; Shine 2005; Bestion et al. 2015; Boretto et al. 2017).

The mass of the offspring is another reproductive characteristic of *P. copei* that, if influenced by environmental temperature, suggests a rapid life history strategy for Tenango animals. According to the PROD index, the total mass of offspring produced in a year is greater in Tenango than in San Lorenzo Acopilco. This pattern is similar to that observed in another temperate-adapted skink species, *Eulamprus tympanum* (Rohr 1997); in populations living at higher environmental temperatures and lower elevations, the total offspring mass is significantly greater than that in populations living at colder temperatures and higher elevations. In conclusion, female lizards living in colder environments, as in the case of San Lorenzo Acopilco, evolve a slow strategy characterised by a combination of sexually mature females with larger body sizes and lower offspring masses (Adolph and Porter 1996; Rohr 1997; Badyaev and Ghalambor 2001; Pérez-Mendoza and Zúñiga-Vega 2014; López-Alcaide et al. 2020).

Our analysis of the masses of individual *P. copei* neonates revealed marked differences both within and between litters (see Fig. 3), which have been attributed to the availability of resources in the environment (Bleu et al. 2013; Wang et al. 2017) or predation pressures (Shine and Downes 1999; Bestion et al. 2014) to which the females are exposed during gestation. However, other factors could also explain this observed variation, such as sperm storage by females or multiple paternity events (Bateson et al. 2011; Chávez 2012; Muñoz 2015). Such factors have been suggested to be important in species of the genus *Plestiodon* (Ramírez-Bautista et al. 1996; Bateson et al. 2011) and may matter for *P. copei* as well, although this has not yet been demonstrated for this species.

Moreover, the differences in MLM observed between years suggest that there are other factors that could influence the reproductive investment of *P. copei* females in Tenango. Possible factors include differences in the SVL of females or in environmental conditions, such as temperature variation and food availability (Ballinger 1977; Ji et al. 2007; Warner et al. 2007; Bleu et al. 2013;

Cruz-Elizalde and Ramírez-Bautista 2016; Guo et al. 2022), which could be responsible for the heavier litters produced in 2014 compared to those in the three subsequent years. First, we ruled out the possibility that the greater MLM in 2014 was due to female size variation because the female SVL did not significantly differ across the four years. Second, data from the nearest meteorological station showed that there was no significant variation in environmental temperature that might account for the heavier litters in 2014 than in 2015–2017.

However, the lower MLMs recorded since 2015 could be attributed to reduced food availability, as the collection site showed repeated signs of human-caused grass fires due to traditional agricultural and grazing activities that allowed fires to spread into the forest. This type of vegetation disturbance has been shown – due to the lethal surface temperatures caused by fire – to negatively impact the abundance of ground-dwelling beetles which, in turn, are an important food source for *P. copei* (Nunes et al. 2006; Elia et al. 2012). The quantity and quality of the diet of females strongly influence their reproductive output (Selman and Huston 1996; Warner et al. 2007; Lovern and Adams 2008). Low feeding during fire years reduced MLM not only during that year, but also in subsequent years, as food resources for *P. copei* females decreased (Ballinger 1997; Warner et al. 2015). Bleu et al. (2013) documented that food availability is correlated with reproductive investment in *Zootoca vivipara*. Furthermore, in *Vipera aspis*, the size of the neonate is influenced by the food intake of the female immediately before ovulation and litter size depends on both long-term reserves and recent food intake (Bonnet et al. 2001). Thus, if human-caused grass fires in Tenango indeed resulted in a significant decrease in prey items consumed by females prior to fertilisation and during pregnancy, this could explain why MLM decreased in 2015–2017; however, this hypothesis needs to be tested in future studies.

In conclusion, by comparing the RLM, INV and PROD indices used to evaluate reproductive effort, we observed that *P. copei* had slightly greater values than the mean estimated for species in the *P. brevirostris* group (Table 1). The high reproductive effort values obtained for *P. copei* might be a result of inhabiting areas with extreme environmental conditions (e.g. high altitude) within the TMVB. Elevation is considered an important factor influencing the evolution of life history traits, especially in *P. copei*, as it is the most important abiotic factor determining its geographic distribution within the TMVB (Alvarado-Avilés et al. 2020). For example, colder temperatures and limited food availability at higher altitudes have been shown to lead to greater reproductive effort in high-altitude species, such as *P. copei* (Rohr 1997; Badyaev and Ghalambor 2001). Overall, we observed that the RLM obtained for *P. copei* was similar to the estimated values for other species of the Scincidae family (Vitt and Price 1982; Qualls and Shine 1997). However, when we examined data from only the species *Plestiodon* from Mexico, we observed that the RLM estimated for *P. copei* was slightly greater than those reported for *P. dugesii* and *Plestiodon* sp. PT from Jalisco and Tlaxcala, which live

**Table 1.** Reproductive effort estimations for several Mexican species of *Plestiodon*.

Species	Location	RCM / RLM	INV (g)	PROD (g × year <sup>-1</sup> )	Reference
<i>Plestiodon bilineatus</i> (n = 1)	Valparaíso, Zacatecas	—	—	1.820	Bañuelos et al. (2016)
<i>Plestiodon</i> sp. PT* (n = 7)	Volcán La Malinche, Tlaxcala	0.231	0.432	0.850	Muñoz (2015)
<i>Plestiodon</i> sp. PT* (n = 17)	Chilchota, Puebla	0.334	0.325	1.168	Chávez (2012)
<i>Plestiodon</i> sp. OX* (n = 1)	Santa Inés del Monte, Oaxaca	—	0.515	1.240	López et al. (2008)
<i>P. indubitus</i> (n = 1)	Sur de Tres Marias, Morelos	—	—	0.640	López et al. (2008)
<i>P. copei</i> (n = 3)	San Lorenzo Acopilco, CDMX	—	—	1.020	García (2009)
<i>P. copei</i> (n = 24)	Tenango, Estado de México	0.301	0.428	1.236	This study
<i>P. dicei</i> (n = 1)	Pablillo, Nuevo León	—	—	1.212	Feria-Ortiz et al. (2007)
<i>P. dicei</i> (n = 1)	San Antonio de las Alazanas, Coahuila	—	—	1.164	Feria-Ortiz et al. (2007)
<i>P. dugesii</i> (n = 21)	Mazamitla, Jalisco	0.292	0.362	1.001	Muñoz (2015)
Averages		0.290	0.412	1.135	

\* Undescribed *Plestiodon* species reported by Pavón-Vázquez et al. (2018): *Plestiodon* sp. PT from Puebla and Tlaxcala; *Plestiodon* sp. OX from Oaxaca.

at lower elevations (Muñoz 2015). Conversely, the RLM obtained for *P. copei* was slightly lower than that estimated for the population of *Plestiodon* sp. PT from Puebla (Chávez 2012). We also observed that the PROD index calculated for *P. copei* from Tenango was greater than that (0.830) estimated by Meiri et al. (2012) for this species.

The observations presented here suggest that the reproductive strategy of *P. copei* from Tenango may have been shaped by the prevailing extreme environmental conditions (Castro-Franco et al. 2011; Bestion et al. 2015; Muñoz 2015), although it will be necessary to evaluate this hypothesis in future studies using both larger sample sizes and additional study sites. Furthermore, it will also be important to evaluate the effects of global warming and habitat loss on the reproductive strategies and sex ratio of this specialist skink.

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## Supplementary material 1

### Games-Howell post-hoc multiple comparisons

Authors: Hermilo Sánchez-Sánchez, Adriana Jocelyn Morales-Gonzaga, Ken Oyama, J. Carlos Alvarado-Avilés

Data type: xlsx

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Link: <https://doi.org/10.3897/herpetozoa.36.e97705.suppl1>

## Supplementary material 2

### Mean monthly temperature based on 59 years of records (1951–2010) for four populations of *Plestiodon copei*

Authors: Hermilo Sánchez-Sánchez, Adriana Jocelyn Morales-Gonzaga, Ken Oyama, J. Carlos Alvarado-Avilés

Data type: docx

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Artikel/Article: [Reproductive effort of \*Plestiodon copei\* \(Squamata, Scincidae\), a highland viviparous lizard from Central Mexico 1-10](#)