

Variation in female reproduction between populations of the arboreal lizard *Urosaurus bicarinatus* (Squamata: Phrynosomatidae) from two different environments in Mexico

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Manuscript received: 13 February 2016

Accepted: 3 October 2016 by EDGAR LEHR

Abstract. Local and geographic variation in several life history characteristics (body size at sexual maturity, clutch size, clutch frequency, egg volume, offspring size) were analysed in the arboreal lizard *Urosaurus bicarinatus* in three populations (Chamela, Jalisco; Jojutla, Morelos; and Paso del Chivo, Michoacan) from two different environments (tropical dry forest and thorn bush) in Mexico. Variations in these life history traits were found to exist between populations. Adult females from Chamela exhibited smaller snout–vent length (SVL) than females from Jojutla and Paso del Chivo. A similar pattern was found in others reproductive characteristics, including clutch size, relative clutch mass, egg volume, and hatchling SVL. These differences could be interpreted in terms of trade-offs, where some populations or species under conditions of low resource availability and high mortality tend to expend higher costs on reproduction; such could be the case in the population of Chamela. However, more studies are needed in many species with a broad geographic distribution to better understand the effects of the environment and genetics on variation in life histories.

Key words. Geographic distribution, life history characteristics, lizard, reproduction.

Introduction

Comparative studies of life history traits across multiple species of lizard were first initiated by TINKLE (1969) and TINKLE et al. (1970). These studies, largely based on previously published data from single populations of individual lizard species, tested hypotheses for the evolution of life history traits such as snout–vent length (SVL), age at sexual maturity, growth rate, survivorship, clutch size, egg size, and other reproductive characteristics in species from different families and environments. FITCH (1970, 1985) examined differences in the breeding period and reproductive characteristics of members of several lizard families, including the genus *Sceloporus* of the family Phrynosomatidae (FITCH 1985).

These pioneering studies provided the basis for further contributions to the study of life history evolution, both

across lizard species (BALLINGER 1973, DUNHAM 1980, RAMÍREZ-BAUTISTA & VITT 1997, 1998) and between populations of a single species (FERGUSON et al. 1980, DUNHAM 1982, BENABIB 1994, RAMÍREZ-BAUTISTA et al. 2004, HERNÁNDEZ-SALINAS et al. 2010). Geographic variation in life history traits across populations of a single species has been addressed in a high number of phrynosomatid species, such as *Sceloporus undulatus* (FERGUSON et al. 1980), *S. grammicus* (LEMONS-ESPINAL et al. 1998, RAMÍREZ-BAUTISTA et al. 2004, HERNÁNDEZ-SALINAS et al. 2010), *S. minor* (RAMÍREZ-BAUTISTA et al. 2008), and *Urosaurus ornatus* (DUNHAM 1982), as well as some other genera of lizards such as *Anolis* (*A. carolinensis*; MICHAUD & ECHTERNACHT 1995).

Variations in life history characteristics reported in earlier studies may represent adaptations to different selective pressures in local environments; however, relatively little

information about the possible role of resource availability, predators, or climate on the regulation of populations was available at that time (FERGUSON et al. 1980, BENABIB 1994). Other studies of lizard life histories have attempted to obtain empirical data to test current hypotheses of life history evolution (TINKLE et al. 1970, VITT & CONGDON 1978, DUNHAM 1982, BENABIB 1994, LEMOS-ESPINAL et al. 1998, RAMÍREZ-BAUTISTA et al. 2004, HERNÁNDEZ-SALINAS et al. 2010). Nevertheless, intraspecific studies of reproductive patterns within individual species have revealed geographic variation in a variety of life history characteristics, such as clutch size, egg size, clutch frequency, and SVL at sexual maturity between populations (BENABIB 1994, MACEDONIA et al. 2003, RAMÍREZ-BAUTISTA et al. 2004, HERNÁNDEZ-SALINAS et al. 2010). Variations in these reproductive characteristics might be related to environmental factors. For example, food availability (prolonged food shortage in the environment may prevent females from reproducing in a particular season or year; BALLINGER 1977, DUNHAM 1982, BENABIB 1994), duration of appropriate environmental conditions (extended optimal environmental conditions improves egg incubation; BENABIB 1994), mortality rates (gravid females are usually subject to higher predation risks, in part due to their reduced locomotory performance; PÉREZ-MENDOZA et al. 2014), and phylogenetic history (even when food is available and lizards are well fed, they fail to obtain the maximum size observed in other species of a given monophyletic group; DUNHAM & MILES 1985, RAMÍREZ-BAUTISTA et al. 2004).

Urosaurus bicarinatus is a small, oviparous, arboreal lizard distributed throughout much of western Mexico, including coastal areas and islands of the Mexican Pacific

(HERNÁNDEZ-SALINAS et al. 2013, 2014). This range includes Pacific coastal areas in the states of Jalisco and Nayarit, as well as more interior areas of Michoacán, Guerrero, and Morelos States (Cuenca del Río Balsas or Río Balsas region). Lizards of the genus *Urosaurus* are generally short-lived (≤ 1 yr), with rapid growth rates and a capacity to deposit multiple clutches within a given reproductive season (RAMÍREZ-BAUTISTA & VITT 1998). However, relatively little is known regarding variation in reproductive characteristics across populations of *U. bicarinatus*, and even less between populations found in different environments. In this study, we compared reproductive characteristics of three populations of this species located in two different areas of central Mexico. These populations were selected given that individual populations of one species with wide distributions often are exposed to various selective regimes and evolutionary trajectories as a result of their living in different environments, at various altitudes, and in different vegetation types (e.g., *A. carolinensis*, MICHAUD & ECHTERNACHT 1995; *U. ornatus*, DUNHAM 1982; *S. aeneus*, RAMÍREZ-BAUTISTA et al. 2016a). Therefore, we predicted that the reproductive characteristics of female *U. ornatus* we measured would differ between populations.

Material and methods

Study sites

We studied three populations of *U. bicarinatus* (Fig. 1). The first study site was Chamela, Jalisco (19°30' N, 105°03' W; datum WGS84; Fig. 1), located at an altitude of about 584 m above sea level. The dominant vegetation type here is tropi-

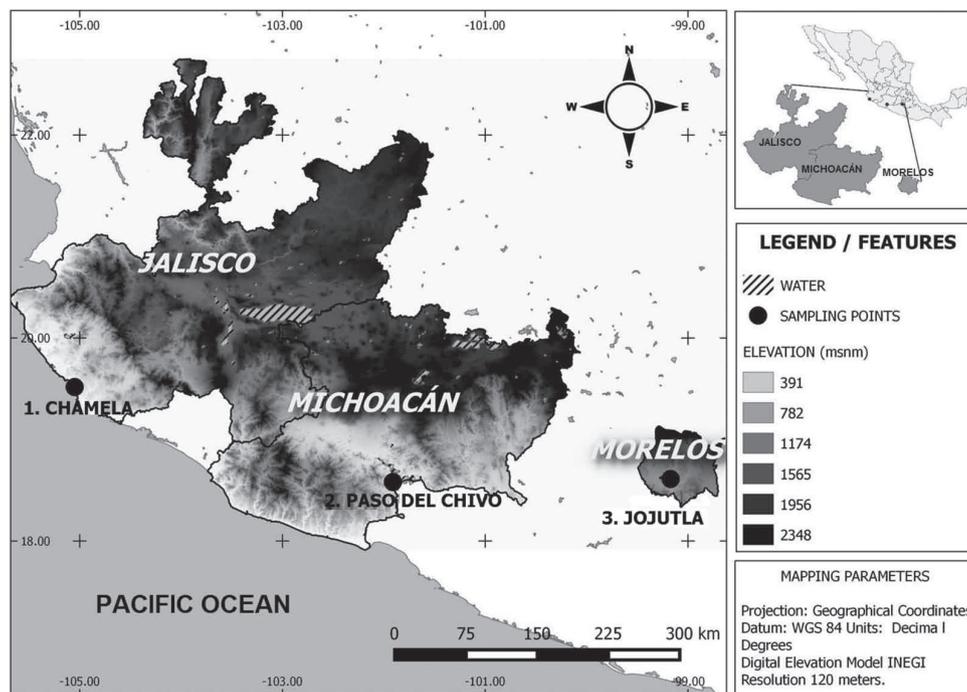


Figure 1. Locations of the three populations of *Urosaurus bicarinatus* in Mexico analysed in this study.

cal dry forest, supported by rains in late spring and summer. The mean annual temperature is 24.9°C, with an average annual rainfall of 748 mm (BULLOCK 1986). Our second site was Jojutla de Juárez, Morelos (18°30' N, 99°30' W; datum WGS84; Fig. 1) located at an altitude of 1,000 m above sea level. This region has a warm subhumid climate with a mean annual rainfall of 838 mm and mean annual temperature of 24°C. The dominant vegetation type is tropical dry forest (RZEDOWSKI 1978). The third study site was Paso del Chivo, Michoacan (18°35' N, 101°55' W; datum WGS84; Fig. 1), located at 350 m above sea level. It has a semi-arid climate with rain in the summer, and total mean rainfall of 700 mm (GARCÍA 1981); the mean annual temperature is 28°C. The dominant vegetation is thorn bush (scrub) mixed with large cacti that can reach > 10 m in height (MIRANDA 1974, URIBE et al. 1981). These populations will subsequently be referred to as Chamela, Jojutla and Paso del Chivo populations, respectively.

Field methods

During our fieldwork, we collected adult females and offspring by hand or with rubber bands. The largest numbers of lizards were mainly collected on sunny days under a schedule from 10:00 to 16:00 h. Adult females were collected at the locality of Chamela from June through December 1988, April through December 1989, and March through August 1990 (n = 79; see Appendix); females at Jojutla were collected from January through November 1984 (n = 81; see Appendix); while females at Paso del Chivo were collected from January through December 1984 (n = 69; see Appendix). We also collected hatchlings at each site (Chamela, n = 92; Jojutla, n = 18; Paso del Chivo, n = 14; see Appendix) during the reproductive season (see Results). The total sample size of adults was 229 females, and the total number of juveniles was 124. Specimens from Chamela (ARB-CHA-UB-0001-0171), Jojutla (ARB-MOR-UB-0001-0099) and Paso del Chivo (ARB-MICH-UB-0001-0083) were deposited in the Colección Nacional de Anfibios y Reptiles (CNAR) of the Universidad Nacional Autónoma de México (UNAM).

Laboratory techniques

All adult lizards used in analyses of reproductive cycles were euthanised with an overdose of pentobarbital (0.01%), subsequently fixed in formalin (10%), and preserved in ethanol (70%). All adult specimens had snout-vent length (SVL) of > 40.5 mm. A previous study showed that females of 40 mm or larger were sexually mature (i.e., exhibit vitellogenic follicles in the ovary or eggs in the oviduct; RAMÍREZ-BAUTISTA & VITT 1998). The reproductive anatomy of each female was examined in order to confirm the presence of non-vitellogenic follicles (NV), vitellogenic follicles (VF) in the ovary, and/or eggs in the oviduct. NVE, early or late VF, and embryos were removed and weighed

(to the nearest 0.0001 g) with an analytic precision scale. In reproductive females, we measured the mass of the largest egg (embryos in the uterus), or vitellogenic or non-vitellogenic follicle (i.e., follicular mass) on each side of the body to the nearest 0.0001 g. We then multiplied this result by the total number of eggs (oviductal eggs [OE], NVE, FV) on that side of the body to estimate the total gonadal mass (RAMÍREZ-BAUTISTA et al. 2002). Clutch size was quantified by counting only the number of eggs in the oviducts of adult females during the reproductive season, and clutch mass was the total mass of all eggs in the oviduct. Following VITT & CONGDON (1978), we calculated the Relative Clutch Mass (RCM) as: clutch mass/(female mass - clutch mass). Egg volume was calculated by measuring the length and width of the largest vitellogenic follicles or OE on the left and right sides of the body to the nearest 0.1 mm using a digital calliper and applying the formula for an ellipsoid (SELBY & GIRLING 1965), $V = (4/3)\pi a^2b$, where 'a' is half the shortest diameter and 'b' half the longest diameter.

Statistics

We used ANOVA to test for population variation in female SVL, and between other reproductive characteristics (clutch size, RCM, egg mass, hatchling SVL, egg volume) using population as a factor. When ANOVAs were significant, we used Bonferroni post hoc tests to identify specific differences between populations. We calculated a Pearson's product-moment correlation coefficient to test for a relationship between clutch size and female SVL (ZAR 1999). Finally, we identified the hatching period of offspring considering the number of months in which they were collected.

Normality of the data was confirmed by means of Shapiro-Wilk W tests (SHAPIRO et al. 1968, ZAR 1999). Means are presented ± 1 standard error (SE), and statistical analyses were performed with the software Statistica 7.0 (Statsoft), with the significance level set at $p \leq 0.05$.

Results

Body size at sexual maturity

Mean body size (SVL) of sexually mature female *U. bicarinatus* differed between populations (ANOVA, $F = 35.9$, $df = 2, 226$, $p < 0.001$; Table 1). A post-hoc Bonferroni test indicated that the females from Chamela were smaller than females from both Paso del Chivo and Jojutla ($p = 0.0001$ in both comparisons), but there was no difference in size between females from Paso del Chivo and those from Jojutla (post-hoc Bonferroni test, $p = 0.561$; Table 1).

Reproductive traits

We found that reproductive activity and offspring size varied between populations (Table 1). Females from Jo-

Table 1. Reproductive characteristics of female *Urosaurus bicarinatus* from each of three populations in Mexico. Means are given \pm 1 SE. Ranges and sample sizes (n) are shown in parentheses. RCM = Relative Clutch Mass.

Variables	Populations		
	Chamela	Jojutla	Paso del Chivo
Vitellogenesis	May–October	February–October	April–August
Egg production	June–September	June–August	May–September
Hatching period	August–December	August–November	August–September
Clutch size	5.4 \pm 0.23 (4–8, n=25)	7.8 \pm 0.72 (5–11, n=10)	6.6 \pm 0.42 (2–9, n=21)
Egg volume (mm ³)	168 \pm 5.2 (108–206, n=24)	276 \pm 47.4 (123–575, n=10)	421 \pm 29.9 (141–616, n=20)
RCM (g)	0.339 \pm 0.02 (0.239–0.534)	0.497 \pm 0.04 (0.300–0.642)	0.507 \pm 0.03 (0.166–0.712)
Clutch frequency	3	2	2
Hatchling SVL (mm)	22.3 \pm 0.31 (18.0–27.0, n=92)	23.9 \pm 0.53 (20.0–27.0, n=18)	24.7 \pm 0.63 (21.0–27.0, n=14)
Female SVL (mm)	43.1 \pm 0.23 (40.0–49.0, n=79)	46.7 \pm 0.38 (40.0–54.0, n=81)	46.5 \pm 0.39 (40.3–54.0, n=69)

jojutla exhibited a longer period of vitellogenesis (February through October, 9 months) than females from Chamela (May through October, 6 months), and those from Paso del Chivo (April through August, 5 months; Fig. 2A–C). Egg production was limited to a shorter period in Jojutla (June–August, 3 months; Fig. 2B) and Chamela (June–September, 4 months; Fig. 2A), than at Paso del Chivo (May–September, 5 months; Fig. 2C).

Clutch size differed between populations (ANOVA, $F = 7.28$, $df = 2,53$, $p < 0.001$; Table 1). A Bonferroni test indicated that the females from Chamela produced smaller clutches (mean = 5.4 ± 0.23) than did females from both Paso del Chivo (mean = 6.6 ± 0.42 ; $p = 0.003$) and Jojutla (mean = 7.8 ± 0.72 ; $p = 0.004$). Females from Jojutla and Paso del Chivo did not differ in clutch size (post hoc Bonferroni test; $p = 0.498$). Egg volume also varied among populations (ANOVA, $F = 26.8$, $df = 2,53$, $p < 0.0001$; Table 1). A post-hoc Bonferroni test indicated that females from Chamela had eggs with smaller volumes (mean = $168 \pm 5.2 \text{ mm}^3$) than did females from Jojutla (mean = $276 \pm 47.4 \text{ mm}^3$; $p = 0.009$) or Paso del Chivo (mean = $421 \pm 29.9 \text{ mm}^3$; $p = 0.001$; Table 2). Relative clutch mass (RCM) also varied between populations (ANOVA, $F = 17.4$, $df = 2,53$, $p < 0.0001$). A post-hoc Bonferroni test indicated that the females from Chamela had lower RCMs (mean = 0.339 ± 0.02) than females from Jojutla (mean = 0.497 ± 0.04 ; $p = 0.010$) or Paso del Chivo (mean = 0.507 ± 0.03 ; $p = 0.001$). However, there was no difference in RCM between females from Jojutla and Paso del Chivo (post-hoc Bonferroni test; $p = 0.507$). Clutch size was significantly correlated with SVL in females from Chamela ($r = 0.77$, $p < 0.0001$), but not in females from Jojutla ($r = 0.31$, $p = 0.37$) or Paso del Chivo ($r = 0.12$, $p = 0.617$).

As snout–vent length (SVL) of hatchlings from Chamela did not vary across years (1988, 1989, and 1990, $n = 92$; ANOVA, $F = 0.825$, $df = 2,89$, $p = 0.441$), all samples were

Table 2. Clutch size by month in each of three populations of *Urosaurus bicarinatus* from Mexico. * Variation between months (all instances).

Month	Chamela*	Jojutla*	Paso del Chivo*
May	–	–	7.5 \pm 1.5
June	6.3 \pm 0.42	8.4 \pm 1.0	7.0 \pm 0.76
July	5.5 \pm 0.26	7.0 \pm 1.3	7.3 \pm 0.88
August	5.3 \pm 0.88	8.0	5.8 \pm 0.30
September	4.0	–	3.0

* $F_{4,49} = 3.39$, $p = 0.01$

grouped together and compared with body sizes of hatchlings from Jojutla ($n = 18$) and Paso del Chivo ($n = 14$). Offspring SVL varied between populations (ANOVA, $F = 6.0$, $df = 2,121$, $p = 0.003$). A post-hoc Bonferroni test indicated that hatchlings from Chamela had smaller SVLs (mean = $22.3 \pm 0.31 \text{ mm}$) than hatchlings from Jojutla (mean = $23.9 \pm 0.53 \text{ mm}$; $p = 0.029$) and Paso del Chivo (mean = $24.7 \pm 0.63 \text{ mm}$; $p = 0.004$; Table 1). However, there was no difference in the size of hatchlings between those from Jojutla and Paso del Chivo (post-hoc Bonferroni test; $p = 0.457$). The total hatching period also varied between populations, with a longer hatching period occurring at Chamela (5 months) as compared to Jojutla (4 months) or Paso del Chivo (2 months; Table 2). However, the peak hatching period was limited to a relatively short time in all three populations, from August to October (Table 1).

Discussion

Interpopulational variation in body size between individuals of one sex is a commonly observed phenomenon in liz-

ards (FERGUSON et al. 1980, DUNHAM 1982, HERNÁNDEZ-SALINAS et al. 2010). Such a pattern could result from some local adaptations to prevailing environmental pressures, as

well as non-adaptive processes, such as population bottlenecks. In this study, we found that female SVL differed between study populations: adult females from Chamela were

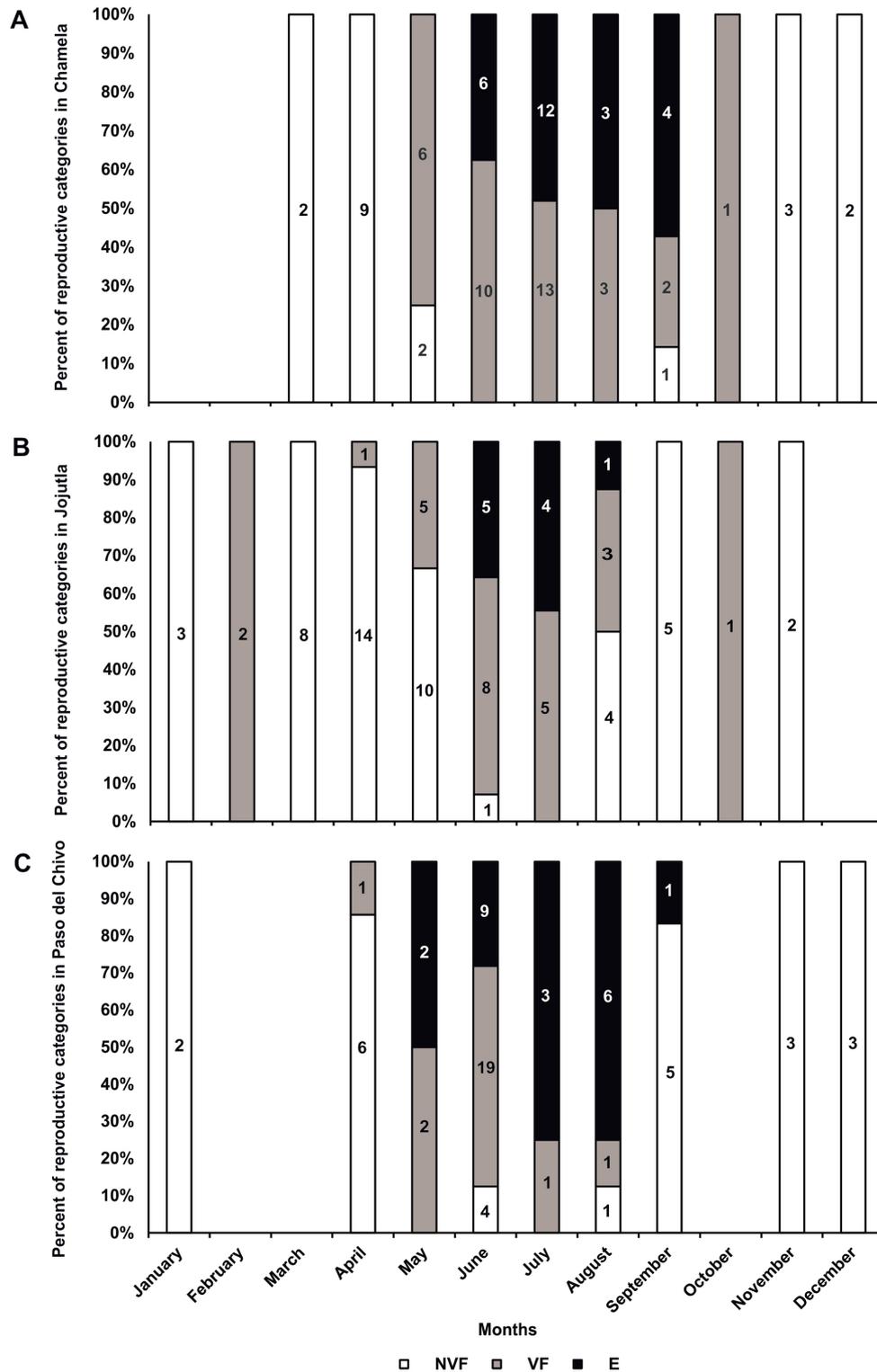


Figure 2. Percentages and numbers of reproductive categories for females of *Urosaurus bicarinatus* from three populations in Mexico (A - Chamela; B - Jojutla; C - Paso del Chivo). NVF - non-vitellogenic follicles; VF - vitellogenic follicles; E - mature eggs.

smaller than those from Jojutla or Paso del Chivo (Table 1). The smaller size of females from Chamela could be a function of selection for accelerated onset of sexual maturity relative to other populations of *U. bicarinatus*: females from Chamela become sexually mature as early as at 7 months post-hatching (RAMÍREZ-BAUTISTA & VITT 1998, RAMÍREZ-BAUTISTA et al. 2016b), and have a short reproductive period (vitellogenic follicles and egg production ending by early September, Tables 1 and 2), adjusting their life history characteristics according to some selective factors of an environment (i.e., predation, competition), allowing them to maximize their fitness (ANGILLETTA et al. 2004).

Females of *U. bicarinatus* from Chamela were smaller but had greater clutch frequencies than females from Jojutla and Paso del Chivo (Table 1). As *U. bicarinatus* is a relatively short-lived species (RAMÍREZ-BAUTISTA & VITT 1998; RAMÍREZ-BAUTISTA et al. 2016b), we suggest that females from Chamela invest more energy into reproduction than growth, a strategy observed in many other species of lizards occurring in tropical environments as well (BELL 1980, STEARNS 1992). Conversely, females from Jojutla and Paso del Chivo may be subjected to contrary trade-offs, investing more energy into growth than reproduction. If so, *U. bicarinatus* can be considered to exhibit high phenotypic plasticity, with populations in different localities experiencing different climatic regimes (temperature, altitude, precipitation), resource distributions, and perhaps social environments, which all are factors that can interact and so generate variation in body size and various reproductive characteristics (BALLINGER 1979, MICHAUD & ECHTERNACHT 1995, JIN & LIU 2007, RAMÍREZ-BAUTISTA et al. 2004, 2008, HERNÁNDEZ-SALINAS et al. 2010).

For females from Chamela, attaining early sexual maturity may reflect a trade-off between maximizing growth and minimizing risk of mortality (EDWARD & CHAPMAN 2011). For example, early reproduction can evolve in response to strong predation pressure (BELL 1980, STEARNS 1992), so that these females prioritise reproduction early in life, rather than pay the costs associated with the deposition of greater numbers of clutches later in life; perhaps as a result, females from Chamela produce smaller overall clutches compared to those from Jojutla and Paso del Chivo, and smaller offspring at hatching (Table 2). Likewise, availability of food in the environment can be a factor that generates another trade-off between quantity and quality of food intake, as compared to current and expected future survival and reproduction rates (EDWARD & CHAPMAN 2011) in *U. bicarinatus*. For example, females from Chamela laid more clutches than females from Jojutla and Paso del Chivo, possibly because the amount and/or quality of food in their environment had been higher in Chamela during the previous breeding season than at Jojutla and Paso del Chivo. However, females from Chamela could also pay higher costs associated with predation, because gravid females became heavier and slower than non-gravid females (MARTIN 1977, DUNHAM 1982). It is likely that local reproductive strategies by female *U. bicarinatus* represent phenotypic variation arising in large part in response to

local environmental pressures (DUNHAM 1982, RAMÍREZ-BAUTISTA et al. 1995, VILLAGRÁN-SANTA CRUZ et al. 2009).

Reproductive characteristics

Female reproductive activity is clearly seasonal in *U. bicarinatus* (Table 1; Figs 2A–C). However, the extent of the reproductive period varied across populations (Table 1). Females initiated vitellogenesis earliest at Jojutla (February), later at Paso del Chivo (April), and latest at Chamela (May; Figs 2A–C). Females with vitellogenic follicles were found in May in all three populations, although the proportion of females with VF in May varied (Figs 2A–C). Females from Chamela exhibited the longest period of vitellogenesis (May–October; Fig. 2A), as compared to Jojutla (May–August; Fig. 2B) and Paso del Chivo (May–August; Fig. 2C). In contrast, the egg deposition period was longest at Paso del Chivo (May–September), intermediate at Chamela (June–September), and shortest in Jojutla (June–August; Table 2). A similar pattern was reported by DUNHAM (1982) for four populations of *U. ornatus* in the southwestern United States, who found that the variations between populations in reproductive activity and related morphological characteristics were positively correlated with relative humidity in the environment, food availability, and intensity of predation (RAMÍREZ-BAUTISTA et al. 1995).

Clutch size in females from Chamela was smaller than that in females both from Jojutla and Paso del Chivo. In this regard, the Chamela population resembles the Animas population of *U. ornatus* described by DUNHAM (1982) in that it exhibits life history traits that are characteristic of classic r strategists (i.e., early sexual maturity and high reproductive effort; TINKLE & DUNHAM 1983, VAN LOBEN SELS & VITT 1984). In all three populations of *U. bicarinatus* we studied, clutch size varied between months (Table 1), declining across all populations from May to September (Table 1). This is consistent with earlier studies in *Urosaurus* species that demonstrated that the total number of eggs per clutch would decline with successive clutches within a given reproductive season (MARTIN 1977, DUNHAM 1982, RAMÍREZ-BAUTISTA & VITT 1998), even though female *U. bicarinatus* may produce up to four clutches per year (RAMÍREZ-BAUTISTA & VITT 1998). However, it is also understood that clutch size and clutch frequency are components of a reproductive strategy adapted to the particular environmental pressures associated with individual lizard populations (MARTIN 1977, DUNHAM 1982, RAMÍREZ-BAUTISTA & VITT 1998). Although females may lay up to four clutches annually, their reproductive period (for all three populations) is shorter than that of many other oviparous lizard species with a similar clutch frequency, such as *Phyllodactylus lanei* (RAMÍREZ-SANDOVAL et al. 2006), or *Sceloporus variabilis* (BENABIB 1994, RAMÍREZ-BAUTISTA et al. 2006).

The differences in the period of female reproductive activity observed across populations of *U. bicarinatus* could be related to clutch frequency, food availability, and/or

other differences in environmental factors (e.g., mortality rates). A shorter reproductive period (i.e., the total period of vitellogenesis, egg production, and egg deposition) in females from Paso del Chivo could be related to greater energy investment in clutch size, egg volume, or RCM (Table 2), as well as food availability, as described by BALLINGER (1977) and DUNHAM (1982) in *U. ornatus*. These authors showed that the investment of energy in reproduction is strongly dependent on food availability in the environment between seasons and years, as has been observed for other lizard species (*S. undulatus*, FERGUSON et al. 1980; *S. variabilis*, BENABIB 1994; *S. mucronatus*, VILLAGRÁN-SANTA CRUZ et al. 2009).

In the same context, variation in RCM – which affects offspring size – between populations of *U. bicarinatus* could reflect different selection pressures in the environment that lizards inhabit (VITT & PRICE 1982). One possibility is that females from Chamela exhibit a trade-off with lower clutch size to maximize their RCM. However, more information on both reproductive characteristics from over an extended period of time is needed to support this hypothesis.

The Paso del Chivo population receives somewhat less rainfall annually (700 mm) than does Chamela (748 mm); although we do not know whether this difference is significant, a greater amount of moisture leads to improved functioning of the somatic structures responsible for nurturing offspring and aiding the development of their immune systems (EDWARD & CHAPMAN 2011). This can result in the production of offspring of greater size and therefore greater RCM, as may be happening in the females of Jojutla and Paso del Chivo. Thus, females from these two populations may give birth to larger offspring as compared to females from Chamela, because females of the former populations are perhaps better fed during the sampling period, or are subject to less intense predation pressure (DUNHAM 1982, ZÚÑIGA-VEGA et al. 2008, BOCK et al. 2010).

Hatchlings from Chamela were smaller than those from Jojutla and Paso del Chivo (Table 2). This may be tentatively explained under the hypothesis of a trade-off between reproductive success (number of offspring) and survival (STEARNS 1992, EDWARD & CHAPMAN 2011). This hypothesis predicts that females from Chamela will invest more energy in reproduction, producing fewer and smaller offspring, but with more clutch frequencies to survive compared to females from Jojutla and Paso del Chivo. This trade-off was observed in other reproductive characteristics like clutch size, RCM, and egg volume, which could be related to local environmental adaptation where life history traits change in response to certain environmental factors (i.e., predation, declining resources, competence), resulting in a maximization of fitness, such as occurs in species from both tropical (*S. variabilis*, RAMÍREZ-BAUTISTA et al. 2006) and arid environments (*S. grammicus*, PÉREZ-MENDOZA et al. 2014).

Life history variation along the geographic range of a given species arises or can be explained by proximate environmental (GRANT & DUNHAM 1990, SEARS 2005), genetic or ultimate factors (SMITH et al. 1994, BALLINGER et

al. 1996), or the interaction of both proximate and genetic factors (IRAETA et al. 2006). In these populations of *U. bicarinatus*, the environmental factors (local environment) probably play a key role in the evolution of life history, specifically reproductive strategies. However, the evolutionary potential of a given species is constrained by the phylogeny (evolutionary history) of *Urosaurus* more generally. Lizards of this genus usually live one year or less, exhibit rapid growth rates, and are capable of depositing multiple clutches within a given reproductive season (RAMÍREZ-BAUTISTA & VITT 1998, RAMÍREZ-BAUTISTA et al. 2016b).

Finally, more studies of populations of individual species are needed in order to understand the relative influence of environmental factors and evolutionary history on life history variation (NIEWIAROWSKI 2001). The three populations of *U. bicarinatus* studied here exhibit some similarities (e.g., body size, reproductive period, clutch frequency, hatchling size), but also several key differences (e.g., most reproductive characteristics), mainly in Chamela as compared to Jojutla and Paso del Chivo. These differences could be related to the differences in the environmental factors at each locality (population), as has been proposed in other studies (BALLINGER 1979, FERGUSON et al. 1980, DUNHAM 1982, HERNÁNDEZ-SALINAS et al. 2010). Further research should help elucidate the source of similarities and differences in life history evolution (FERGUSON et al. 1982).

Acknowledgements

We thank the Estación de Investigación Experimentación y Difusión Biológica de Chamela of the Universidad Nacional Autónoma de México (UNAM) and their staff for making facilities available during the study. Regional authorities from Morelos and Michoacan provided administrative support. We also thank three anonymous reviewers for their comments, which greatly improved our manuscript. Fieldwork was conducted under scientific permits SEMARNAT08-017-A, with environmental register number HESSX1304811.

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Appendix

Specimens of *Urosaurus bicarinatus* collected for use in this study.

Chamela, Jalisco. Adult females: ARB-CHA-UB-0001, 0002, 0003 [June-1988], 0004, 0005, 0006, 0007, 0008, 0009, 0010, 0011, 0012, 0013, 0014 [July-1988], 0015, 0016, 0017 [September-1988], 0018 [October-1988], 0019, 0020, 0021 [November-1988], 0022 [December-1988], 0023, 0024, 0025, 0026 [April-1989], 0027, 0028, 0029 [May-1989], 0030, 0031, 0032, 0033, 0034, 0035, 0036 [June-1989], 0037, 0038, 0039, 0040, 0041, 0042, 0043, 0044, 0045 [July-1989], 0046, 0047 [August-1989], 0048, 0049, 0050, 0051 [September-1989], 0052 [December-1989], 0053, 0054 [March-1990], 0055, 0056, 0057, 0058, 0059 [April-1990], 0060, 0061, 0062, 0063, 0064 [May-1990], 0065, 0066, 0067, 0068, 0069, 0070 [June-1990], 0071, 0072, 0073, 0074, 0075 [July-1990], 0076, 0077, 0078, 0079 [August-1990]. Hatchlings: ARB-CHA-UB-0080, 0081 [August-1988], 0082, 0083, 0084 [October-1988], 0085 [November-1988], 0086, 0087, 0088, 0089, 0090 [August-1989], 0091, 0092, 0093, 0094, 0095, 0096, 0097, 0098, 0099, 0100, 0101, 0102, 0103, 0104, 0105, 0106, 0107, 0108, 0109, 0110, 0111, 0112, 0113 [September-1989], 0114, 0115, 0116, 0117, 0118, 0119, 0120, 0121, 0122, 0123, 0124, 0125, 0126, 0127, 0128, 0129, 0130, 0131, 0132, 0133, 0134, 0135, 0136, 0137, 0138, 0139, 0140, 0141 [October-1989], 0142 [December-1989], 0143, 0144, 0145, 0146, 0147, 0148, 0149, 0150, 0151, 0152, 0153, 0154, 0155, 0156, 0157, 0158, 0159 [August-1990], 0160, 0161, 0162, 0163, 0164, 0165, 0166, 0167 [September-1990], 0168, 0169, 0170, 0171 [October-1990].

Jojutla de Juárez, Morelos. Adult females: ARB-MOR-UB-0001, 0002, 0003 [January 1984], 0004, 0005 [February 1984], 0006, 0007, 0008, 0009, 0010, 0011, 0012, 0013 [March 1984], 0014, 0015, 0016, 0017, 0018, 0019, 0020, 0021, 0022, 0023, 0024, 0025, 0026, 0027 [April 1984], 0028, 0029, 0030, 0031, 0032, 0033, 0034, 0035, 0036, 0037, 0038, 0039, 0040, 0041, 0042 [May 1984], 0043, 0044, 0045, 0046, 0047, 0048, 0049, 0050, 0051, 0052, 0053, 0054, 0055, 0056 [June 1984], 0057, 0058, 0059, 0060, 0061, 0062, 0063, 0064, 0065 [July 1984], 0066, 0067, 0068, 0069, 0070, 0071, 0072, 0073 [August 1984], 0074, 0075, 0076, 0077, 0078 [September 1984], 0079 [October 1984], 0080, 0081 [November 1984]. Hatchlings: ARB-MOR-UB-0082, 0083, 0084 [January-1984], 0085, 0086, 0087, 0088 [August-1984], 0089, 0090, 0091, 0092, 0093, 0094 [September-1984], 0095 [November-1986], 0096, 0097 [August-1986], 0098, 0099 [October-1986].

Paso del Chivo, Michoacán. Adult females: ARB-MICH-UB-0001, 0002 [January 1984], 0003, 0004, 0005, 0006, 0007, 0008, 0009 [April 1984], 0010, 0011, 0012, 0013 [May 1984], 0014, 0015, 0016, 0017, 0018, 0019, 0020, 0021, 0022, 0023, 0024, 0025, 0026, 0027, 0028, 0029, 0030, 0031, 0032, 0033, 0034, 0035, 0036, 0037, 0038, 0039, 0040, 0041, 0042, 0043, 0044, 0045 [June 1984], 0046, 0047, 0048, 0049 [July 1984], 0050, 0051, 0052, 0053, 0054, 0055, 0056, 0057 [August 1984], 0058, 0059, 0060, 0061, 0062, 0063 [September 1984], 0064, 0065, 0066 [November 1984], 0067, 0068, 0069 [December 1984]. Hatchlings: ARB-MICH-UB-0070-0071, 0072, 0073, 0074, 0075, 0076, 0077, 0078, 0079, 0080, 0081, 0082, 0083.