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Thermal Dependence of Incubation Duration Under a Cycling Temperature Regime in the Lizard, *Podarcis hispanica atrata*

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ABSTRACT.— We report the effects of incubation temperature on the duration of incubation and hatchling size in the insular lizard *Podarcis hispanica atrata*. Freshly-laid eggs were placed in artificial nests that were exposed to a natural cyclical variation of microclimate. We monitored substrate temperatures and egg size throughout the incubation period, and measured hatchling size at birth. The mean incubation period was 54 days at average incubation (substrate) temperatures that ranged from 23.5 to 26.5 C. We found a negative relation between the duration of incubation and mean incubation temperature. Overall survival of eggs to hatching was high (83%), even though eggs were frequently exposed for short periods (1-5 h) to high substrate temperatures (>35 C). We found no effect of duration of incubation or incubation temperature on the size of hatchlings.

The rate of development of reptilian embryos is temperature dependent, such that increasing temperatures accelerate embryonic development. This is usually observed in the length of the incubation period, because as incubation temperature increases, hatching occurs earlier (Packard and Packard, 1988). In addition, incubation temperatures can have long-term effects on the morphology, physiology, behavior, and survival of hatchling reptiles (e.g., Packard and Packard, 1988; Burger, 1989, 1990; Janzen, 1993b; Overall, 1994). Hence, part of the variation in body size and other hatchling attributes can be induced by the physical environment that is encountered during incubation (Packard, 1991; Van Damme et al., 1992; Janzen, 1993a; Miller, 1993; Phillips and Packard, 1994). However, most of the available evidence is based on results of laboratory investigations, where the eggs were generally exposed to a constant temperature throughout the incubation period. As

such conditions are rarely, if ever, encountered in nature, the physiological potential revealed in laboratory experiments may not be realized in the field (Cagle et al., 1993).

One of the main obstacles to studying the effects of various microclimatic variables on egg development in lizards has been the difficulty in locating nesting sites. Unlike turtles (Cagle et al., 1993) and crocodiles (Ferguson, 1985), the location of lizard nests in nature is very hard and labour intensive. For this reason little information is available concerning environmental conditions in natural nests of lizards (but see Bock and Rand, 1989; Christian et al., 1991; Christian and Lawrence, 1991; Burger, 1993).

Given these difficulties, alternative research policies have to be designed. One approach consists of mimicking natural cyclicity of one or more microclimatic variables in a laboratory setting (Andrews and Rose, 1994). Alternatively, eggs can be placed in "outdoor incubators" and can be exposed to natural variation of microclimate. Here we report results of a study that followed the latter approach.

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We designed and created artificial nesting sites for the lacertid lizard *Podarcis hispanica atrata* (Castilla and Swallow, 1995). As a biological assay for the suitability of the artificial nests, we buried recently-laid eggs in each container, and subsequently monitored their development until hatching. Our aims here are: (1) To examine the duration of incubation in the artificial nests as a function of temperature; and (2) To examine hatchling characteristics in relation to incubation temperature.

MATERIALS AND METHODS

Study Area and Animal.—The study was conducted between May and August 1993 on the island Columbrete Grande (39°54'N, 0°41'E; Castellón, Spain). This is the largest (13 ha) islet of the Columbretes archipelago. The climate of the archipelago is characterized by an average annual temperature of 17 C and low rainfall (265 mm/year). Most precipitation occurs during Autumn (September–October) and Spring (March–May). Vegetation consists mainly of perennial shrubs (*Suaeda vera*, *Lobularia maritima*), herbs (*Lavatera mauritanica*), and patches of grasses. The vegetative cover of herbs exhibits dramatic seasonal fluctuations, and depends strongly on precipitation levels. Trees are absent, except for one introduced individual of *Ficus carica*. Large expanses of rock without any vegetative cover are also present.

Podarcis hispanica atrata is an endangered, heliothermic, and actively foraging lizard endemic to the Columbretes islands (see details in Castilla and Bauwens, 1991a, b) whose entire world range is about 20 ha. As other Lacertidae, this species possesses sex chromosomes (Odierna et al., 1993). Females attain sexual maturity within their first year of life and may produce at least three clutches per year. Clutch size varies from 1–5 eggs and increases with female body size (Castilla and Bauwens, in press).

Artificial Nests.—Artificial nests (N = 15) were constructed of commercially available plastic cages (20 × 15 × 7 cm). They were open above and filled with 5 kg of dry volcanic sand from the same island. We used three different types of nests. In five we placed two flat rocks 10 cm in height covering about 40% of the sand surface (type rock). In another five we placed a large stone shingle used for house construction which covered ca. 80% of the sand surface (type shingle). The last five nests had only sand (type sand) (see details in Castilla and Swallow, 1995). All nests were covered with a stone slab allowing ventilation and shading. About 1.2 g of rain water, collected in cisterns, was added for each 10 g of dry sand to establish initial moisture levels. The resulting degree of humidity matched that in a sand sample taken from a

natural nest site (described in Castilla and Bauwens, in press). To estimate natural humidity levels, we weighed a sample of wet sand (to the nearest 0.1 g), dried it by three days exposure to sun, and then reweighed it. As evaporation in artificial nests was rather high, we maintained humidity (visually estimated) by adding every other day from 0.1 to 0.3 l of water to each nest.

Artificial nests were placed in two different areas. Area I (N = 7 nests) was rocky, sparsely vegetated and oriented to the west, and area II (N = 8 nests) had high vegetation cover and was oriented to the east. All nests in both areas were placed at ground level in a horizontal position and near a *Suaeda vera* scrub of ca. 50 cm height, from 19 May until 10 August 1993.

Acquiring Experimental Eggs.—To obtain eggs, we captured gravid females with a mean snout-vent length of 62.3 mm (range = 54.3–66.5 mm) and kept them in terraria until they laid their eggs. All terraria were placed under natural conditions and provided with food, water, partial sun/shade and an area with humid sand. Eggs that were buried by females in humid sand were removed from the terraria 15 minutes to four h after they were laid. They were weighed and measured (maximum length and width) to the nearest 0.01 g and 0.1 mm, respectively. They were individually marked with a permanent marker pen and three eggs were buried 6 cm deep in each artificial nest at three different positions (south, east and west). We monitored size and mass of the eggs weekly. All eggs within a single nest proceeded from different females and were incubated on different dates.

Temperature Measurements in the Nests.—From 20 May until 28 July 1993, we manually measured sand temperature in the center of each nest at 6 cm deep, with a digital thermometer (Digitap Therma 3; to the nearest 0.1 C). Temperatures in all cages were recorded every other day, between 0800–0900 h and 1400–1500 h (all times are Mean European Time: MET), as approximations of the daily minimum and maximum soil temperatures. On three different days (15 June, 27 June, 13 July) we tracked the diel variation in each nest by measuring the soil temperature every three hours during the intervals: 0500–0600, 0800–0900, 1100–1200, 1400–1500, 1700–1800, 2000–2100, and 2300–2400 h. On the same days and times, we also recorded soil temperature in one natural nest site.

We estimated the daily average temperature in each nest by calculating the mean of the readings obtained at 0800–0900 h and 1400–1500 h. To assess the reliability of this estimate, we compared the value for each day and nest, with the corresponding mean obtained from the temperature measurements at 3 h intervals for the three days for which these data were available.

The regression with the pooled data for all three days was highly significant ($R^2 = 0.858$, $P < 0.001$); the value (± 1 SE) of the slope (0.928 ± 0.058) does not differ significantly from unity and the intercept (2.331 ± 1.436) is not different from zero. Similar results were obtained for each day separately. Hence, our estimate of the average daily temperature is close to the actual daily mean. At the very least, it provides an index of the relative temperature differences among artificial nests.

The mean incubation temperature for a given egg was calculated as the mean value of the daily average temperatures recorded in the corresponding nest over the entire period that the egg was incubating.

Hatchling Characteristics.—Hatchlings that emerged from eggs incubated in the artificial nests were weighted (to nearest 0.01 g) and measured (snout-vent length and tail-length; to nearest 0.1 mm) on their day of birth. To compare hatchlings from the artificial nests to those born in the field, we captured and measured a separate sample of 68 hatchlings in the study area. They were captured by hand and with a "baited noose" (Castilla et al., 1994) between 9 July and 2 August 1993. We have only included for the analysis those individuals with complete tails and with an open umbilical mark.

Statistical Analysis.—Duration of incubation (log-transformed) was analyzed as a dependent variable using multiple regression (SPSS/PC+ version 5.0) with the following independent variables: initial egg mass, average temperature of the nest (log-transformed), oviposition date, type of artificial nest (sand, rock, or shingle), position (South, East, or West) in the nest, female SVL, and identity of the female ($N = 13$).

Hatchling mass at eclosion was also analyzed as a dependent variable using multiple regression with the same independent variables listed above plus duration of incubation (log-transformed).

RESULTS

Incubation Temperatures and Duration of Incubation.—Substrate in all nests was subject to natural cyclic variation of temperature. Soil temperatures attained daily minimum values during the interval 0500–0800 h, increased steadily during the morning and midday hours, and were maximal at 1700 h (Fig. 1). Variation in soil temperature among nests was highest during the warmest part of the day, whereas nighttime temperatures converged strikingly (Fig. 1). Temperatures recorded at both 0800–0900 h and 1400–1500 h increased gradually from May to July (Fig. 2). The average value of the daily mean temperature over the entire period for the different nests situated in areas I and II was 24.2

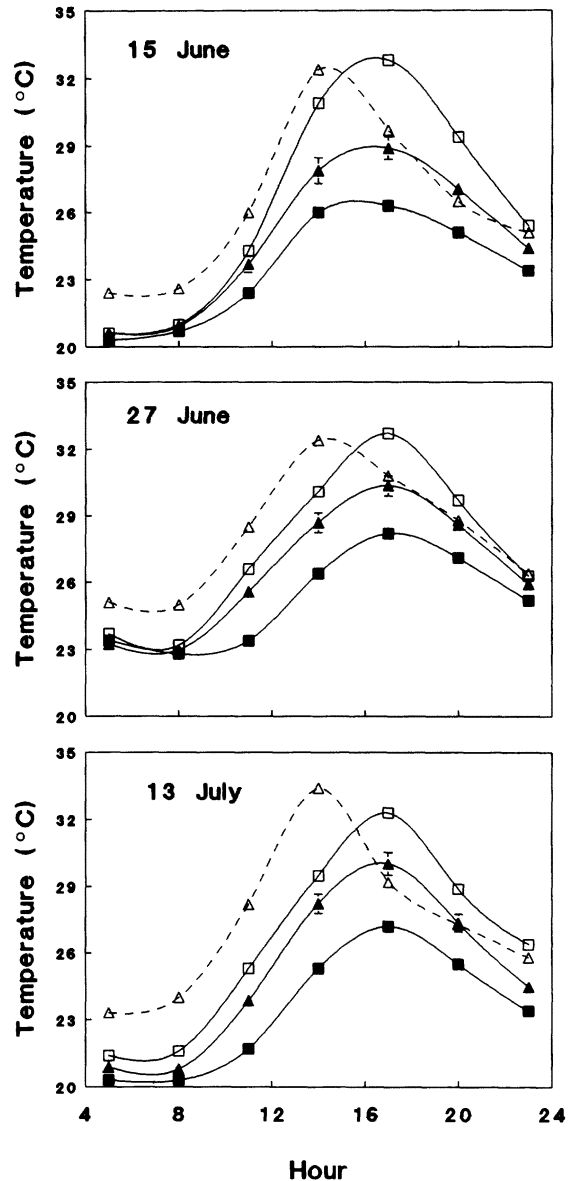


FIG. 1. Diel variation of sand temperature (6 cm deep) in artificial nests during three days in June and July 1993. Given are the mean values (± 1 SE) for the 15 artificial nests (black triangle), and the maximum (white square) and minimum (black square) temperatures recorded in each interval. Temperatures at a natural nest site (white triangle) are shown for comparison.

and 24.4 C respectively, and did not differ significantly (ANOVA: $F = 2.061$, $df = 1,523$, $P > 0.10$).

During incubation, eggs increased in mass by a factor of 3.7 (mass before eclosion divided by mass at laying time), and in length and width by factors of 1.4 and 1.6, respectively (Fig. 3).

The mean incubation period for the eggs in the artificial nests was 54.0 days ($N = 24$, range = 44–69). The results of the multiple regression

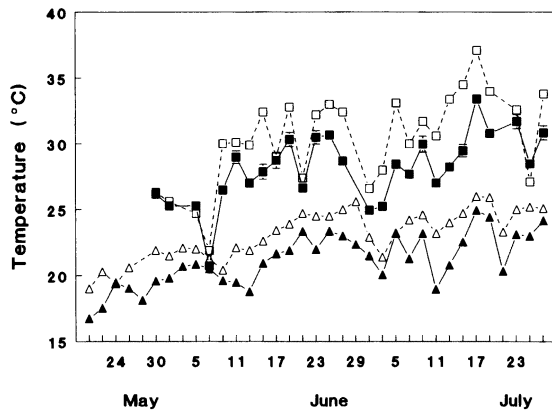


FIG. 2. Substrate temperatures (6 cm deep) recorded on different days in May–July 1993, during the intervals 0800–0900 (triangles) and 1400–1500 (squares). Shown are the daily mean (± 1 SE) values for the 15 artificial nests (black symbols), and temperatures recorded at one natural nest area (white symbols).

analysis indicated that only mean incubation temperature explained a significant amount of the variation in duration of incubation ($F = 16.08$, $df = 1, 23$, $P < 0.01$). Incubation temperature alone explained 78% of the variation in duration of incubation ($r = -0.885$, Fig. 4). However, some of the independent variables were highly correlated (multicollinearity), which may create a problem with interpretation of the data (e.g., female A and position west were both correlated with date of oviposition at $r = -0.751$ and $r = -0.860$, respectively). Therefore, several other models were fitted to see whether they explained the variation more

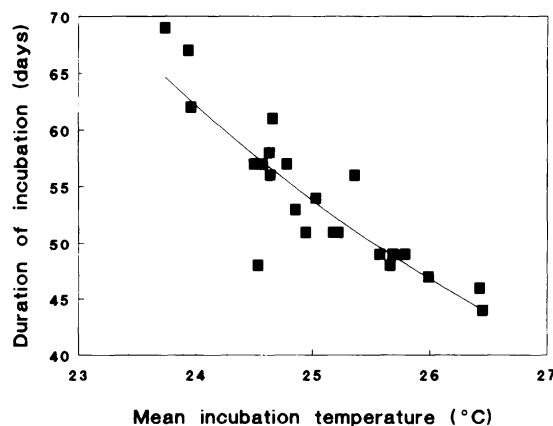


FIG. 3. Temporal changes in the mass of eggs during the complete incubation period in the artificial nests (white squares). Values are means (± 1 SE). The mean body mass of hatchlings at birth is also shown (black square). Numbers indicate sample size.

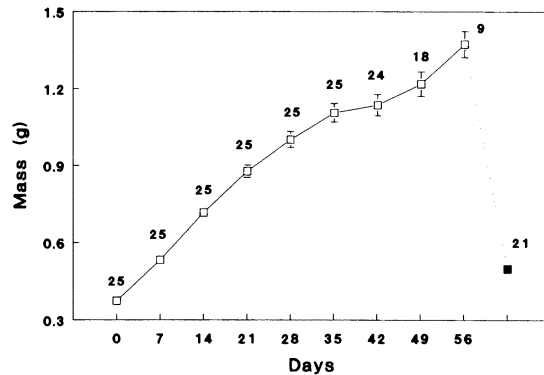


FIG. 4. Relationship between the duration of incubation and mean incubation temperature of *P. hispanica atrata* eggs in artificial nests.

adequately. The data were analyzed omitting position west, female A, both female A and position west, and omitting all variables for female identity and position in the nest. All of these analyses yielded the same model, with only mean incubation temperature explaining a significant portion of the variance.

Hatchling Characteristics.—The multiple regression analysis of the variation in hatchling mass evidenced that only the egg mass at oviposition explained a significant portion of the variation. Hatchling mass was positively correlated with the mass of the eggs at the time of laying ($r = 0.533$, $P = 0.01$), so large hatchlings tended to come from large eggs.

Hatchlings from the artificial nests were significantly larger in body mass (ANOVA, $F = 7.515$, $df = 1, 61$, $P < 0.01$) but significantly shorter in both SVL and tail length than those captured in the field (ANOVA, SVL: $F = 5.47$, $df = 1, 62$, $P = 0.02$; tail length: $F = 15.04$, $df = 1, 62$, $P < 0.001$) (see Table 1). An analysis of covariance, with body mass as the covariate, was used to confirm the morphological differences between the two groups of hatchlings. Hatchlings from the artificial nests had statistically shorter SVL (ANCOVA; $R^2 = 0.601$, $F = 44.468$, $df = 2, 59$, $P < 0.001$) and tail length (ANCOVA; $R^2 = 0.565$, $F = 38.284$, $df = 2, 59$, $P < 0.001$) for their body mass. Furthermore, hatchlings from the artificial nests had shorter tails for their SVL (ANCOVA; $R^2 = 0.561$, $F = 31.975$, $df = 2, 60$, $P < 0.001$).

DISCUSSION

Nest Temperatures.—The majority (83%, $N = 47$) of the eggs successfully finished their development in the artificial nests (details in Castilla and Swallow, 1995). Hence they provided an environment that seemed suitable for egg incubation. This may have important practical

TABLE 1. Size (mean \pm 1 SE, range between brackets) of hatchlings from the artificial nests (N = 21) and of hatchlings captured in the field during July and August 1993. Measurements of hatchlings with the presence of an umbilical mark still open (N = 41), or closed (N = 13) are given separately.

	Body mass (g)	Body length (mm)	Tail length (mm)
Artificial nests	0.51 \pm 0.01 (0.43–0.60)	28.05 \pm 0.36 (25.4–30.6)	45.36 \pm 0.88 (36.0–51.0)
Nature: open umbilical mark	0.45 \pm 0.01 (0.29–0.70)	29.03 \pm 0.23 (25.0–32.0)	50.11 \pm 0.75 (36.7–61.6)
Nature: closed umbilical mark	0.45 \pm 0.02 (0.23–0.56)	28.90 \pm 0.56 (23.0–30.8)	51.06 \pm 1.57 (37.3–58.8)

applications for the conservation of lizard populations that live in areas where natural oviposition sites are scarce (Castilla and Swallow, 1995). In addition, the man made nests can be considered as "outdoor incubators," offering opportunities to study characteristics of embryo and egg development under conditions that closely mimic temporal variability in nature.

Although daily average temperatures differed among artificial nests due to differences in the structure of the surrounding habitat, the pattern of diel cyclicity was rather similar in all man-made nests. Temperatures were lowest during the interval 0500–0800 h, and attained maximal levels near 1700 h. This pattern differed somewhat from that recorded at a single, communal nesting site in the study area. Temperatures at the latter site were lowest between 0500–0800 h, and attained their highest value near 1400 h, when temperatures in the artificial nests were still rising. Maximum and minimum temperatures at the natural nesting site were also higher than in most of the man-made nests. This difference occurred mainly because of the differences in position of natural and artificial nests, the different cover, and the consequent differences in the timing and duration of exposure to direct sun. It is not surprising that temperatures in the artificial nests were somewhat lower than in the natural nesting site, because we devoted special attention to protecting the nests from excessive heat. We deliberately chose to insulate the eggs against high temperatures because eggs of the closely related *P. hispanica hispanica* and *P. muralis* exposed to constant temperatures of 32 C or higher suffer a high mortality rate (Van Damme et al., 1992; D. Bauwens and R. Van Damme, pers. comm.).

Our measurements indicate that soil temperatures in the man-made sites and the natural nest regularly rose to levels well above 30 or even 35 C for short periods (1–4 h) of time. Yet, the probability of survival to hatching was high for eggs in both artificial nests and in the natural site (Castilla and Bauwens, *in press*). This

suggests that the eggs of *P. h. atrata* tolerate short term exposures to temperatures that are at the edge of tolerance for constant maintenance in some closely related species.

Duration of Incubation.—Eggs in warmer nests tended to incubate for a shorter period of time. A negative relation between the duration of incubation and temperature has been described previously for numerous other species of lizards (e.g., Muth, 1980; Packard and Packard, 1988; Galán, 1992; Van Damme et al., 1992). However, the former studies were performed in the laboratory, where the eggs were incubated over a wide range of constant temperatures (most typically 25–35 C). Our study, in contrast, was performed in the field, where the eggs were exposed to a natural cycle of fluctuating temperatures. Moreover, the mean incubation temperature varied only between 23.5 and 26.5 C. It is therefore remarkable that we have found such a strong relationship between the duration of incubation and substrate temperature.

The foregoing result implies that the eggs laid early in the season (April–May), when environmental temperatures are lower, will need more time to develop than will those laid late in the season (July). This prediction is confirmed by the strong negative correlation found between the duration of incubation and date of laying.

Hatchling Characteristics.—Other studies have shown that incubation temperature affects the size of hatchling lizards at birth. Higher incubation temperatures produce smaller hatchlings, even after correcting for the effect of initial egg size (e.g., Beuchat, 1988; Phillips et al., 1990; Van Damme et al., 1992; Phillips and Packard, 1994). In our study, however, incubation temperature did not affect hatchling size. Given that the average incubation temperatures were rather low (23.5–26.5 C), perhaps this finding is not so surprising. The effect of temperature on hatchling size observed in one congeneric and one conspecific lizard (*Podarcis muralis* and

P. h. hispanica) was evident only at high, constant incubation temperatures (32–35 °C; Van Damme et al., 1992; D. Bauwens and R. Van Damme, pers. comm). Also, the range of temperature variation among our sites might have been too small to induce differences in hatchling size. Yet, Overall (1994) reported variation in hatchling body mass that was associated with short-term (1–3 h) increases of incubation temperature.

Hatchlings from the artificial nests weighed more than those captured in the field, but had shorter body and tail lengths. These differences might be artificial, because the field-caught hatchlings could have lost or gained mass in a short time. Assuming that the difference is a real one, it might be partially attributable to diverging conditions between the man-made and the natural nesting sites. As we have information for only a single natural nesting area, any comparison remains extremely preliminary, and no firm conclusions can be drawn. The available data indicate that temperature in the artificial nests was lower than in the natural nesting area. Eggs incubated at lower temperatures generally give rise to heavier hatchlings (e.g., Beuchat, 1988; Phillips et al., 1990; Van Damme et al., 1992; Phillips and Packard, 1994). Also, soil humidity in our cages was probably different from that in natural nests. Hatchling size increases with humidity of the incubation substrate in several turtles (e.g., Packard, 1991; Packard et al., 1993) and lizards (Phillips et al., 1990; Phillips and Packard, 1994). However, other studies have failed to find this relation (e.g., Overall, 1994), including the only one that involved a lacertid lizard (D. Bauwens and M. Gil, pers. comm.).

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SHORTER COMMUNICATIONS

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Descriptions of *Bufo* Tadpoles from the Southwestern Coast of Jalisco, México

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There are approximately 200 species of *Bufo* worldwide (Blair, 1972). The genus includes a number of species with undescribed tadpoles and many *Bufo* tadpoles are difficult to distinguish even when descriptions have been published.

Three species of *Bufo* are common in the lowlands of western México: *B. marinus* (Linnaeus, 1758), *B. marmoratus* (Wiegmann, 1833), and *B. mazatlanensis* (Taylor, 1940, Casas-Andreu, 1982). *Bufo marinus* is a eurytopic species that ranges through all lowland neotropical environments from wet forest to tropical and

subtropical scrub (Blair, 1972). *Bufo marmoratus* and *B. mazatlanensis* are Mexican endemics that inhabit coastal lowland thorn forests. Tadpoles of *B. marinus* have been described elsewhere (Ruthven, 1919; Kenny, 1969; Duellman, 1978; Zug and Zug, 1979), but those of *B. marmoratus* and *B. mazatlanensis* have not. In this paper we describe all three species from an area of sympatry (Ramírez-Bautista, 1994).

Bufo marinus and *B. mazatlanensis* have a generalized bufonid life history pattern, with many eggs laid in strands in water, followed by an aquatic larval stage and then metamorphosis. *Bufo marmoratus* follows this same pattern except that it lays single adhesive eggs (Blair, 1972). All three species are opportunistic breeders, reproducing when there is adequate rainfall to fill the breeding ponds (Blair, 1972). Based on rainfall data and the presence of metamorphosed toadlets, larval development in the field was no greater than one month for all three species.

Tadpoles came from four sites within a 19 km radius in Jalisco, México; the Estación de Biología "Chamela" of the Universidad Nacional Autónoma de México, the villages of Chamela and Emiliano Zapata, and Zarco Dam. We used a dip net to collect from rivers, ditches, temporary ponds, and a pool behind a dam. A portion of the tadpoles from each collection locality was preserved in 5% formalin or 2.5% glutaraldehyde and the remainder was reared through metamorphosis to confirm the identifications. Collections were made between 20 June and 13 July, 1991.

Descriptions and drawings were made from tadpoles preserved in formalin. We measured 20 tadpoles indiscriminately selected from the collections of each species in Gosner stages 33-36 (Gosner, 1960) to 0.1 mm with digital calipers, and included body length,

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