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Variation in parental investment and relative clutch mass of the spiny-tail iguana, *Ctenosaura pectinata* (Squamata: Iguanidae) in central México

Variación en la inversión parental y masa relativa de la nidada en la iguana de cola espinosa *Ctenosaura pectinata* (Squamata: Iguanidae) en el centro de México

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Abstract. We measured the length, width, volume, and weight of 871 freshly laid eggs of 28 clutches of *Ctenosaura pectinata*. The iguanas were obtained from a tropical dry forest area in central Mexico. The relative clutch mass was related positively to the average egg weight but not to average egg volume. Unlike what usually occurs in lizards, where the body length strongly predicts egg production, in *C. pectinata* clutch size and egg size were not correlated with female weight or snout-vent length. Observed differences revealed variation in the weight-size of the egg within an individual clutch. Therefore, there is not an optimization of the egg in the studied population of *Ctenosaura*, as usually occurs in small lizards. This variation associated with reproduction takes place in the middle of the dry season, and may be interpreted as an adaptation to facilitate the adjustment of different phenotypes in environments with extreme drought.

Key words: *Ctenosaura pectinata*, Mexico, parental investment, clutch variation.

Resumen. Medimos la longitud, amplitud, volumen, y peso de 871 huevos recién puestos de 28 nidadas de *Ctenosaura pectinata*. Las iguanas fueron obtenidas en un área de bosque tropical seco en el centro de México. La masa relativa de la nidada estuvo relacionada positivamente con el peso promedio de los huevos pero no con el volumen promedio del huevo. A diferencia de lo que ocurre usualmente en lagartijas, donde la longitud del cuerpo determina la producción de huevos, en *C. pectinata* el tamaño de la puesta y el tamaño del huevo no se correlacionan con el peso y tamaño de las hembras. Las diferencias observadas revelan variación en el tamaño y peso de los huevos dentro de las puestas individuales. En consecuencia, no hay una optimización del huevo en la población estudiada de *Ctenosaura*, como usualmente ocurre en lagartijas de tamaño pequeño. Esta variación asociada con la reproducción tiene lugar a mitad de la estación seca, y puede ser interpretada como una adaptación para facilitar el ajuste de diferentes fenotipos en ambientes con sequía extrema.

Palabras clave. *Ctenosaura pectinata*, México, inversión parental, variación en la puesta.

Introduction

Reproductive strategies in reptiles involve variation in clutch size, incubation time, and intra-clutch variation in egg weight and size (Sinervo and Licht, 1990; Craig et al., 1990; Rodríguez-Romero et al., 2004; Wilkinson and Gibbons, 2005). These patterns of variation usually have been considered to be promoted by environmental factors. Within lizards, patterns of variation in clutch and egg

size (Van Marken and Albers, 1993; Rand, 1994; Ji and Brana, 2000; Shanbhag et al., 2000) have been attributed to variation in climate conditions among high and low elevations/latitudes, and their effects on the environment temperature and humidity variations (Fitch, 1985). Within the same population, variation among years is considered to result from responses to food availability, predation intensity, female size, and other local environmental factors (Vitt and Price, 1982; De Marco, 1989; Abell, 1999). Previous studies have shown that in lizards, clutch size variation is related to female size or weight in both oviparous and viviparous species and the pattern is

consistent in semelparous and early-maturing iteroparous species (Rodríguez-Romero et al., 2004; Du et al., 2005; Herrman and Herrman, 2005). However, this pattern is less common and not consistent within iteroparous, long-lived and late-maturing lizard species (Shanbhag et al., 2000). According to previous studies among lizards, *Iguana iguana* show unusually large clutches and these are not related to female size (Van Marker and Albers, 1993). Moreover, notable egg size variation within clutches was recorded (Rand, 1994; Alvarado et al., 1995). Variation in clutch size in lizards can also result from the effect of proximate environmental factors and from changes in the physiological condition of females (Dunham et al., 1989). This lack of a generalized pattern is not only seen in these long-lived lizards, but also in some turtles (i.e., *Gopherus* and *Kinosternon*), lizards (i.e. *Amphibolurus muricatus* Warner et al., 2008) and snakes (*Vipera aspis*, Bonnet et al., 2001) where variation in clutch size was not explained by mother's size or weight (Andrew and Aguirre, 1995; Wilkinson and Gibbons, 2005), and was attributed to such proximate factors as resource availability and the metabolic rate of the mother. The mother may present differences in metabolic rate during follicle recruitment and vitellogenesis (Warner et al., 2008; Bonnet et al., 2001), which can last from fall through spring.

The present paper addresses the study of variation in clutch size and relative clutch mass in the spiny-tail iguana (*Ctenosaura pectinata*). Our results support the fact that iteroparity in large and long-lived lizards is commonly associated with 1) a pattern in which clutch-size variation is related to weight of females instead of snout-vent length, and 2) significant within-clutch variation in the size of eggs depending on the weight of females.

Material and methods

Subjects came from a tropical dry forest with a sub-humid climate in central México, Sierra de Huautla, Morelos (18° 24' N and 99° 03' W; 930 m elevation). The most common species are *Ipomoea intrapilosa*, *Pithecellobium dulce*, *Acacia acatlensis*, *Plumeria rubra*, *Acacia cymbispina* and *Ceiba parvifolia*. The driest months are January (10.8 mm), March (0.0 mm) and April (6.3 mm), and the hottest months are April to 26.2 °C and May with 26.3 °C. The average annual temperature in this area is 24.9 °C (23.6-26.3 ± 0.89).

Gravid females ($n = 28$) were collected during April in different years: 1995 $n = 7$, 2003 $n = 14$, and 2005 $n = 7$. Each female was kept and watched during the last week of gravidity in a plastic box (60 x 40 x 15 cm) with vermiculite (horticulture grade Terra/Lite), moisture between 15 – 20

%, dim light, and temperature between 28 – 30° C. Freshly-laid eggs were measured and weighed and females were returned to their natural habitat.

Data recorded from each female were snout-vent length (SVL), total weight (TW), and clutch size. All the eggs from each clutch were measured with digital calipers (0.01 mm) and weighed on a digital balance (0.1 g). Clutch size was considered as the total count of eggs produced by each female. Volume of each egg was obtained by the equation for an ellipsoid, $V = 4/3 \pi (1/2 L) (1/2 W)^2$, where L is the longest diameter and W is the shortest diameter. Total volume and total weight of the clutch were obtained by summing these individual measurements for all freshly-laid eggs produced by each female. Relative clutch mass was calculated by the egg weight/ female mass quotient after having laid the eggs (Cuellar, 1984; Rodríguez-Romero et al., 2002). The variation in relative clutch mass (RCM) and clutch size was calculated among females, whereas that of egg size and egg volume was calculated within the individual clutches. We used the coefficient of variation ($CV = \text{standard deviation}/\text{mean} \times 100 \%$) as a measure of variation considering ($CV < 5\%$ as invariant, and $> 5.1\%$ as variable). To evaluate whether the weight of females might affect their reproductive characteristics, both the female weight and the residuals of the regression of female weight against SVL (which is a measure of female body nutritional condition) were used as the independent variables in separate regressions with number of eggs and average weight of the eggs as dependent variables. Additionally, to analyze whether variation in the volume and weight of eggs was explained by the traits of the females, SVL and weight of females after oviposition were compared by regression analyses with CV of volume and weight of freshly-laid eggs.

To analyze whether the amount of precipitation might influence reproductive characteristics like clutch size, egg volume, and egg weight, a regression analysis was applied considering the amount of rainfall (May to September) from the previous year. Considering that reproductive season analyzed as vitellogenesis and mating occur from January to February. All analyses were conducted in Statistica 6.0 (StatSoft).

Results

A total of 871 eggs were collected from 28 females with an average size of 289.3 mm SVL (± 23.5 , range of 240.0-340.0) across the 3 years of the study. Average clutch size was 31.1 eggs (± 11.6 , range of 12.0 – 52.0, $CV = 37.5 \%$), with a mean egg volume of 7.39 cm³ (± 2.07 range of 3.3 – 17.27, $CV = 28.07 \%$), maximum diameter

of 30.9 mm (± 2.2 , range of 18.0 - 40.5, CV = 7.3 %), minimum diameter of 21.16 mm (± 2.4 , range of 16.2 - 32.0, CV = 11.3 %), and a mean weight of 7.46 g (± 1.7 , range of 5.1 - 15.6, CV = 23.48 %). Average relative clutch mass was 0.40 (± 0.09 , range of 0.23 - 0.56, CV = 22.5 %), and was related to average egg weight ($r = 0.411$, $R^2 = 0.168$, $F_{1,26} = 5.07$, $P = 0.033$), and not related to the average egg volume ($r = 0.293$, $R^2 = 0.085$, $F_{1,26} = 2.43$, $P = 0.13$). A positive relationship between clutch size and average egg weight was found ($r = 0.408$, $R^2 = 0.16$, $F_{1,26} = 5.0$, $P = 0.034$). In contrast, clutch size was not related to maximum egg diameter ($r = -0.025$, $R^2 = 0.0006$, $F_{1,26} = 0.01$, $P = 0.899$) nor to average egg volume ($r = 0.040$, $R^2 = 0.0016$, $F_{1,26} = 0.04$, $P = 0.836$). Average egg length was significantly related to female weight (Table 1). Clutch size was not correlated with robustness of female (body condition) (Fig. 1A). Average weight of eggs was not related to female robustness (Fig. 1B). Neither clutch nor egg characteristics were explained by the SVL females

Table 1. Regression analysis (r) between reproductive traits and female weight and length of the spiny-tail iguana, *Ctenosaura pectinata*. ns = non significant. Clutch size and Relative clutch mass $n=28$; Average egg size, Average egg volume and Average egg weight $n=871$ eggs

| | Clutch size | Average egg size | Average egg volume | Average egg weight | Relative clutch mass |
|--------------------------------------|---------------------|---------------------|---------------------|---------------------|----------------------|
| Weight of females ($n=28$) | 0.460 ^{ns} | 0.450 ^{ns} | 0.223 ^{ns} | 0.125 ^{ns} | 0.364 ^{ns} |
| Snout-vent length females ($n=28$) | 0.372 ^{ns} | 0.332 ^{ns} | 0.140 ^{ns} | 0.183 ^{ns} | 0.080 ^{ns} |

(Table 1), Clutch size ($r = 0.250$, $R^2 = 0.062$, $F_{1,26} = 1.68$, $P = 0.206$), average volume ($r = 0.161$, $R^2 = 0.026$, $F_{1,26} = 0.66$, $P = 0.421$) and weight of eggs ($r = 0.142$, $R^2 = 0.020$, $F_{1,26} = 0.51$, $P = 0.478$) were not affected by the rainfall amount of the year previous to reproduction.

The regression analyses showed that the coefficient of variation (CV) of weight of freshly laid eggs was neither related to female SVL ($r = 0.163$, $R^2 = 0.026$, $F_{1,26} = 0.71$, $P = 0.404$) nor to female weight ($r = 0.215$, $R^2 = 0.0465$, $F_{1,26} = 1.26$, $P = 0.270$).

Females of *Ctenosaura pectinata* laid clutches with a wide variation in egg size and weight (Fig. 2). 75 % of clutches showed an average CV of 9.47 (± 3.90 , range of 5.3- 21.0), whereas only 25 % produced more evenly

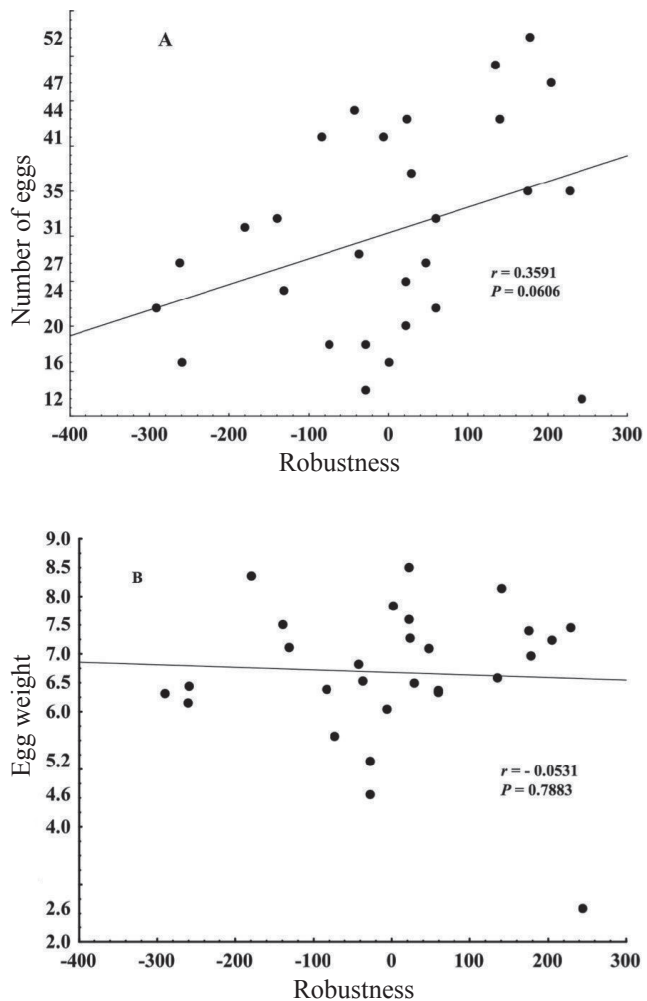


Figure 1. Relationship between the residuals from female weight against female snout-vent length (robustness a measure of body nutritional condition) and (A), the number of eggs produced per female, and (B), the weight of the eggs.

sized eggs (CV < 5%). Within-clutch variation of egg volume (measured as CV) was neither related to SVL ($r = 0.239$, $R^2 = 0.488$, $F_{1,26} = 1.57$, $P = 0.219$), nor to female weight ($r = 0.302$, $R^2 = 0.549$, $F_{1,26} = 2.61$, $P = 0.117$).

Discussion

With some exceptions, in general, variation in the clutch size of lizards is explained by a positive relationship of clutch size and female snout-vent length (Fitch, 1985). In addition, the egg has been considered to be under a high evolutionary pressure to be relatively invariant in size (Shine and Greer, 1991; Shine, 2005). In *Ctenosaura pectinata* clutch size was not found to be related to the

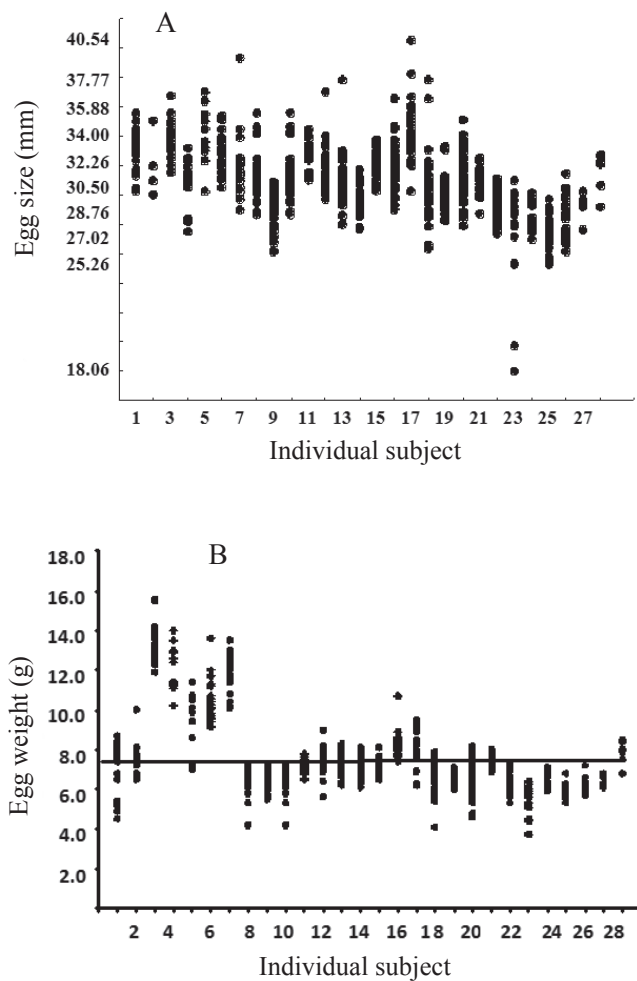


Figure 2. Within clutch variation in egg size (A), and weight (B) of freshly-laid eggs of *Ctenosaura pectinata*. The horizontal lines show average size (30.92 mm) and weight (7.72 g) of eggs for all females.

weight of females, nor to snout-vent length. The substantial variation observed in the clutch size among females of *Ctenosaura pectinata* is similar to that in *Iguana iguana*, *Ctenosaura similis*, several species of *Cyclura*, *Sauromalus*, and *Xenosaurus* (Van Marker and Albers, 1993; Zamora-Abrego et al., 2007).

In turtles the nutritional condition of females determined egg size and was associated with number and position of follicles (Wilkinson and Gibbons, 2005). Egg size also varied among the first, second, and third clutches due to decrease in resource availability. In *C. pectinata*, we found only 1 clutch per year, but we observed considerable variation in clutch size (12–52 eggs) and in the sizes of eggs within a clutch (from 18.06 to 30.92 mm in length).

According to Wilkinson and Gibbons (2005) smaller eggs may correspond to those that were incorporated late to the clutch, when the availability of resources from the mother was depleted. The utilization of both endogenous energy stores “capital”, and recently acquired food to fuel reproduction “income”, has been previously observed in agamid lizards (Warner et al., 2008). Vitellogenic follicles of different size were observed in the ovary of *C. pectinata* with platelets of 3 different sizes and various kinds of morphology (Uribe et al., 1996).

Considerable variation in clutch size of *C. pectinata* has been observed previously in lizards (Uller et al., 2008) and other large reptiles, such as tortoises and crocodiles (Fitch, 1985; Casas-Andreu, 2003; Roosenburg and Dennis, 2005). All these taxa are late-maturing, long-lived, and produce variable large clutches.

Relative clutch mass is considered to be influenced by foraging mode and predator escape tactics (Vitt and Price, 1982), although it does not appear to be consistent. Species with the widely foraging mode usually show low relative reproductive outputs, whereas sit-and-wait species show higher values (Vitt et al., 2003). Therefore, *C. pectinata* may be considered a sit and wait forager (Vitt and Congdon, 1978) considering its feeding habits with adaptations for herbivory (Iverson, 1982) and that it shows a high relative reproductive output of 0.40 with a high CV = 24.68.

Relative clutch mass and its variability are directly related in lizards. Several members of the genera *Anolis*, *Tropidurus*, *Niveoscincus*, *Sceloporus*, *Calotes*, and *Tiliqua* exhibit low mean RCM values as well as low variability in this trait (less than 10 %, Feria et al., 2001; Chapple et al., 2002; Ji et al., 2002; Milne and Bull, 2002; Wiederhecker et al., 2002; Rodríguez-Romero et al., 2004; Vitt and Zani, 2005). Lizards with moderate reproductive output exhibit moderate variation in RCM index (11.0–17.0 %), for example *Oedura lesuerii*, *Aspidoscelis lineatissima*, and *S. aeneus* (Doughty, 1997; Ramírez-Bautista et al., 2000; Rodríguez-Romero et al., 2002). Finally, Xenosaurid and Iguanid lizards, Australian skinks, *Ctenophorus fioni* and *S. bicantalis* (Johnston, 1999; Rodríguez-Romero et al., 2002; Knapp and Shedd, 2003; Zamora-Abrego et al., 2007) invest the highest values of RCM and show the highest variation (from 20.0 to 42.0 %).

Lizards that show the highest values are not phylogenetically close, but all of them occur in extreme environments (high altitude or desert conditions), which suggests that high values of RCM and its variability might be selected in severe environments, as an adaptive mechanism.

The environment that *Ctenosaura pectinata* inhabits may be considered a harsh environment because of the dry conditions (when the laying period occurs) that last 8

months (from October to May). The RCM and the variation of it in *C. pectinata* are relatively high and may be as a consequence of the environment, specifically during the reproductive season.

Within-clutch variation in *Ctenosaura pectinata* could have been selected to facilitate fitness of different phenotypes in changing and unpredictable conditions. Long-lived iteroparous species (i.e., iguanas) have more chances to test different reproductive outputs and phenotypes during longer periods of time. This variability has been interpreted in terms of a plasticity model, considering that the same genetic load may respond to differences in environmental opportunities (Wilkinson and Gibbons, 2005).

Low values of relative clutch mass are associated with low variation in the size and weight of eggs. Low variation implies either an optimization of the individual egg or an evolutionary constraint (Harvey and Pagel, 1991). In contrast, high values of RCM are related with high variation in the size and weight of eggs. In general, large species are associated with long life spans, high values of RCM, and considerable variation in egg size as a strategy to produce variation in their progeny. Differences in the size and weight of the progeny within the same clutch, as in turtles and iguanas, may be interpreted in terms of the highest chances of hatchling survivorship, while facing extreme or unpredictable environments (Roff, 1982; Charnov, 2002). High values of annual juvenile survival (0.47- 0.81) were observed previously in several species of turtles (Pike, et. al., 2008). We consider that *Ctenosaura pectinata* represents a good model to test this theory in iguanas, considering that its eggs show extensive variation in size and weight, in opposition to species that lay eggs optimized in size and weight, i.e., with restricted variation.

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