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Relative clutch mass of *Basiliscus vittatus* Wiegmann, 1828 (Squamata, Corytophanidae): female morphological constraints

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Abstract

Clutch size (CS) and relative clutch mass (RCM) are considered important features in life history descriptions of species within Squamata. Variations in these two characteristics are caused by both biotic and abiotic factors. The present study provides the first account related to CS and RCM of *Basiliscus vittatus* in Mexico within a population that inhabits an open riverbed juxtapositioned to tropical rainforest habitat in Catemaco, Veracruz, Mexico (170 m a.s.l.). Twenty-nine gravid females were collected and kept in captivity under favorable conditions that promote oviposition. The CS within this population was 6.2 ± 0.2 and was correlated positively with snout vent-length (SVL); while the RCM was 0.17 ± 0.006 and was correlated positively with both CS and width of egg. Factors, such as female morphology and environmental conditions, should influence these reproductive traits in *B. vittatus*. The data collected in this study could provide a framework for comparisons of the life history traits across populations of *B. vittatus* in Mexico and within other species of the family Corytophanidae and provide a model for testing how abiotic and biotic factors may influence the CS and RCM in basilisk lizards throughout their range.

Key Words

clutch size, Corytophanidae, female morphology, lizard, reproduction, reproductive effort

Introduction

Reptiles vary in terms of reproductive output, such as the clutch size (CS), egg dimensions, time that reproduction occurs during their lifespan, age, and relative clutch mass (RCM). Normally in many species of reptiles, these life history traits show complex relationships to both female body size (Radder and Shanbhag 2003) and intra- and inter-population variation (Castilla and Bauwens 2000; Kiefer et al. 2008). Thus, when these parameters are determined, information is provided on reproductive strategies that are utilized by different populations of a single species

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(Shine and Greer 1991). These variations of reproductive outputs have been attributed to both (1) abiotic factors that mainly include temperature and rainfall (Fitch 1985; Ji and Brana 2000), and (2) biotic factors such as body size, morphology, and age (Goodman et al. 2008). Thus, the study of life history traits may increase our understanding of how individuals of each species interact with the environment and the environment's role in reproductive output.

The relative clutch mass has been considered one of the most important life history traits in reptiles (Tinkle et al. 1970; Vitt and Price 1982), and studied as the ratio of clutch mass with respect to the female mass (Pianka and Parker 1975; Gerald and Miskell 2007) or as the proportion of energy destined for reproduction (Vitt and Congdon 1978), and is considered an indirect estimate of reproductive effort in squamates (Tinkle 1969; Seigel and Fitch 1984). Several hypotheses have been proposed from the study of life history traits in reptiles that suggest that female body morphology and both clutch size and relative clutch mass have coevolved with foraging mode (Vitt and Congdon 1978). Therefore, sit-and-wait foragers tend to have robust bodies, high clutch size and relative clutch mass values, and low escape velocities; while active foragers show cylindrical bodies, low clutch size and relative clutch mass values, and high escape velocities (Vitt and Congdon 1978; Vitt and Price 1982; Rodríguez-Romero et al. 2005; Mesquita et al. 2016).

Basiliscus vittatus Wiegmann, 1828 is an oviparous lizard of the family Corytophanidae and is widespread in tropical regions of America. In Mexico, the Brown Basilisk has been recorded in Jalisco, Michoacán, Puebla, Tamaulipas, Veracruz, and also throughout Central America down to Panama (Campbell 1998; Castañeda-Hernández et al. 2011). The Brown Basilisk is also now registered in Florida as an introduced and invasive species (Krysko et al. 2006). For its habitat preferences, *B. vittatus* can be semi-aquatic, terrestrial, and a semi-arboreal lizard. According to previous studies, *B. vittatus* neonates show a habitat preference close to water bodies, while juveniles and adults tend to move away from permanent aquatic sources and have perch sites more elevated (Hirth 1963; Fitch 1973).

Particularly within the family Corytophanidae, studies about life history characteristics are scarce. In the genus *Basiliscus*, there are a few studies detailing aspects of natural history, which provide characteristics by habitat preferences, thermoregulation, and spatial movements (Hirth 1963; Fitch 1973; Laerm 1974), and others have related ecological and life history data (Van Devender 1982; Vaughan et al. 2007; Lattanzio and LaDuke 2012; Hernández-Córdoba et al. 2012). Unfortunately, much of the information obtained in these studies does not correspond to recently oviposited eggs and most samples were taken from different populations (Ortleb 1965; Lieberman 1980); in addition the limited samples size could promote variations in life history traits. The Brown Basilisk is classified as a type of passive forager (Cooper et al. 2013), however the wide range of microenvironments it can occupy (aquatic, terrestrial and arboreal) may possibly promote restrictions in its relative clutch mass. Recently, in a Mexican *B. vittatus* population localized in Ejido López Mateos, Catemaco, Veracruz, characteristics in regard to nesting site choice and dimensions of eggs were recorded for the first time (Suárez-Varón et al. 2016). It is now possible, using this new data, to make comparisons with populations of basilisk lizards distributed more to the south of this nesting description, for example, in Costa Rican populations (see, Hirth 1963; Fitch 1973), and to observe the effects of biotic/abiotic factors on reproductive output among different populations of *B. vittatus* in Mexico and other Central American locations. Thus, the purpose of the present study is to provide clutch traits and relative clutch mass data for a single population of *B. vittatus* that inhabits an open riverbed juxtapositioned to tropical rainforest habitat in Catemaco, Veracruz, Mexico. This study may help: (1) to elucidate if a relationship exists between life history traits (i.e., CS and RCM) and different biotic/abiotic factors (including morphological traits of females), (2) allow a comparison of these female reproductive traits within different populations of Mexican *B. vittatus*, and other lizards especially within the family Corytophanidae.

Materials and methods

Study area

The study was carried out in the community of La Selva del Marinero, Ejido Adolfo López Mateos, Catemaco, Veracruz, Mexico (18°26'36.3"N, 94°37'81.9"W, ca. 170 m a.s.l.). The climate is warm-humid with a mean temperature of 27 °C and 4964 mm of annual precipitation; the rainy season extends from June to February and the dry season occurs from March to May (Ibarra-Manríquez and Sínaca 1987).

Animal collection

We sampled monthly from April to July 2016, and June 2018 corresponding to the months in which gravid females (Fig. 1) were registered in earlier studies (Suárez-Varón 2015). The females were found in areas close to the water, on branches, trunks, riparian vegetation, soil, and rocks in an open riverbed near tropical rainforest habitat. We captured females manually and with the help of a noose. To evaluate their reproductive condition, an abdominal palpation and a visual assessment were performed, where the gravid females showed a contour in the abdomen region (Castilla and Bauwens 2000; Boretto et al. 2014). Once the reproductive condition of the females was determined, the following morphological data were recorded just for gravid females: snout-vent length (SVL), and inter-limb distance (ILD) to the nearest millimeter with a digital caliper; additionally, the body weight was measured and we considered the total weight (equal to the female weight +

Figure 1. Gravid female of *Basiliscus vittatus* from La Selva del Marinero, Catemaco, Veracruz. Photo by Kevin M. Gribbins.

clutch mass, TW). Female lizards were then transported to the laboratory within large cotton bags.

Within the lab, each female was maintained in individual terrariums of 1 m × 50 cm × 50 cm (length, width and height, respectively) made with glass and wood. Soil substrate from the study site was added to tanks and mounds of soil were formed in these terrariums. Moreover, branches and rocks were also included as refuges, as well as resting/basking sites for the captive females.

Laboratory conditions

To maintain a thermal gradient between 20–40 °C, incandescent lamps of 75 watts were placed inside the terrariums to provide light and heat on one end of the tank, a photoperiod of 12/12 hrs (photofase/scotophase) was maintained respectively, the terrariums were sprayed daily with water to maintain the proper humidity. Finally, females were fed every third day with crickets (*Acheta domesticus*) and larvae (*Tenebrio molitor*), and water was provided *ad libitum* until the termination of oviposition.

The terrariums were monitored daily and the presence of eggs in the terrarium or abdominal flaccidities of females were observed. After the oviposition process (no later than 3 hours post-oviposition), the body mass of each female was recorded; this value was considered as the absolute mass of the female (AM). Next, the eggs morphology were measured: clutch size was calculated as the total number of eggs in the nest, clutch mass (CM) was determined from the sum of the masses of all eggs recently oviposited, maximum length and width of the eggs was measured (ML and MW); to estimate the volume of the eggs (VE) we used the equation of an ellipsoid $V = 4/3\ \pi\ (½\ L)\ (½\ W)^2$ where L is the maximum length and W is the maximum width (Shanbhag et al. 2000). The relative clutch mass index was also calculated by Tinkle's method (1969), which corresponds to the ratio of the clutch mass to total weight.

Statistical analysis

We evaluated differences between the residuals of regression of clutch size and SVL between years. Additionally, we used a normality test (Kolmogorov-Smirnov, Zar 1999) on all variables analyzed, descriptive statistics were estimated (mean ± standard error, minimum and maximum), and the coefficient of variation (CV = standard deviation / mean × 100) was calculated as a measure of the variability observed for parameters of the clutch data to elucidate the highest percentage of variation of traits. To evaluate whether the female morphology condition (robustness) had an effect on the clutch size and clutch mass, the residuals of the regression between the log SVL and the log absolute mass were used as independent variables in regression analysis with clutch size and clutch mass as dependent variables (Shanbhag et al. 2000). Pearson's correlations were also used to analyze if there are relationships between female morphology traits (SVL, AM, and ILD) and their reproductive traits/effort (CS, CM, MW, ML, VE, and RCM). All statistical analyses were performed in STATGRAPHICS (V 16.1), results were deemed significant if $p < 0.05$.

Results

Clutch size and dimension of the eggs

One hundred and eighty-two eggs were analyzed from 29 gravid females (n = 18, 2016; n = 11, 2018) of *B. vittatus*. The dates were analyzed overall given that the residuals between sampling years did not differ significantly (p = 0.17). The female with the smallest SVL that was palpated positive for the presence of eggs was 106 mm. The female morphology trait with the lowest variation was SVL (CV = 6.5%), and conversely the absolute mass show the highest variation (CV = 21.6%). In the case of reproductive traits, maximum length and maximum width of the eggs were the characteristics that showed the smallest variation (CV = 6.5 and 6.4 %, respectively), while relative clutch mass (CV = 20.7%) and clutch size (CV = 20.3%) are the traits with the most variation for reproductive traits. Additional information about descriptive statistics related with morphology of the female and their reproductive traits (mean, standard error, range and CV) are also shown in Table 1.

With the female morphological traits, SVL was associated with inter-limb distance (r = 0.48, p = 0.008), and absolute mass (r = 0.80, p = 0.001) while the regression analyses within reproductive traits display additional relationships: clutch size with both maximum width (r = 0.41, p = 0.02), and volume of eggs (r = 0.46, p = 0.01). Also, the comparison between female morphological traits with reproductive traits show that SVL was correlated with clutch size (r = 0.58, p = 0.001; Fig. 2), and both maximum width (r = 0.44, p = 0.01), and volume of eggs (r = 0.54, p = 0.002; Fig. 3), but was not correlated with other traits of the eggs (Table 2). Absolute mass was correlated with clutch size (r = 0.48, p = 0.009), maximum width (r = 0.37, p = 0.04), and volume of the eggs (r = 0.40, p = 0.02). Robustness of females was not significant in terms of both clutch size (r = 0.01, p = 0.92) and clutch mass (r = 0.18, p = 0.32).

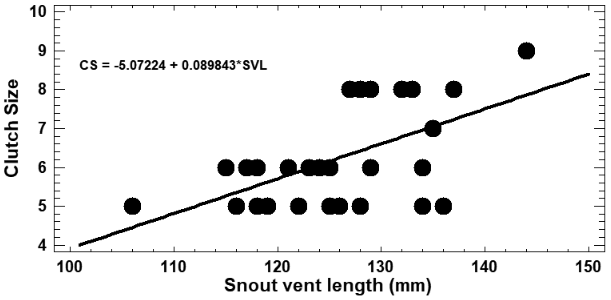

Figure 2. Relationship between snout vent length (**SVL**) and clutch size (**CS**) in *Basiliscus vittatus* from La Selva del Marinero, Catemaco, Veracruz.

Relative clutch mass

The mean of relative clutch mass was 0.17 ± 0.006 (Table 1) and was positively correlated with clutch size (r = 0.51, p = 0.004), clutch mass (r = 0.52, p = 0.004), and maximum width of the eggs (r = 0.39, p = 0.03). Otherwise, when relative clutch mass was analyzed with other female morphology traits, no correlations were observed (Table 2).

Table 1. Statistical summary for female morphology: SVL (snout-vent length), AM (absolute mass), and ILD (inter-limb distance), and reproductive traits: RCM (relative clutch mass), CS (clutch size), CM (clutch mass), ML (maximum length), MW (maximum wide), and VE (volume of egg) in *Basiliscus vittatus* from La Selva del Marinero, Catemaco, Veracruz.

Trait	Mean	SE	Min	Max	CV %	N
SVL (mm)	126.3	1.500	106.00	144.00	6.5	29
AM (g)	46.4	1.800	26.80	67.00	21.6	29
ILD (mm)	62.7	1.000	53.90	74.70	9.3	29
RCM	0.17	0.006	0.06	0.22	20.7	29
CS	6.2	0.200	5.00	9.00	20.3	29
CM (g)	1.5	0.010	0.80	2.20	16.5	182
VE (mm^3)	1331.9	15.200	827.40	1782.01	15.4	182
ML (mm)	19.7	0.090	16.50	22.70	6.5	182
MW (mm)	11.3	0.050	8.90	12.70	6.4	182

Table 2. Linear regression analysis of the relationship between female traits (SVL = snout vent length, ILD = inter-limb distance, AM = absolute mass), and reproductive traits (CS = clutch size, CM = clutch mass, ML = maximum length, MW = maximum wide, VE = volume of egg, and RCM = relative clutch mass) of *Basiliscus vittatus* from La Selva del Marinero, Catemaco, Veracruz. The * indicates a relationship between both traits.

Trait	R^2	p	Trait	R^2	p	Trait	R^2	p
SVL vs RCM	1.7	0.490	AM vs RCM	10.10	0.090	ILD vs RCM	9.500	0.100
SVL vs ILD	22.8	0.008*	AM vs CS	22.60	0.009*	ILD vs CS	1.600	0.500
SVL vs AM	64.5	0.001*	AM vs CM	5.30	0.220	ILD vs CM	0.350	0.760
SVL vs CS	33.8	0.001*	AM vs ML	0.83	0.630	ILD vs ML	0.002	0.970
SVL vs CM	5.1	0.230	AM vs MW	14.10	0.040*	ILD vs MW	1.800	0.480
SVL vs ML	0.7	0.660	AM vs VE	16.30	0.020*	ILD vs VE	10.400	0.080
SVL vs MW	19.2	0.010*						
SVL vs VE	29.7	0.002*						

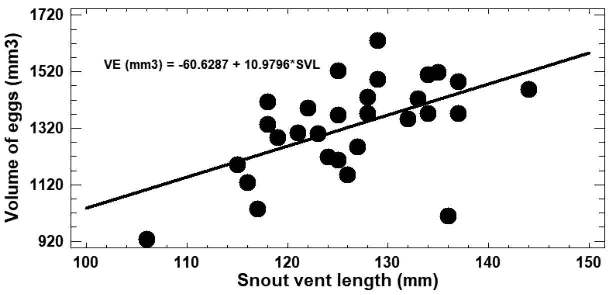

Figure 3. Relationship between snout vent length (**SVL**) and volume of eggs (**VE**) in *Basiliscus vittatus* from La Selva del Marinero, Catemaco, Veracruz.

Discussion

The mean clutch size of *B. vittatus* in this study is 6.2 eggs (range 5–9 eggs/female), which is within the known range for this species (range 3.9–12 eggs), for the genus (range 3.9–18 eggs), and for the family Corytophanidae (Table 3). Although in squamates clutch size varies between congeners distributed in regions with different requirements (Hamilton et al. 2008), it is also affected by strategies of reproduction within populations. For example, if there are one or more clutches per season, variation in clutch size should occur in later clutches (Vitt 1977). In the present study, we do not know if there are multiple clutches in our study population; however, according to previous evidence *B. vittatus* shows multiple clutches (Fitch 1973). In this study, we did not consider the effect of multiple clutches on clutch size and relative clutch mass since we are unsure if multiple clutches occur in our population. A future study will investigate whether single or multiple clutches occur within our population at our study site.

Our results show that females of *B. vittatus* with larger body sizes have larger clutch sizes compared to smaller females (Fig. 2). Although there are some lizards that do not show this relationship of body size to clutch size (Wen-San 2010; Ljubisavljević et al. 2012), this pattern is common in many squamates (Radder and Shanbhag 2003), and includes other genera of tropical lizards such as *Tropidurus* (Vitt and Goldberg 1983), *Eurolophosaurus* (Galdino et al. 2003), and *Emoia* (Hamilton et al. 2008). Also, the association between SVL with inter-limb distance is important, since larger abdominal cavities allow the storage of more eggs (Williams 1966; Castilla and Bauwens 2000; Kratochvil and Kubicka 2007). Thus, the body size of the female allows for an increase in clutch size and maximum width of the eggs (Table 2). In addition, the increase in body size of squamates has been closely related to its reproductive response; females with higher SVL tend to maximize their fitness by increasing the numbers of eggs (Rutherford 2004). However, their chances of reproducing in future events may be restricted due to their increased susceptibility to predation because of decreased locomotor capacity and escape velocity (Galdino et al. 2003). Likewise, the increase in body size should be an evolutionary advantage that allows females not only to fill the larger abdominal space, but also increase the capacity to store energy reserves (e.g., food reserves, fat bodies) allocated towards reproduction (Williams 1966; Qualls and Shine 1995). Energy reserves in some reptilian species are reduced considerably during the gestation period by a cessation of food intake, which has been observed to affect growth and physical condition of the female (Shanbhag et al. 2000). In the present study, the effect of robustness (female body condition) on the variations of clutch size and clutch mass was not supported because no significant association between these variables was observed as recorded in previous studies of others lizards (Shanbhag et al. 2000). Thus, much of the available energy stores within reproducing females may be allocated immediately to reproduction (Shine 1980; Wilkinson and Gibbons 2005; Warner et al. 2008).

A central theory in vertebrate life histories is the trade-off between clutch size and dimensions of eggs (Stearns 1992). In regards to this theory, the clutch size of *B. vittatus* was related to maximum width and volume of the eggs regardless of the SVL of the female. Our data suggest that the variations present in the dimensions of the eggs show limitations imposed by the clutch size supporting this

Table 3. Clutch size in family Corytophanidae, the data correspond to mean values.

Species	Clutch size	Reference
Basiliscus vittatus	6.2	This study
	4.2	Hirth 1963
	3.9	Fitch 1973
	12.0	Alvarez del Toro 1982; Guyer and Donnelly 2004
	4.0	Campbell 1998
	5.2	Meiri et al. 2012
	5.4	Scharf et al. 2015
B. basiliscus	18.0	Ortleb 1965
	6.2	Fitch 1973
	8.0	Lieberman 1980
	9.2	Meiri et al. 2012
B. galeritus	5.0	Almendárez and Brito 2012
Corytophanes hernandezii	3.0–4.0	Alvarez del Toro 1982
C. cristatus	6.0	Ream 1965
Laemanctus serratus	3.0–5.0	Martín 1958
L. longipes	4.0–6.0	Alvarez del Toro 1982

trade-off hypothesis. Thus, the volume of eggs is more variable in comparison with consistent and less variable measures of maximum length and width of the eggs. This supports the adaptative canalization hypothesis, which suggests that maternal investment is related to body size, promoting a higher clutch size, but not larger eggs (Brockelman 1975). In contrast, clutch mass and volume of egg were traits that displayed more variation within reproductive traits, which have been strongly correlated to female body size (Fig. 3) or body mass because these traits can limit/enhance the amount of available abdominal space for carrying eggs (Shine 1992). In contrast, egg size is invariant to different selective pressures, such as physiologic mechanisms, predation, climatic tolerance, as well as the agility of the females during gravidity (Shine and Greer 1991). Then, the size of egg is most likely limited by: 1) the length and arrangement of eggs within the oviduct (Ford and Seigel 1989), and 2) by the size of both the pelvic girdle (Congdon and Gibbons 1987) and vent of the females to facilitate the oviposition process.

Furthermore, clutch size is molded by environmental characteristics attributed to abiotic factors such as precipitation, seasonality, or temperature (Ji and Brana 2000; Lepage and Lloyd 2004) because these factors modify the availability of resources (e.g., food) and thus, the energy that females can acquire prior to reproductive events (Ballinger 1977; Seigel and Fitch 1984). Consequently, clutch size is a trait that has evolved as an adaptive mechanism to environment pressures (Fitch 1985), especially in those species that are widely distributed and whose adult body size shows a range of variability (e.g., *B. vittatus*). Thus, changes in clutch size are expected (Fitch 1970) as a result of different selective pressures to local environment constraints (Shine and Downes 1999), which is balanced by maintaining an optimal number of eggs that allows greater fitness in females (Fitch 1970; Shine and Greer 1991). The variation in clutch size among populations probably reflects differences in the availability of energy resources that females obtain and which are influenced by the biotic and abiotic conditions of each local study area.

Within our data, female *B. vittatus* raise their relative clutch mass at the same time that their clutch size increases; the inversion towards reproduction can increase or decrease with respect to the age, weight, and size of the females, in such a way that the energy available for reproduction is allocated in an optimum amount within each egg (Doughty and Shine 1998; Radder and Shanbhag 2004; Orrell et al. 2004).

The fact that there is no observable relationship between relative clutch mass and SVL in *B. vittatus* suggests that larger females do not proportionally exhibit greater reproductive effort (Stuart-Smith et al. 2007). However, in *B. vittatus* clutch size and relative clutch mass are limited by body morphology (SVL and absolute mass respectively) rather than by foraging mode or escape velocity, thus the only way females can increase their reproductive responses are to be larger in order to produce more eggs. According to the regression model ($CS = -5.07224 + 0.089843 * SVL$, Fig. 2), which estimates the body size that allows the females to increase their clutch size; then, substituting our CS (= to 6.2 eggs) into this model equates to an increase in 8% female SVL for each egg added since the difference between our SVL (mean =126.3 mm) and the estimated SVL = 136.596 mm (for 7.2 eggs in the model equation) implies an increase of 10.2 mm of female SVL. This indicates that the reproductive response in *B. vittatus* is strongly linked to the body morphology, which involves the SVL and absolute mass of the females. Future studies should incorporate abdominal-volume data (Shine 1992) to evaluate if body shape (more than inter-limb distance) restricts or promotes reproductive output. This should offer a model for the index of available space in the abdominal cavity and the egg carrying capacity of the female squamates.

The relative clutch mass of *B. vittatus* (0.17) in the present population is similar to other studied species within the family Corytophanidae, as reported by Scharf et al. (2015): genus *Basiliscus* (= 0.21, *B. plumifrons* Cope, 1875); (= 0.18, *B. galeritus* Duméril, 1851); (= 0.16, *B. basiliscus* Linnaeus, 1758), and genus *Laemanctus* (= 0.17, *L. longipes* Wiegmann, 1834), which contrast to the highest relative clutch mass recorded in *Corytophanes cristatus* Merrem, 1820 (= 0.27), an extreme passive foraging lizard (Andrews 1979). Mesquita et al. (2016) also obtained a lower relative clutch mass value (= 0.08) for *B. vittatus*; and it appears that the variation in relative clutch mass is more easily observed at the population level rather than at the species level (Du et al. 2005). It has also been hypothesized that relative clutch mass has coevolved with foraging mode (Vitt and Congdon 1978); however, in this study there is no supportive evidence for this hypothesis; since the value of relative clutch mass index obtained for *B. vittatus* is close to that of active foragers (RCM = 0.17, Mesquita et al. 2016). Therefore for this study, we suggested that both traits are under independent selective pressures regarding foraging mode for *B. vittatus*. Although *B. vittatus* is classified as a sit and wait forager based on low movements per minute and percentage of activity (Cooper et al. 2013), it has lower values in its reproductive investment when compared with other sit and wait species, such as: *Phrynosoma orbiculare* Linnaeus, 1789 (= 0.27, Suárez-Rodríguez et al. 2018), *Sceloporus clarkii* Baird & Girard, 1852 (= 0.30, Shine 1992), and *Sceloporus grammicus* Wiegmann, 1828 (= 0.28, Rodríguez-Romero et al. 2005). These lizards have been associated with high values in relative clutch mass, low escape velocities, and robust bodies (Vitt and Congdon 1978; Vitt and Price 1982). This contrast in *B. vittatus* versus other sit and wait squamates may be due to the fact that the relative clutch mass of *B. vittatus* is considerably limited by its body morphology, since it has an elongated body and tail such as those observed in active foragers (Teiidae) (Ramírez-Bautista et al. 2000) and longer posterior extremities that facilitate running to high speeds even across the surface of water (Hirth 1963). According to this, it is suggested that *B. vittatus* may hold an intermediate position between both foraging modes, which may provide information on the evolution of more complex adaptations, such as escape mechanisms (Cooper 2005). In this way, the reproductive effort in B. vitt*atus* has been molded to maintain its locomotor skills such as: velocity of escape, attachment to branches, submersion, etc., all making the Brown Basilisk less vulnerable to predation (Geral and Miskell 2007; Suárez-Varón unpublished results). Consequently, natural selection may favor individuals in this population of lizards with an optimal relative clutch mass that allows for escape performance in different microhabitats in which these lizards occupy, but still maintains little variation in the dimensions of the egg, which has been associated with low values in relative clutch mass index (Harvey and Pagel 1991). This implies that an optimization of the clutch size and clutch mass is in play to maximize fitness. Finally, the clutch size and relative clutch mass may show a response to multiple selective pressures caused by: 1) local environmental effects (Vitt 1981; Zamora-Abrego et al. 2007), 2) constraints associated to the body morphology (Vitt and Price 1982), 3) microhabitat (Vitt 1981), and 4) foraging and escape strategies, as well as the use of crypsis (Vitt and Congdon 1978; Rodríguez-Romero et al. 2005), which limit the reproductive output and should influence both clutch size and relative clutch mass.

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