# Reproductive biology of a viviparous lizard (*Mabuya dorsivittata*) from the subtropical Wet Chaco of Argentina: geographical variations in response to local environmental pressures

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**Abstract:** Herein we studied the reproductive biology of a viviparous lizard (Mabuya dorsivittata) from the Wet Chaco region (northeastern Argentina) and compared the results with other populations from the Espinal (central Argentina) and the Atlantic Forest (southeastern Brazil), and with other Neotropical species of Mabuya to better understand the possible causes of its reproductive phenotype variation. Males and females of M. dorsivittata from the Wet Chaco exhibited associated, seasonal, and annual reproductive cycles. Spermatogenic activity related positively to a lengthening photoperiod reaching maximum activity in late spring (December). Females displayed an extended gestation period of 11 months, from mid-summer (February) to late spring or early summer (December) when births occur. Embryonic development was associated with temperature and historical rainfall. Litter size ranged from 3 to 8 (mean = 5.3 ± 1.3 SD) and increased with body size and body mass of females. Fat-body mass varied seasonally and was inversely correlated with spermatogenesis and to embryonic development. Females were larger in body size and interlimb length, and smaller in head length than males. We observed interpopulational differences in minimum body size, litter size, and timing of birth, probably as a result of phenotypic plasticity, genetic divergence or both.

**Key words:** reproductive cycle, sexual dimorphism, ecotypic variation, lizard, Squamata.

## INTRODUCTION

Different environmental conditions can lead to variation in life history traits such as age and size at sexual maturity, maximum body size, fecundity, reproductive timing, and lifespan among individuals, populations, and species, as the result

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of phenotypic plasticity, genetic divergence or both (Dunham et al. 1988, Wapstra and Swain 2001, Radder 2006). Geographical variations in life history traits correspond to gradients of environmental factors such as temperature, photoperiod, food availability, predation, and competition (Adolph and Porter 1993, Seigel and Ford 2001, Zeng et al. 2013). The comparative study of populations provides information to identify the possible causes

of variation, and their ecological and adaptive value (Radder 2006).

In this sense, temperate montane environments with cool temperatures, short growing seasons, and summer rainfall, play a role in the evolution of a suite of reproductive characteristics shared by evolutionarily distant viviparous lizard species inhabiting these harsh climates (Shine 1985, Ramírez-Bautista et al. 1998, 2002). Nevertheless, the genus *Mabuya* Fitzinger, 1826, characterized by a highly specialized placentotrophic viviparity (Vitt and Blackburn 1983, 1991, Jerez and Ramírez-Pinilla 2001, 2003, Blackburn and Vitt 1992, 2002, Leal and Ramírez-Pinilla 2008), inhabits tropical and subtropical latitudes, so it is a particularly interesting group for reproductive studies because it contrasts with the "cold climate" hypothesis proposed to explain the origin of viviparity in Squamata (Shine 1985). The hypothesis of maternal manipulation of thermal conditions for embryogenesis offers an explanation for viviparous squamates species living in tropical zones (Webb et al. 2006). According to this hypothesis, pregnant females prefer a range of body temperatures different from non-pregnant females and adjust their body temperature producing offspring phenotypes that enhance their fitness (Webb et al. 2006, Ji et al. 2007, Rodríguez-Díaz and Braña 2011).

*Mabuya* belong to the Scincidae family, with 26 species (Jerez 2012) distributed in tropical and subtropical environments of South America (Mausfeld et al. 2002). Placentotrophy is considered by Mausfeld et al. (2002) to be one of the synapomorphies of the South American *Mabuya* species, and represents a strong convergence with eutherian mammals (Blackburn 1992). The Scincidae family and the genus *Mabuya* have been the focus of recent taxonomic reviews. Hedges and Conn (2012) proposed to elevate the subfamilies Acontiinae, Egerniinae, Eugongylinae, Lygosominae, Mabuyinae, Scincinae and Sphenomorphinae to the family level, whereas

Pyron et al. (2013) argued that Scincidae family is a monophyletic clade and concluded that the degree of divergence among the various scincid subfamilies is insufficient to justify elevating them to the family level. Here, we follow Pyron et al. (2013) in restricting the genus *Mabuya* to a monophyletic clade of Neotropical species of Scincidae, an interpretation supported by multiple phylogenetic analyses and several morphological synapomorphies (Mausfeld et al. 2002, Whiting et al. 2006, Miralles and Carranza 2010).

Despite the broad distribution of genus *Mabuya* in South America, the reproductive biology has been studied mainly in the Amazon biomes (*M. nigropunctata* [= *M. bistriata*], Vitt and Blackburn 1991; *M. mabouya*, Duellman 1978; Dixon and Soini 1986) and in the Brazilian biomes, the latter including the Atlantic Forest, (*M. frenata*, Vrcibradic and Rocha 1998; *M. macrorhyncha* and *M. agilis*, Rocha and Vrcibradic 1999), the Cerrado (*M. frenata*, Vitt 1991, Pinto 1999; *M. nigropunctata*, Pinto 1999; *M. guaporicola*, Mesquita et al. 2000), and the Caatinga (*M. agilis* [= *M. heathi*], Vitt and Blackburn 1983; *M. arajara,* Ribeiro et al. 2015). These studies have described a seasonal reproductive cycle in both sexes, with a unimodal pattern of births. However, in a Colombian population from the tropical wet forest (*M. mabouya*, Ramírez-Pinilla et al. 2002), males and females exhibited a continuous reproductive cycle, with a bimodal pattern of births.

The species *Mabuya dorsivittata* (Cope, 1862) is distributed across Bolivia, Paraguay, Brazil, Uruguay and Argentina, occupying a variety of habitats including grasslands, forests and rocky outcrops (Cei 1993, Vrcibradic et al. 2004, Aun et al. 2011, Williams and Kacoliris 2011, Núñez 2012). The reproductive cycle has been studied in the Espinal biome of Argentina and is characterized by a seasonal reproductive pattern (Aun et al. 2011). Litter sizes in southeastern Brazil were reported by Vrcibradic et al. (2004), but no information exists

on *Mabuya* from the subtropical Wet Chaco region, which is one of the largest South American biomes with the greatest herpetofaunal diversity (Alvarez et al. 2002). In the present study of *M. dorsivittata*, we describe the male and female reproductive cycles, the fat-body cycle and the extent of sexual dimorphism for a subtropical population from the Wet Chaco, and the results are compared among populations and congeneric species to understand the possible causes of the reproductive phenotype and its relationship with the environment they inhabit.

## MATERIALS AND METHODS

### STUDY AREA AND CLIMATE

*Mabuya dorsivittata* was studied in the grasslands of Corrientes Province (Argentina), part of the Eastern District of the Chaco Phytogeographic Province known as Wet Chaco (Cabrera and Willink 1973, Cabrera 1976, Carnevali 1994), belonging to the South American Chaco region an area of approximately 200.000 km$^2$ (Cabrera 1976, Ginzburg and Adámoli 2006). The climate in Corrientes Province is mainly warm and subtropical; there is no dry season although winter rainfall is significantly lower (Cabrera 1976, Bruniard 1997), and the average annual rainfall varies from 1000 to 1500 mm. Mean annual temperatures varies from 20-22 °C. Mean maximum temperatures occur in January (26-28 °C), while the mean minimum temperatures are recorded in July (13-16 °C); frosts are uncommon (Cabrera 1976, Carnevali 1994, Bruniard 1997).

Historical records of mean temperature, photoperiod and rainfall from 1990 to 2010 and during the sampling period from 2011 to 2013 were provided by the Servicio Meteorológico Nacional and the Servicio de Hidrografía Naval Argentino (Figure 1). During 2011 and 2012 a La Niña climatic event occurred, characterized by particular patterns of temperature and rainfall, which alter

seasonal climate conditions. Consequently, we also include historical data from 1990 to 2010 to discuss the results of the present study.

### SAMPLING AND LABORATORY METHODS

Most specimens (n = 36; 13 adult males; 2 juvenile males, 18 adult females and 3 juvenile females) were collected from September 2011 to May 2013 in San Cayetano (27º33'22" S, 58º40'33" W), Capital Department, Corrientes Province by hand, drift-fences with pitfall traps, or by using artificial shelters. We completed the sample with two additional adult females from the herpetological collection of the UNNE of Corrientes (UNNEC: 10574, 10586) collected in October 2009 in the localities Paraje Loma Alta, Concepción Department (28°25'21" S, 57°56'57" W) and Paraje Maloyas, San Luis del Palmar Department (27°42'37" S, 58°09'40" W) from environments similar to those in Corrientes Province. Specimens collected in 2011-2013 were euthanized by intraperitoneal administration of anesthesia (carticaine L-adrenaline), following the recommendation of the European Commission (Close et al. 1997), and the ASIH/HL/SSAR Guidelines for the Use of Live Amphibians and Reptiles as well as the regulations detailed in Argentinean National Law #14346.

The specimens were fixed in Bouin's solution for 24 hours, stored in 70% ethanol and deposited at the herpetological collection of the Universidad Nacional del Nordeste (UNNEC), Corrientes province. Prior to fixation, lizards were sexed and weighed (body mass, BM) to the nearest 0.01 g with a digital balance (Ohaus® traveler scale TA320) and measured using a digital caliper (Essex®, 0.01 mm) to 0.1 mm. Fat bodies were excised after the necropsy of each adult lizard and weighed to nearest 0.01 g with a digital balance. Sexual dimorphism was described *sensu* Boretto et al. (2007) and Boretto and Ibargüengoytía (2009). The following variables were measured using a digital caliper:
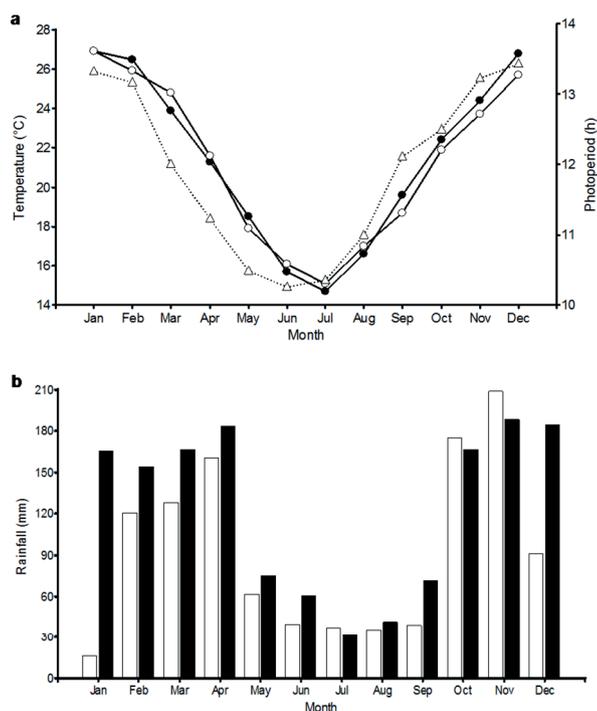
**Figure 1 -** Monthly means of climatic variables in Corrientes, Argentina. (**a**) Temperature from 2011 to 2013 (solid circles), historical temperature from 1990 to 2010 (open circles) and photoperiod (triangles). (**b**) Rainfall from 2011 to 2013 (white bars) and historical rainfall from 1990 to 2010 (black bars). Climatic data were obtained from the Servicio Meteorológico Nacional and Servicio de Hidrografía Naval Argentino.

snout-vent length (SVL), head length (HL), head width (HW) and head height (HH) at interparietal-scale level, neck width (NW), distance between front and hind limbs (Interlimb length, IL; *sensu* Olsson et al. 2002), diameter of the front leg (FLD) and hind leg (HLD) at the insertion to the shoulders and pelvic girdles respectively, hip width (HipW), measured as the body width at the insertion of hind legs, maximum body width (BW), tail width immediately posterior to vent (TWV), and status of the tail (ST; intact, cut or regenerated).

MALE REPRODUCTIVE CYCLE

The male gonadal cycle was determined based on macro- and microscopic observations. Testes size (TS) was measured as an antero-posterior diameter

using a digital caliper (± 0.1 mm). Gonads were dehydrated in an ethanol series and embedded in paraffin for 24 hours at 52 ºC. Following a conventional histological protocol (Humason 1979), 5-µm sections were cut with a rotary microtome (Arcano®) and stained with hematoxylin and eosin.

Spermatogenic stages were determined by the most advanced cell type present in the seminiferous tubules following Mayhew and Wright (1970), and cell types were recognized based on Gribbins (2011). Five spermatogenic stages were defined: (I) only spermatogonia, (II) primary and secondary spermatocytes, (III) spermatozoa in the seminiferous tubules, (IV) early regression with cellular debris and scarce spermatozoa in tubular lumen, and (V) complete regression, characterized by no cell division and no lumen (modified from Mayhew and Wright 1970). The presence or absence of spermatozoa in the epididymes and/ or ductus deferens was also registered. Minimum SVL at sexual maturity in males was determined by the shortest specimen with spermatogenic activity (stages II–V) or spermatozoa in the epididymes or ductus deferens.

FEMALE REPRODUCTIVE CYCLE

The female reproductive cycle was defined based on macroscopic and microscopic observations of the reproductive tract and the presence and number of oviductal embryos and corpora lutea. Pregnant females were classified (*sensu* Leyton et al. 1980) based on embryonic development as initial (from cleavage to somatic embryos), medium (from curvate trunk to elongated limbs with 5 fused fingers), and advanced (fetus with scales and pigmented skin). Embryos from left oviduct were used to estimate the embryos size based on the diameter taken as the distance across the chorionic vesicle (Vitt and Blackburn 1991). Embryos were observed with a stereoscopic microscope (Olympus® SZH10/

AB3639, Tokyo, Japan) and measured through digital images using an Image-Pro Plus analyzer (Media Cybernetics, Inc., Rockville, MD, USA). Litter size was determined by counting the number of embryos in uterus (Ibargüengoytía and Cussac 1998). Minimum SVL at sexual maturity of females was estimated considering the shortest female with embryos in uterus or corpora lutea. Female with oviducts without folds or presence of small folds were classified as juveniles, following the definition of Ibargüengoytía and Cussac (1998).

STATISTICAL ANALYSES

Statistical analyses were conducted using INFOSTAT (version 2011), SPSS (version 17.0), and SIGMAPLOT (version 10.0). Assumptions of normality and homogeneity of variance were tested with the Shapiro-Wilk test and Levene's test, respectively. Dependence between variables was tested performing simple regression, Pearson and Spearman correlations. When correlation between independent variables and SVL was found, residuals of linear regression were used to perform further analysis (Ramírez-Bautista and Vitt 1997).

To analyze sexual dimorphism in mean SVL, we used a t-test. All morphometric variables (BM, HL, HW, HH, NW, IL, FLD, HLD, HipW, BW, and TWV) were ln-transformed and then regressed against ln-transformed SVL. The residuals of these regressions were used in the Stepwise discriminant analysis (based on p-value with $\alpha = 0.05$ and $\alpha = 0.10$ as input and output significance levels) to determine the variables that better explain the differences between the sexes. In order to determine the possible causes of intersexual differences in the frequency of caudal autotomy, a $\chi^2$ test was performed to compare intact versus broken or regenerated tails between males and females. The significance level used was $p < 0.05$ for all statistical tests and results are presented as means ± standard deviation (SD).

**RESULTS**

ANNUAL ACTIVITY, BODY SIZES AND SEXUAL DIMORPHISM

Adult males and females were captured through the year (Figure 2), whereas juveniles were captured only from mid-summer (February) to early winter (July). The smallest SVL of any lizard was recorded in February. The minimum adult size for males was 51.2 mm SVL, corresponding to a specimen with spermatocytes in the seminiferous tubules (stage II). In females, the minimum adult size was 49.0 mm SVL, corresponding to a gravid specimen with embryos in initial stage of development. The SVL of adult males ranged from 51.2 to 70.9 mm (mean = 60.7 ± 6.4, n = 13), and the BM from 2.32 to 5.25 g (mean = 3.54 ± 0.85 g, n = 12). Adult females ranged from 49.0 to 82.4 mm SVL (mean = 67.0 ± 9.0, n = 20), and 1.25 to 9.32 g BM (mean = 5.17 ± 2.18 g, n = 20). Male and female juveniles ranged from 42.2 to 52.6 mm SVL (mean = 48.3 ± 4.45, n = 5), and from 0.97 to 2.70 g BM (mean = 1.93 ± 0.76, n = 5).

Adult females exhibited larger body size (SVL; T = -2.10, p = 0.043, n = 33; Figure 3) and larger interlimb length than adult males, while males showed larger heads (discriminant analysis; λ = 0.502, $\chi^2$ = 19.99, df = 2, p < 0.001, n = 33). Adult males and females did not differ in the frequency of
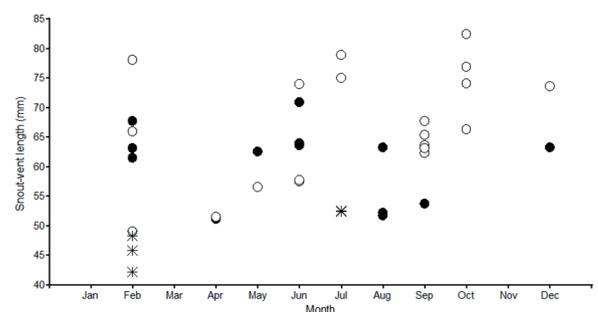
**Figure 2 -** Snout-vent length distribution by month in *Mabuya dorsivittata*. Adult males (solid circles), adult females (open circles), juveniles (asterisks).

caudal autotomy ($\chi^2 = 0.53$, df = 1, p = 0.466, n = 33). Broken and regenerated tails were recorded in 77% of males (10 of 13 individuals) and in 65% of females (13 of 20 individuals). Males and females with intact tails were not different in snout-vent length or body mass from those with broken or regenerated tails ($SVL_{males}$, T = -1.72, p = 0.113; $BM_{males}$, T = -0.95, p = 0.367; $SVL_{females}$, T = -0.60, p = 0.556; $BM_{females}$, T = -0.45, p = 0.661).

MALE REPRODUCTIVE CYCLE

The relationship between male SVL and testicular size was positive (Linear Regression; $r^2 = 0.47$, $F_{1,11} = 9.67$, p = 0.009, n = 13); therefore, residual testicular size (TS) was used for the following analyses. The smallest TS values were observed in late autumn (June), and increased gradually in mid-winter (August) until late spring when the TS reached the highest value (December; Figure 4a). The TS was positively correlated with the photoperiod (Spearman correlation, $r_s = 0.57$, p = 0.04), but not with temperature or rainfall ($temperature_{(2011-2013)}$; $r_s = 0.16$, p = 0.61; historical $temperature_{(1990-2010)}$; $r_s = 0.39$, p = 0.19; $rainfall_{(2011-2013)}$; $r_s = -0.02$, p = 0.94; historical $rainfall_{(1990-2010)}$; $r_s = 0.18$, p = 0.56).

The histological study of gonads revealed that juvenile males with spermatogonia in testes (stage I, n = 2) occurred in winter (July; Figure 5), whereas adult males with primary and secondary spermatocytes (stage II, n = 4) were captured from early autumn (April) to early spring (September), and those with spermatozoa in the seminiferous tubules (stage IV, n = 3) were found in summer (December and February). Males with early testicular regression (stage V, n = 2) were captured from mid-summer (February) to late autumn (June), and males with complete regression (stage VI, n = 4) were found between mid-autumn (May) and mid-winter (August). In addition, sperm in the epididymis was recorded only in males with testes in stage IV.
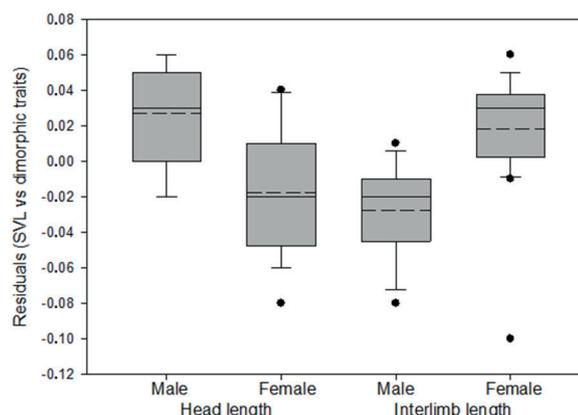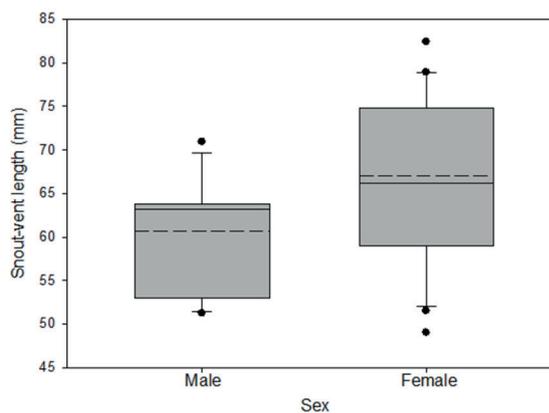




**Figure 3** - Box plot of the significant dimorphic traits (p < 0.05) of female and male *Mabuya dorsivittata*. Median (black horizontal line), mean (dashed line), whiskers (10th and 90th percentiles) and outliers (solid circles) are indicated.

FEMALE REPRODUCTIVE CYCLE, EMBRYONIC DEVELOPMENT AND LITTER SIZE

Gravid females (n = 20) were observed from mid-summer (February) to late spring (December), showing a progressive advance in the embryonic development (Figure 4b). Gravid females collected in mid-summer (February) showed embryos with evidence of initial developmental stages and small chorionic vesicles (largest diameter of the chorionic vesicle = 1.3 mm, n = 3). Very little embryonic growth occurred between February and October, followed by fast growth from October to December (Figure 4b). From mid-summer (February) until late winter (September)
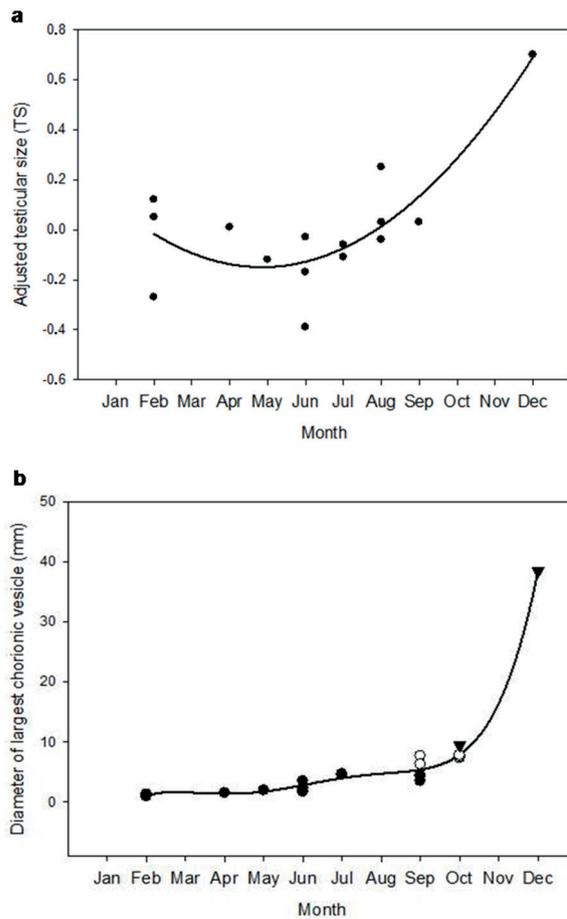
**Figure 4 -** Reproductive cycle of *Mabuya dorsivittata*. (**a**) Variation in adjusted testicular size of adult males throughout the year. Solid circles correspond to the residuals from snout-vent length versus testicular diameter regression. (**b**) Variation of size of the largest chorionic vesicle of different embryonic stage: initial (solid circles), medium (white circles) and advance (triangles). Lines show change in testicular and chorionic vesicle size corresponding to a second and fifth order polynomial equation respectively.



**Figure 5 -** Male reproductive cycle of *Mabuya dorsivittata*. Spermatogenic stage: (1) only spermatogonia (white circles); (2) primary and secondary spermatocytes (black circles); (3) spermatozoa in the tubule (white squares); (4) early regression with cellular debris and scarce spermatozoa in tubular lumen (black squares); and (5) complete regression, characterized by no cell division and no lumen (white triangles). Asterisks indicate presence of spermatozoa in the epididymis. The values in brackets are the number of observations; no value shown indicates a single observation.

females exhibited initial embryonic developmental stage (n = 13). Females with medium embryonic developmental stage (n = 5) were found from late winter (September) to early spring (October), while females with advanced embryonic developmental stage (n = 2) were captured in spring (October and December). During October one female showed embryos in an advanced stage of development, with fingers completely separated, but the skin not yet pigmented. However, another female with
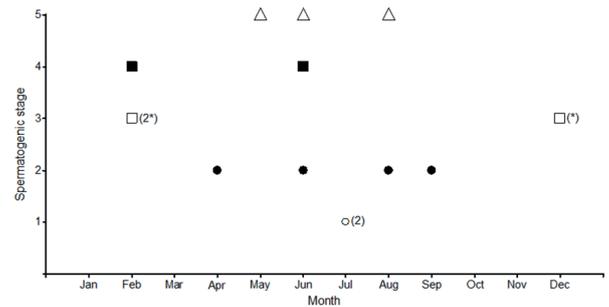
near-term embryos was collected on December 7 (embryos with scales and skin completely pigmented), suggesting that parturition occurs during December. Litter size varied from 3 to 8 offspring (mean = 5.3 ± 1.3, n = 20) and increases with SVL (Pearson Correlation; r = 0.66, p = 0.002, n = 20) and body mass (r = 0.46, p = 0.04, n = 20). Embryonic development was positively correlated with monthly mean temperature$_{(2011\text{-}2013)}$ (Spearman Correlation; $r_s$ = 0.53, p = 0.023), and historical rainfall$_{(1990\text{-}2010)}$ ($r_s$ = 0.47, p = 0.049), but not with photoperiod ($r_s$ = 0.46, p = 0.057), rainfall$_{(2011\text{-}2013)}$ (r = 0.10, p = 0.705) or historical temperature$_{(1990\text{-}2010)}$ (r = 0.33, p = 0.181).

FAT-BODY CYCLES

Fat-body mass was correlated with SVL of adult males and females (Linear Regression; $r^2$ = 0.14, p = 0.033, n = 33). The adjusted fat-body mass of males showed a negative correlation with TS (Spearman Correlation; $r_s$ = -0.57, p = 0.04, n = 13; Figure 6a). Similarly, in females we found a negative correlation between the adjusted fat-body mass and the embryonic development ($r_s$ = -0.67, p = 0.001, n = 20; Figure 6b).
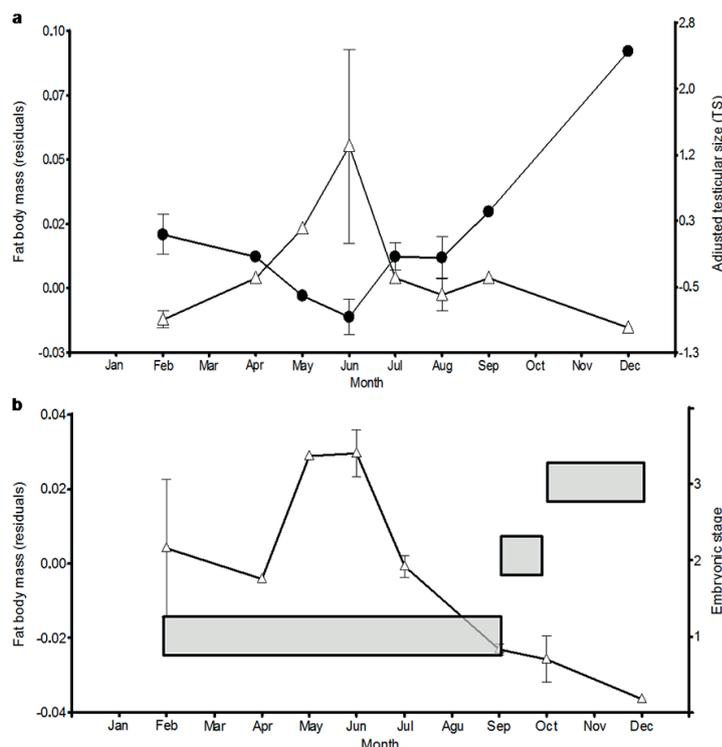
**Figure 6 -** Fat body annual cycle of *Mabuya dorsivittata* adults. (**a**) Monthly means of the residuals obtained from the linear regressions between fat body mass and snout-vent length (triangles) and between means of testicular diameter and snout-vent length (solid circles). (**b**) Monthly of the means residuals of fat bodies (triangles) and embryonic stages: 1) initial, 2) medium, and 3) advanced. Vertical bars indicate 1 SE.

DISCUSSION

*Mabuya dorsivittata* from the wet environments of Corrientes exhibited associated, seasonal and annual reproductive cycles in both males and females. Females displayed a long gestation period, showing embryos with an early stage of development in mid-summer (February), and an advanced stage in late spring (December), indicating that births occur during late spring (December) after 11 months of gestation. The gestation time estimated for *M. dorsivittata* from the Wet Chaco biome is coincident with the time span documented for congeners from other biomes of Brazil and Colombia (Amazon, Caatinga, Atlantic Forest and Cerrado biomes, Brazil, 9-12 months; Vitt

and Blackburn 1983, 1991, Vrcibradic and Rocha 1998, Rocha and Vrcibradic 1999, Ribeiro et al. 2015, and tropical wet forest, Colombia, Ramírez-Pinilla et al. 2002). Males showed the maximum spermatogenic activity in late spring (December), after females have completed gestation, and are ready to mate and begin a new reproductive cycle.

The testicular cycle of *M. dorsivittata* in the Corrientes population varied positively with the photoperiod, while the female reproductive cycle was linked to temperature and historical rainfall. However, the male reproductive cycle in tropical species of *Mabuya* is more strongly associated with the female cycle rather than environmental factors; the maximum spermatogenic activity usually coincides with birth and ovulation times (Rocha

and Vrcibradic 1999) as is seen in *M. dorsivittata* from Corrientes. Furthermore, the reproductive cycles of females in *Mabuya* are probably more dependent on the rainfall regime, as suggested by the observation that births occur during the transition period between the dry and wet seasons (see Vrcibradic and Rocha 2011), when there is greater availability of prey, which probably increases the offspring survival (Vitt and Blackburn 1991, Vrcibradic and Rocha 1998, Ramírez-Pinilla et al. 2009). Births in *M. dorsivittata* from the Wet Chaco region occur from late spring seemingly to early summer (December and January; Table I), while in the population in the Espinal biome from Córdoba (Argentina) births occur only during the summer (January and February; Aun et al. 2011), when temperatures and rainfall are high in both biomes.

The comparative analysis reveals that there is a delay in parturition as latitude increases, shifting from early spring to early summer. In tropical populations, the availability of food for hatchlings could determine the time of births (Vitt and Blackburn 1983); nevertheless, in the more southern populations the environmental temperature could play a more important role, and births in summer probably occur as a result of differences in the opportunities of females to maintain optimum temperature for embryonic development through thermoregulation (Wapstra and Swain 2001, Aun et al. 2011). Temperature can also indirectly affect the timing of birth, since increases in the diversity and abundance of arthropods in the summer at more southerly sites could be associated with the increase in temperature (Kearns and Stevenson 2012). Nevertheless, maximum accumulation of lipids in fat bodies occurs in late autumn (June) in *M. dorsivittata* from the Wet Chaco region, when temperature and rainfall drop; thus, availability of food does not seem to be a limitation for this region.

Likewise, a decrease in the fat-body mass during the reproductive season has been registered in numerous squamate species (Rocha 1992, Wiederhecker et al. 2002, Ramírez-Bautista et al. 2009), as exemplified by *M. dorsivittata* from Corrientes. In our study, an inverse relationship was observed between fat-body mass and spermatogenic activity in males, and between fat-body mass and embryonic development in females, indicating the high energetic cost entailed in reproduction in both sexes. In females, lipid resources can be used either in the vitellogenic stage or during embryonic development or in both (Hahn and Tinkle 1965, Guillette and Casas-Andreu 1981, Vitt and Blackburn 1983). Thus, in *M. dorsivittata* from Corrientes, females store lipids in the initial phase of gestation, while lipids deposited in the fat bodies decrease in the medium and advanced stages of embryonic development, similar to the congeneric pattern (Vitt and Blackburn 1983, Ramírez-Pinilla et al 2002), suggesting that lipid storage is responsible for the maintenance of the females during gestation, and even more so during the middle and final stages of embryo growth (Ramírez-Pinilla et al. 2002). However, during the pre-ovulatory phase (follicular growth) a large mobilization of lipids would not be necessary to produce microlecithal oocytes, hence the cycle of fat-body mass in *Mabuya* species seems to be strongly associated with placentotrophy (Gómez and Ramírez-Pinilla 2004). In this sense, the small diameter of oocytes at ovulation in *M. dorsivittata*, as throughout the clade *Mabuya* (Ramírez-Pinilla 2014), indicates the microlecithal character. The small size of the eggs results from a vitellogenic phase reduction as a consequence of the placental matrotrophy present in this group (Ramírez-Pinilla 2010, 2014).

Biotic and abiotic factors are involved in the evolution of the optimal litter size, and therefore it is possible to find differences in the reproductive potential among species or among populations of the same species (Table I), because of the variation in the selective forces on the populations throughout

**TABLE I**

**Summary of reproductive characteristics of the *Mabuya* species. Comparisons among reproductive season, female size at sexual maturity, mean adult female size, litter size, and births period in different biomes and localities (location and altitude). Mean values are presented with ±1 SD or ±1 SE, and range in parentheses.**

| Species | Biome | Reproductive period | Female SVL (mm) at sexual maturity | Female mean size (SVL, mm) | Litter size | Births | Locality (location; altitude) | References |
|---|---|---|---|---|---|---|---|---|
| *Mabuya dorsivittata* | Wet Chaco | February-December | 49 | 64.3 ± 11.31 (42.2-82.4) | 5.3 ± 1.32 (3-8) | December | Corrientes, northeastern Argentina (27°33' S, 58°40' W; 55 m) | Present study |
| *M. dorsivittata* | Espinal | February-December | 41 | 62.65 ± 16.47 (41-94) | 6.4 (5-10) | January - February | Córdoba, central region of Argentina (32°22' S, 62°53' W; 250 m) | Aun et al. 2011 |
| *M. dorsivittata* | Atlantic Forest | no data | 42 | no data (42-84) | 4.8 (3-9) | no data | São Paulo and Paraná, southeastern Brazil (22°50' S, 46°40' W and 25°06' S, 50°10' W; 650-979 m) | Vrcibradic and Rocha 2011 |
| *M. dorsivittata* | "Campos de altitude" | no data | 64 | no data (64-74.3) | 3.5 ± 0.45 (3-4) | February | Rio de Janeiro, southeastern Brazil (22°23' S, 44°40' W, 2460 m) | Vrcibradic et al. 2004 |
| *M. macrorhyncha* | "Restinga" Atlantic Forest | December-November | 59.9 | 68.7 ± 4.0 (59.9-77) | 2.66 ± 0.63 (2-4) | October-December | Rio de Janeiro, southeastern Brazil (22°57' S, 43°50' W; no data) | Rocha and Vrcibradic 1999 |
| *M. macrorhyncha* | Atlantic Forest | no data | no data | no data | 2.7 ± 0.5 (2-3) | November | Queimada Grande island, São Paulo, southeastern Brazil (24°29' S, 46°41' W; 200 m) | Vrcibradic and Rocha 2005 |
| *M. agilis* | "Restinga" Atlantic Forest | November-October | 49.2 | 70.7 ± 5.29 (49.2-77.9) | 3.5 ± 1.04 (2-6) | October-November | Rio de Janeiro, southeastern Brazil (22°57' S, 43°50' W; no data) | Rocha and Vrcibradic 1999 |
| *M. agilis* | "Restinga" Atlantic Forest | no data | 49.0 to 73.5 | 66.6 ± 6.1 (59-81.9) to 75.9 ± 10.7 (59.4-94.4) | 2.8 ± 0.5 (2-3) to 5.6 ± 1.7 (2-9) | no data | Espíritu Santo and Rio de Janeiro, southeastern Brazil (18° to 23° S, 39° to 43° W; 600-800 m) | Rocha et al. 2002 |
| *M. agilis* | "Restinga" Atlantic Forest | January-December | 49 | 73.5 ± 4.4 (65.8-80) | 3.2 ± 1.0 (1-5) | December-January | Rio de Janeiro, southeastern Brazil (23°03' S, 43°32' W; no data) | Vrcibradic and Rocha 2002 |
| *M. mabouya* | Tropical wet forest | Continuous | 60 | 89.41 ± 17.58 (60-103.6) | 6.02 ± 1.61 (4-10) | February and August | Cundinamarca, Colombia (5°37' N, 74°18' W; 800-1350 m) | Ramírez-Pinilla et al. 2002 |

**TABLE I (continuation)**

| Species | Biome | Reproductive period | Female SVL (mm) at sexual maturity | Female mean size (SVL, mm) | Litter size | Births | Locality (location; altitude) | References |
|---|---|---|---|---|---|---|---|---|
| *M. mabouya* | Amazon | June, July and August | 68 | no data (68-116) | no data (3-7) | August-November | Iquitos, northeastern Perú (no data) | Dixon and Soini 1986 |
| *M. mabouya* | Amazon | March-August | 72 | no data | 5.2 (4-6) | October | Dureno and Santa Cecilia, Ecuador (00°03′ N, 76°59′ W; 340 m) | Duellman 1978 |
| *M. frenata* | Cerrado | no data | 50 | 65.4 ± 2.5 (50-80) | 4.0 ± 0.6 (1-8) | December | Mato Grosso, central region of Brazil (no data) | Vitt 1991 |
| *M. frenata* | "Restinga" Atlantic Forest | November-October, November | 50.8 | 75.87 ± 8.92 (47.7-91) | 4.9 ± 1.10 (2-8) | August-November | São Paulo, southeastern Brazil (22°56′ S, 46°55′ W; 700 m) | Vrcibradic and Rocha 1998 |
| *M. frenata* | Cerrado | July-October | 60 | 64.73 | 3.65 (1-6) | August-October | Brasília and Minacu, central region of Brazil (16°00′ S, 48°00′ W; 1000 m) | Pinto 1999 |
| *M. nigropunctata* | Amazon | August-August, September | 55 | 86.3 ± 1.4 (55-109) | 4.7 ± 0.14 (2-9) | August-September | Rondônia and Pará, midwest and north of Brazil (<4° S and 10° S; no data) | Vitt and Blackburn 1991 |
| *M. nigropunctata* | Cerrado | July-October | 75 | 86.71 | 4.7 (1-8) | August-Octobe | Brasília and Minacu, central region of Brasil (16°00′ S, 48°00′ W; 1000 m) | Pinto 1999 |
| *M. heathi* | Caatinga | October-November | 45 | 70.3 ± 0.8 | 5.0 ± 0.1 (2-9) | September-November | Exu, Pernambuco, northeastern Brazil (no data) | Vitt and Blackburn 1983 |
| *M. guaporicola* | Cerrado | no data | 43 | no data (43-82) | 4.25 ± 0.50 (4-5) | no data | Mato Grosso, Pará and Brasília, Brazil (10°26′ S, 50°35′ W and 15°47′ S, 47°55′ W; no data) | Mesquita et al. 2000 |
| *M. arajara* | Caatinga | January-December | 72 | 91.3 ± 9.9 (71.9-114) | 4.9 ± 1.6 (2-9) | October-December | Ceará, northeastern Brazil (07°15′ S, 39°28′ W; 07°16′ S, 39°26′ W; 07°21′ S, 39°17′ W; 07°58′ S, 39°24′ W; 600-800 m) | Ribeiro et al. 2015 |

its distribution (Fitch 1985). Litter size of *M. dorsivittata* suggests a latitudinal and an altitudinal gradient; the populations at lower latitudes, in southeastern Brazil, showed the lowest fecundity (22°23' S, 44°40' W, altitude 2460 m; Vrcibradic et al. 2004; 22°50' S, 46°40' W and 25°06' S, 50°10' W, altitudes 650-979 m; Vrcibradic and Rocha 2011), whereas the southernmost population (Espinal biome from Córdoba, Argentina) showed the highest registered mean fecundity (32°22' S, 62°53' W, altitude 250 m; Aun et al. 2011; Table I). *Mabuya dorsivittata* from the Wet Chaco population exhibited a moderate litter size (27°33' S, 58°40' W, altitude 55 m; present study). Such differences in litter size could be explained by a difference in the female maximum SVL attained in the different populations (Table I), because females from the Espinal biome show larger maximum SVL (Aun et al. 2011) than those in the "campos de altitude" (montane fields in Atlantic Forest) biome in southeastern Brazil (Vrcibradic et al. 2004).

In many taxa, litter or clutch size increases with female body size (Andersson 1994), because larger females have more space for a larger number of offspring or eggs (Andersson 1994, Shine 1988); therefore, female-biased sexual size dimorphism and higher interlimb length in *M. dorsivittata* females from the Wet Chaco biome could be attributed to fecundity selection (Shine 1988). On the other hand, allometric growth of head length of males could be explained by sexual selection for an advantageous characteristic that improves the chance of success in male-male combat (Vitt and Cooper 1985, Anderson and Vitt 1990, Andersson 1994). Larger body size in females and the proportionally larger head size in males have been observed in other species of the genus *Mabuya* (*sensu stricto*; Vitt and Blackburn 1983, Vrcibradic and Rocha 1998, Rocha and Vrcibradic 1999, Ramírez-Pinilla et al. 2002, Ribeiro et al. 2015) and this suggests that the sexual dimorphism

pattern found in *M. dorsivittata* from Corrientes could be a plesiomorphic character for the genus.

The anti-predatory (voluntary) behavior of caudal autotomy can also be different between males and females (Bateman and Fleming 2009, Cromie and Chapple 2013). For example, in *Mabuya heathi* it has been reported that males lose their tails more frequently than females (Vitt 1981). However, although 70% of specimens of *M. dorsivittata* from Corrientes showed caudal autotomy, there was no significant difference between the sexes, regardless of SVL and body mass of individuals. This high frequency in the caudal autotomy is shared with other members of the genus; hence, it is likely that the high frequency of tail loss is a result of the evolutionary history of the group (see Van Sluys et al. 2002).

The reproductive patterns of most squamates that inhabit the Wet Chaco region remain unknown, but interestingly, the few squamate species studied to date (*Tropidurus catalanensis* –formerly *T. torquatus*, Ortiz et al. 2014; *Kentropyx viridistriga*, Ortiz et al. 2016; *Ophiodes intermedius*, Ortiz et al. 2017; *Amphisbaena mertensii*, Aguirre et al. 2017) show a broad spectrum of reproductive styles including continuous, seasonal, associated, and asynchronous cycles, different reproductive modes with different embryonic nutrition strategies, single and multiple clutches, and sperm storage in males. In particular, the reproductive pattern of *M. dorsivittata* from the Wet Chaco region resembles the general pattern of the genus: seasonal reproduction and an associated reproductive cycle, an extended period of gestation, seasonal lipid accumulation and sexual dimorphism. However, it differs in some particular aspects such as the timing of parturition, litter size, and minimum size at sexual maturity, indicating adjustments to local environmental pressures. Usually, the comparative studies showing geographical variation in life-history traits between populations attributes such variations to genetic differences or plastic

responses to different environmental conditions. Future studies under controlled laboratory experiments or using reciprocal transplants are necessary to verify the relative contributions of genotype and environment, and thereby enhance our understanding of geographical life-history patterns.

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## AUTHOR CONTRIBUTIONS

Martín Ortiz, Jorgelina M. Boretto and Nora R. Ibargüengoytía conceived the article; Martín Ortiz collected data and performed the analyses with contributions of Jorgelina M. Boretto and Nora R. Ibargüengoytía. Martín Ortiz, Jorgelina M. Boretto and Nora R. Ibargüengoytía wrote the manuscript.

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