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Reproductive biology of the southernmost *Kentropyx* lizard from the Wet Chaco of Corrientes, Argentina

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Studies on reproductive modes, size at maturity, clutch size and clutch frequency have contributed greatly to our understanding of life history variation among lizard populations, and thereby, to implement conservation strategies. Herein, we studied the reproductive biology of the vulnerable tegu lizard *Kentropyx viridistriga* from Corrientes, northeastern Argentina (Wet Chaco). *Kentropyx viridistriga* are active from early summer to late autumn, with temperature and photoperiod influencing the timing of reproduction and the brumation period. Females showed an annual reproductive cycle, and males exhibited a continuous reproductive cycle during the activity season. Females laid at least two clutches of on average three eggs per reproductive season. Neonates occured in spring, and reached sexual maturity in the first year of life. Females reached sexual maturity at a larger snout-vent length (64.1 mm) than males (54.8 mm). Sexual dimorphism is evident, with males showing greater head size and longer tails than females, while females exhibit larger interlimb length than males. This study reveals that the reproductive strategy of *K. viridistriga* is adjusted to the environmental conditions of the southernmost distribution for the genus.

Key words: life history, *Kentropyx viridistriga*, reproductive cycle, Squamata, Teiidae

INTRODUCTION

Studies on reproductive biology have substantially contributed to life history theory (Tinkle et al., 1970; Dunham et al., 1988), which is essential to understand the diversity of life cycles (Dunham et al., 1988; Mesquita & Colli, 2010). Life history traits like reproductive mode, size at maturity, clutch size and clutch frequency have both theoretical and empirical interest, as it enables us to understand the dynamics of populations and, thereby, implement conservation strategies (Baillie et al., 2004).

Tinkle et al. (1970) in one of the first comparative studies of lizards' life histories proposed two main patterns. The first pattern is more likely to be found in oviparous and viviparous lizards from temperate environments and is characterised by larger females with delayed maturity that produce a single numerous brood per season. The second pattern refers to early maturing oviparous females, which are small-sized at maturity and throughout life, and produce small but multiple broods per season (Tinkle et al., 1970). These yet extant reproductive patterns are based on the dependence of physiological processes upon biotic and abiotic factors. Reproduction depends on temperature, photoperiod (Marion, 1982; Ramírez-Bautista et al., 2000), and rainfall (Rocha, 1992; Watling et al., 2005; Ferreira et al., 2011), which set the annual and daily activity periods during ontogeny. Lizard phenology further depends on phylogenetic history (Miles & Dunham, 1992; Blomberg & Garland, 2002; Mesquita & Colli, 2010), body size and shape (Vitt & Goldberg, 1983; Vitt et al., 1997), social relationships, as well as microenvironments to feed, refuge, thermoregulate and reproduce (Ballinger, 1977; Vitt & Caldwell, 2009).

Lizards adjust the timing of reproductive cycles, especially gametogenesis and births with environmental conditions. Reproduction can be continuous (Hernández-Gallegos et al., 2002; Mojica et al., 2003; Watling et al., 2005) or seasonal (Rocha, 1992; Brown & Shine, 2006; Goldberg, 2012). Seasonal reproductive patterns are most widespread, with principal reproductive events taking place during the warmest months of the year (spring–summer) or during the wet season (see review in Vitt & Caldwell, 2009). Other lizard species show a seasonal reproduction with ovulation, fecundation and development in autumn–winter months, and hatching in spring. This reproductive cycle is frequently observed in high–elevation species in tropical and subtropical latitudes (e.g., Guillette & Casas-Andreu, 1980, 1987; Guillette & Méndez-de la Cruz, 1993; Ramírez-Pinilla, 1991, 1995; Ramírez-Bautista et al., 2014), where births in spring guarantee that offspring find optimal conditions for growth and survival (Brown & Shine, 2006; Warner & Shine, 2007).

In lizards with seasonal activity and a brumation period, lipids are the most efficient way to store energy,

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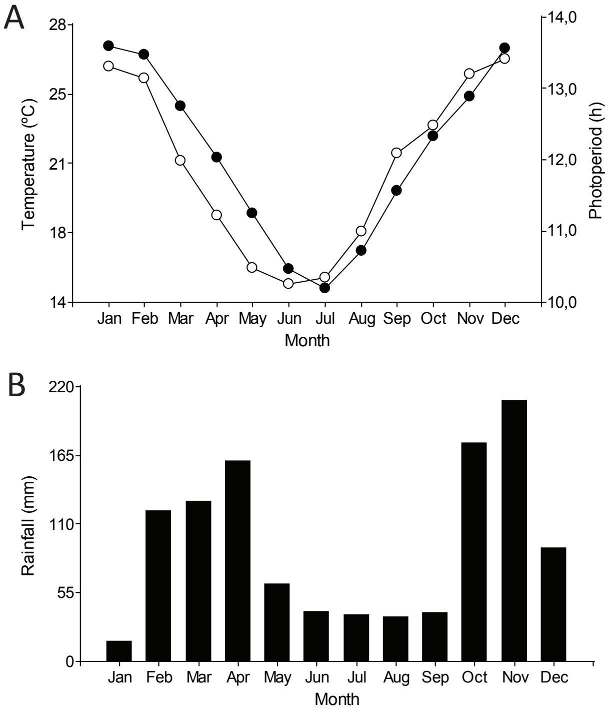

Fig. 1. Monthly means of climatic variables in Corrientes, Argentina. (A) Temperature (solid circles) and photoperiod (open circles); (B) rainfall. Climatic data from 2011 to 2013, obteined from the Servicio Meteorológico Nacional and Servicio de Hidrografía Naval Argentino.

and could be important for both reproduction and/or winter brumation survival (Derickson, 1976; Benabib, 1994). An inverse relationship between abdominal fat body mass and the gonadal cycle has been documented in some species (Ramírez-Pinilla, 1991, 1995; Rocha, 1992)**,** while in others this relationship is not evident (Derickson, 1976; Magnusson, 1987; Serrano-Cardozo et al., 2007). The absence of lipid cycling could be related to foraging mode (Colli et al., 1997), since active foragers can replenish the energy expended on reproduction by continuous foraging (Ramírez-Bautista et al., 2000).

Kentropyx Spix 1825 is a lizard genus distributed in South America, Barbados, and Trinidad (Gallagher & Dixon, 1992; Harvey et al., 2012), comprising nine species (Harvey et al., 2012) which inhabit both tropical and subtropical habitats (Gallagher & Dixon, 1992; Cei, 1993). Gallagher & Dixon (1980, 1992) and Harvey et al., (2012) recognised three groups based on morphological characters: (i) the *calcarata* group (*K. calcarata*, *K. pelviceps* and *K. altamazonica*); (ii) the *paulensis* group (*K. paulensis*, *K. viridistriga*, *K. lagartija* and *K. vanzoi*); (iii) the *striata* group (*K. striata* and *K. borckiana*). Species of the *calcarata* group mainly inhabit in forested habitats of Amazonia, the Guianas, and the Atlantic Forest of Brazil, while species of the *paulensis* and *striata* groups occur in open ecosystems with sandy soils (Werneck et al., 2009; Harvey et al., 2012).

Kentropyx viridistriga (Boulenger, 1894) inhabits open habitats in Brazil, Bolivia, Paraguay, and northeastern Argentina (Embert, 2010, Abdala et al., 2012; Cei, 1993, Acosta et al., 2012). It is a diurnal, oviparous species whose active period occurs from summer (December) to early winter (early July, personal observations) when brumation starts. It has been categorised as a vulnerable species in Argentina (Acosta et al., 2012) due to the anthropic impact which caused its habitat degradation.

In this study we describe the male and female reproductive cycles, size at sexual maturity, reproductive output, mean relative clutch mass, fat bodies cycle and sexual dimorphism of *K. viridistriga* inhabiting the grasslands of the subtropical area of Corrientes province, northeastern Argentina, representing the southernmost species distribution for the genus. Our goal is to address the following questions: (i) When do males and females of *K. viridistriga* start their activity and when do they start their reproductive cycles after the brumation period? (ii) How does climate affect the timing of gametogenesis? (iii) Are male and female reproductive cycles synchronous? (iv) How does lipid storage in fat bodies relate to gametogenesis and seasonality? (v) What are dimorphic sexual traits, and what are the likely causes? Reproductive parameters and cycles of male and female *K. viridistriga* are discussed in relation to the different reproductive responses of other Neotropical congeneric species.

MATERIALS AND METHODS

Study area and climate

Populations of *K. viridistriga* were studied in grassland localised in Capital Department (27°28’50” S, 58°44’24” W), Apipé Island, Ituzaingo Department (27°29’13” S, 56°54’33” W), and Caimán Colony, San Miguel Department (28°02’25” S, 57°41’22” W), Corrientes Province, Argentina. The study site belongs to the Eastern District of the Chaco Phytogeographic Province (Cabrera & Willink, 1973; Carnevali, 1994).

The climate in the north of Corrientes Province is mainly warm and subtropical; there is no dry season although winter rainfalls are lower. Average annual rainfalls in the northern region ranges between 1200–1500 mm; mean annual temperature is 21°C, ranging from 15°C in July to 27°C in January (Carnevali, 1994; Bruniard, 1997). Uncommon frosts are registered only in winter (Carnevali, 1994). Mean temperature, photoperiod and rainfall in the time period 2011–2013 were provided by the Servicio Meteorológico Nacional and the Servicio de Hidrografía Naval Argentino (Fig. 1).

Sampling and laboratory methods

Twenty-five males and 28 females were caught by hand and pitfall traps from March 2011 to July 2013. Specimens obtained from the herpetological collection of the UNNE of Corrientes (one adult female caught in June 2009, and two juveniles caught in November 1994 and December 2007) completed our sample collection. Prior to preservation, lizards were sexed, weighed (body mass, BM) to the nearest 0.01 g with a digital balance (Ohaus® traveler scale TA320). Sexual dimorphism was studied considering the following variables measured using a digital caliper (Essex®, 0.01 mm): 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 at the insertion to the shoulders and pelvic girdles respectively (HLD), 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), tail length (TaL) and status of the tail (ST; intact, cut or regenerated). Specimens were euthanised by intraperitoneal administration of anesthesia (carticaine L-adrenaline) and the testes and ovaries were dissected out to be measured and processed. After fixation in Bouin's solution for 24 hours, the lizards were stored in 70% ethanol and deposited at the herpetological collection of the Universidad Nacional del Nordeste (UNNEC), Corrientes province.

Male reproductive cycle

The male gonadal cycle was determined based on macro- and microscopic observations. Testes were measured on antero–posterior diameter (TS) using a digital caliper (±0.1 mm). Gonads were dehydrated in ethanol series and embedded in paraffin for 24 h in the oven at 52°C. Sections 5 µm thick were cut with a microtome Reichert-Jung Hn40 and following a conventional protocol, stained with hematoxylin and eosin.

Spermatogenic stages were determined based on the most advanced cell type present in the seminiferous tubules following Mayhew & Wright (1970), and cell types were recognised based on Uribe (2002). Five spermatogenic stages were defined: (i) only spermatogonia, (ii) primary and secondary spermatocytes, (iii) round spermatids and in the process of elongation, (iv) spermatozoa in the seminiferous tubules, and (v) regression with cellular debris and scarce spermatozoa in tubular lumen (modified from Mayhew & Wright, 1970). The presence or absence of spermatozoa in the epididymis was also registered. Minimum SVL at sexual maturity in males was determined based on the smallest specimen with spermatogenic activity (stages II–V) or spermatozoa in the epididymis.

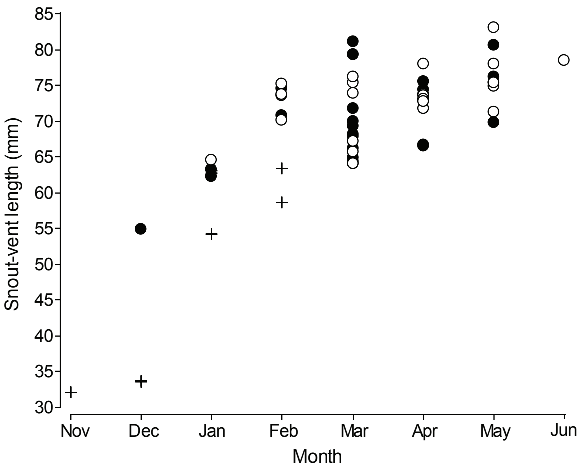

Fig. 2. Body size (snout–vent length) distribution by month in *Kentropyx viridistriga*. Adult males (solid circles), adult females (open circles), and juveniles (plus signs) are represented.

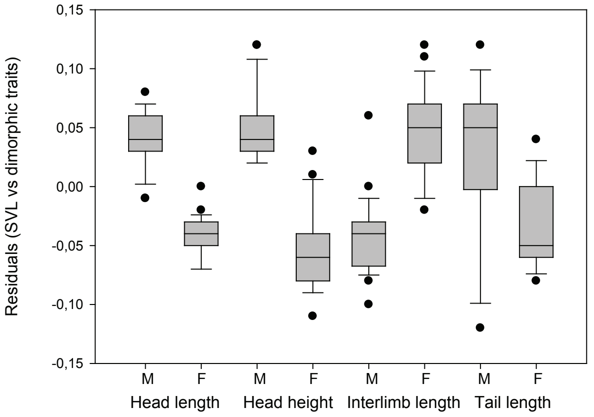

Fig. 3. Box plot of the significant dimorphic traits (p<0.05) of female and male *Kentropyx viridistriga*.

Female reproductive cycle

Female gonadal cycles were defined by the presence and number of vitellogenic follicles, oviductal eggs and corpora lutea. The follicle size was estimated as the diameter of the largest follicle for each female (Ibargüengoytía & Cussac, 1998) and was measured with an ocular micrometer to the nearest 0.1 mm using an Olympus® SZX9 stereoscopic microscope. The largest and smallest diameters of the oviductal eggs were registered with a digital caliper (±0.1 mm) to further calculate their volume with the equation of spheroid: $V=(4/3)\pi(a/2)(b/2)^2$, where V is the egg volume, a is the longest diameter and b is the shortest diameter. Minimum SVL at sexual maturity for females was estimated considering the smallest female containing enlarged vitellogenic follicles, oviductal eggs or corpora lutea. The simultaneous presence of vitellogenic follicles and oviductal eggs, or vitellogenic follicles and corpora lutea, was considered indicative of the occurrence of more than one clutch per reproductive season (multiple clutches). Females without vitellogenic follicles and oviducts with either an absence of folds or presence of small folds were classified as juveniles. This method follows the definition of Ibargüengoytía & Cussac (1998): "Uterus type 1: folds, if present, are small and never spread over the entire uterus."

Clutch size was based on the number of oviductal eggs. Reproductive investment was estimated using the relative clutch mass (RCM). RCM index was calculated following two methods: i) RCMinc=CM/FBM, where CM is clutch mass and FBM is the female's body mass (which includes the clutch mass); and ii) RCMexc=CM/(FBM–CM), where the clutch mass is subtracted from the female's body mass (Rodríguez-Romero et al., 2005).

Fat body cycles

Fat bodies were excised after the necropsy of each adult lizard and weighed to the nearest 0.01 g using a digital balance (Ohaus® traveler scale TA320).

Statistical analyses

Statistical analyses were conducted using INFOSTAT (v.2011), SPSS (v.17.0), and SIGMAPLOT (v.10.0). The assumption of normality was checked with the Shapiro-Wilks tests and Levene's homogeneity of variance test.

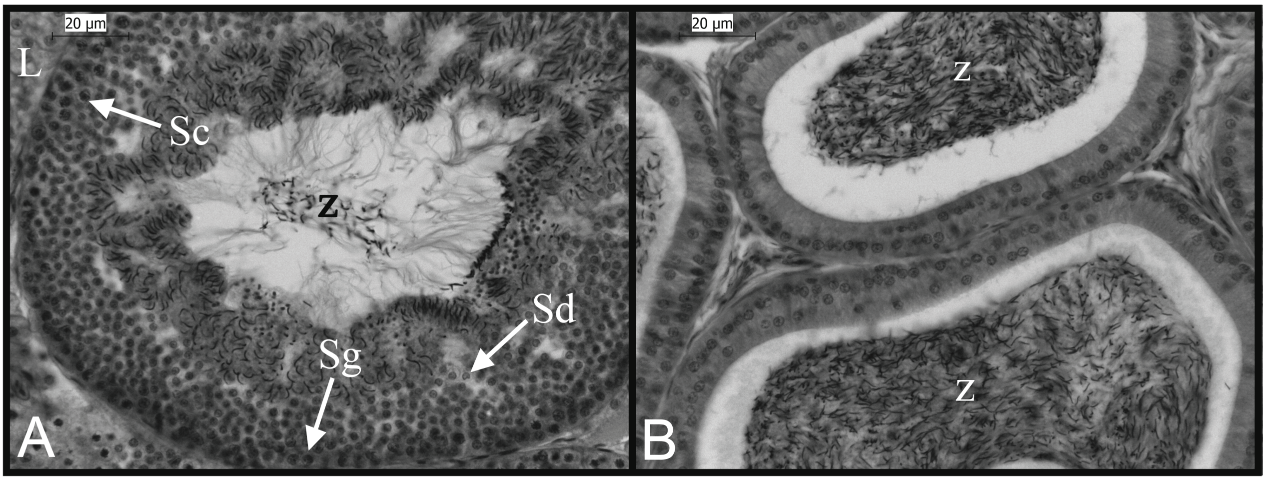

Fig. 4. Photomicrographs of cross-section of seminiferous tubules (A) and epididymis (B) from a male of *Kentropyx viridistriga* collected in March. Leydig cell (L), spermatogonia (Sg), spermatocytes (Sc), spermatids (Sd), and spermatozoas (Z).

Dependence between variables was tested performing simple and multiple regressions (bidirectional stepwise elimination based on *p* value, and significance levels for testing input and output variables were α=0.05 and α=0.10, respectively), and correlations. When correlation between independent variables and SVL was found, residuals of the linear regression were used (Ramírez-Bautista & Vitt, 1997) to perform further analysis. The significance level used was *p*<0.05 for all statistical tests and results are presented as mean±standard deviation (SD).

To analyse sexual dimorphism, we performed a Student's t–test to determine the difference between female and male SVL. Then, the residuals of the regression of the ln–transformed morphological variables (BM, HL, HW, HH, NW IL, FLD, HLD, HipW, BW, and TWV) and ln–transformed SVL were used in the Stepwise discriminant analysis (based on *p* value with α=0.05 and α=0.10 as input and output significance levels) to determine the variables that better explain the differences between the sexes. Analysis of covariance (SVL=covariate) was used to test the sexual dimorphism in tail length (TaL; only the specimens with intact tails were considered). In order to set up the possible causes of intersexual differences in the frequency of caudal autotomy, a χ^2 test was performed to compare intact versus broken or regenerated tails between males and females.

RESULTS

Seasonal activity

The pitfall traps were in the field for two years and checked every week, and adult specimens were only captured from early summer (December) to early winter (July). Particularly, adult males were captured between late spring (December) and mid autumn (May, Fig. 2), while adult females from early summer (January) to late autumn (June). Two specimens of adult size were observed in early winter (early July), but they could not be captured and sexed. In addition, juveniles were captured between mid spring (November) and mid summer (February).

Body size, sexual maturity and sexual dimorphism

Minimum adult size for males was 54.8 mm SVL, corresponding to a specimen with spermatozoa in the seminiferous tubules (stage IV). In females, the minimum adult size was 64.1 mm SVL, corresponding to an individual with oviductal eggs.

Adult males ranged from 54.8 to 81.0 mm of SVL (mean=70.2±6.5, *n*=25), and from 4.11 to 12.98 g of body mass (mean=7.96±2.29, *n*=25), while adults females ranged from 64.1 to 83.0 mm of SVL (mean=73.2±4.6, *n*=23), and from 5.37 to 13.31 g of body mass (mean=8.09±1.86, *n*=23). Although females were on average larger than males, no sexual dimorphism was found in SVL (Student's t–test, *t*=−1.79, df=49, *p*=0.080, *n*=48). Females exhibited larger interlimb length (discriminant analysis, λ=0.166, χ^2=79.88, df=3, *p*<0.000,

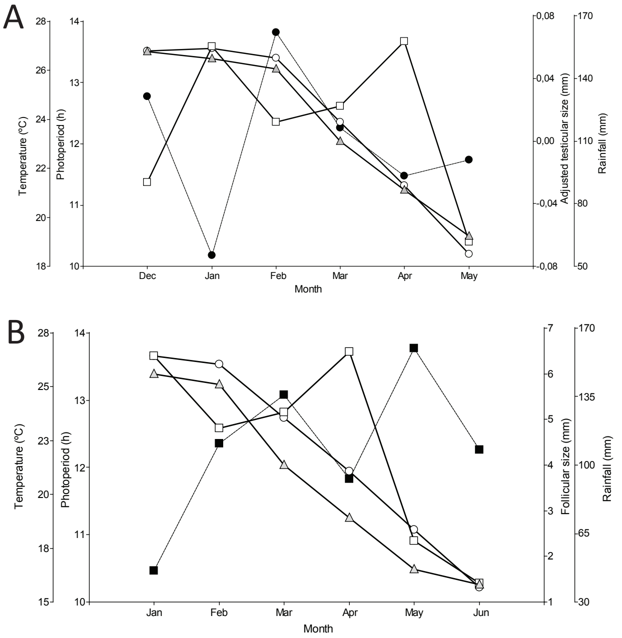

Fig. 5. Climatic variables versus gonadal activity of adults *Kentropyx viridistriga*. Adjusted testicular size (solid circles; A) and follicular size (dark squares; B) with temperature (open circles), photoperiod (gray triangles), and rainfall (white squares).

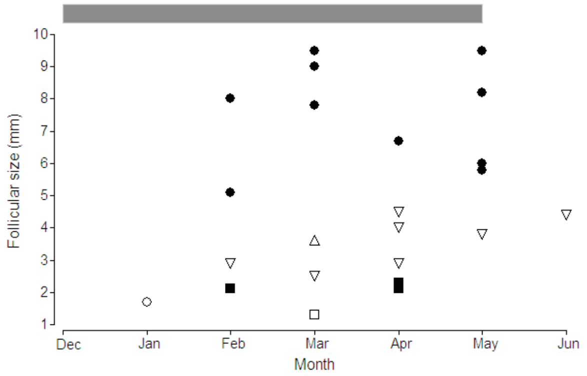

Fig. 6. Follicular size of adult females *Kentropyx viridistriga* versus months during the activity season. Nonvitellogenic follicles (open circles); vitellogenic follicles (solid circles); vitellogenic follicles and oviductal eggs (triangles up); vitellogenic follicles and corpora lutea (triangles down); nonvitellogenic follicles and oviductal eggs (dark squares); nonvitellogenic follicles and corporal lutea (white squares). The grey bar indicates the presence of males with spermatozoa in seminiferous tubules.

n=48, Fig. 3), while males showed longer and higher heads, and longer tails (ANCOVA, $F_{1,28=}$12.03, *p*=0.001, *n*=31, SVL as covariate). In addition, only males have spurs (modified scales) on either side of the cloaca.

Adult males and females did not differ in the frequency of caudal autotomy ($\chi^{2=}$0.01, df=1, *p*=0.929, *n*=48). Broken and regenerated tails were recorded in 36% of males and in 34.8% of females. Males and females with intact tails did not show differences in body size or body mass in comparison with males and females with broken or regenerated tails (Student's *t*–test$_{\text{males}}$, SVL, *t*=–0.74, *p*=0.469; body mass, *t*=0.24, *p*=0.812; *t*–test$_{\text{females}}$, SVL, *t*=–1.62, *p*=0.119; body mass, *t*=0.28, *p*=0.781).

Male reproductive cycle

All males collected during the activity season from early summer to late autumn (December to May) exhibited spermatozoa in the seminiferous tubules (*n*=25, stage IV; Fig. 4A), and a central mass of sperm in epididymis (Fig. 4B), with exception of the single male captured in December. The relationship between male SVL and testicular size (TS) was positive (Linear Regression, r^2=0.36, $F_{1,23}$=13.1, slope=0.50±0.14, *p*=0.001, *n*=25). In consequence, the residuals were used as the adjusted testicular size in the following analyses. Adjusted testicular size showed that the highest mean value was reached in mid summer (February), decreasing during the autumn months when temperature and photoperiod also decreased (Fig. 5A).

Follicular size and female reproductive cycle

Females with vitellogenic follicles occurred from mid summer (February) to late autumn (June). The follicle size showed two peaks, with the highest values in late summer (March) and mid autumn (May, Fig. 6). Presence of females with enlarged vitellogenic follicles (greatest follicle size=8.0 mm), or with oviductal eggs or corpora lutea in February (Fig. 6) indicates that the vitellogenic cycle starts before this period. The last female caught in late autumn (June) showed vitellogenic follicles and corpora lutea (greatest follicle size=4.4 mm, Fig. 6). The reproductive activity was recorded through the months of high rainfall, and extended when temperature and photoperiod decreased during autumn (Fig. 5B). The reproductive state of females do not relate to the female SVL (Fig. 7).

Clutch size, female reproductive investment and hatches

Three hatchlings were registered, one in November (SVL=32.2 mm) and the other two in December (SVL=33.6 and 33.7 mm). Clutch size varied from 2–4 eggs (3.2±0.84, *n*=5) and was not correlated with female SVL (Spearman Correlation, r_s=0.53, *p*=0.36, *n*=5), neither did the volume of the eggs (r_s=0.90, *p*=0.07, *n*=5) which ranged from 402.7 to 582.2 mm^3 (475.4±84.35, *n*=5). The mean fresh total clutch mass was 0.49±0.11 g (range=0.41–0.61, *n*=3), and the mean of fresh egg mass was 0.49±0.1 g (range=0.40–0.62, *n*=8). The analysis of reproductive investment showed that RCMinc ranged from 0.15 to 0.18 (0.16±0.02, *n*=3), and RCMexc ranged from 0.17 to 0.22 (0.19±0.03, *n*=3).

Fat body mass

In total, 87.5% of adult individuals did not have appreciable fat bodies (males: 92%, females: 82.6%). Fat body mass did not exhibit a relationship with SVL neither in females nor in males (Linear Regression r^2_{males}=0.14, *p*=0.068, *n*=25; r^2_{females}=0.001, *p*=0.876, *n*=23). In the male fat bodies cycle, the lowest values are shown from the beginning of the activity (December) until mid summer (February). Then a peak occurs in early autumn (March, Fig. 8A) after the peak of gonadal activity, and then descends during the months following autumn. While in the females fat body cycle, two peaks were observed, one in mid summer (February) and another in early autumn (April, Fig. 8B) alternated with the two peaks of follicular growth.

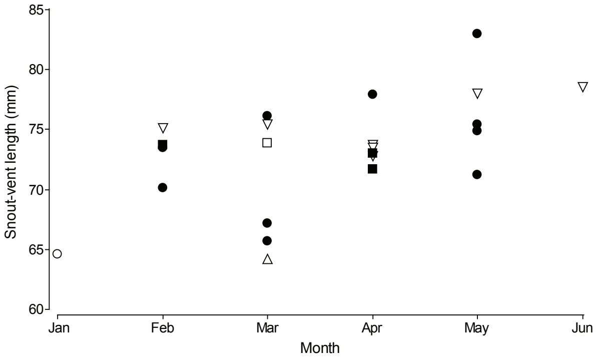

Fig. 7. Female body size (snout–vent length) and reproductive condition in *Kentropyx viridistriga* during the activity season. Females with nonvitellogenic folicles (open circles); vitellogenic follicles (solid circles); vitellogenic follicles and oviductal eggs (triangles up); vitellogenic follicles and corpora lutea (triangles down); with oviductal eggs and nonvitellogenic follicles (dark squares); and females with corporal lutea and nonvitellogenic follicles (white squares) are represented.

Table 1. Summary of reproductive data of *Kentropyx* species. Shown are comparisons of the breeding season, female size at sexual maturity, mean adult female size, clutch size, egg size, reproductive effort (RCM), period of emergence of hatchlings, and number of clutches per reproductive season (CF: S=single, M=multiple) in different biomes and localities. Mean values are presented with ±1 SD or ±1 SE, and range in parentheses. ? no data

Species	Biome	Reproductive period	Female SVL (mm) at sexual maturity	Female mean size (SVL, mm)	Clutch size	Egg volume (mm^3)	RCMinc	RCMexc	Hatching period	CF	Locality	Reference
K. viridistriga	Wet Chaco	January-June, July	64.1	73.2±4.6	3.2 ±0.84 (2-4)	475.4 ±84.35	0.16±0.02 (0.15-0.18)	0.19±0.03 (0.17-0.22)	November-December	M	Corrientes, northeastern Argentina	Present study
K. viridistriga	Pantanal	?	?	?	7.33 ±2.34 (6-12)	804.06 ±87.42	?	?	?	?	Mato Grosso, Brazil	Werneck et al. 2009
K. lagartija	Yungas	February-May, June	?	?	(4-7)	?	?	?	November-December	?	Tucumán, northwestern Argentina	Tulli & Scrocchi 2005
K. paulensis	Cerrado	August, February, March	63.8	70.2±3.8	4.2 ±0.84 (3-5)	?	(0.25-0.28)	?	?	M	São Paulo, southeastern Brazil	Anjos et al. 2002; Mesquita & Colli 2010
K. paulensis	Cerrado	?	?	?	3.9 ±0.78 (3-6)	528.94 ±189.1	?	?	?	?	Paracatu, southeastern Brazil	Werneck et al. 2009
K. vanzoi	Cerrado	?	?	46.9	3.31 ±1.18 (1-6)	510.11	?	?	?	?	Vilhena, Rondônia, northern Brazil	Werneck et al. 2009; Mesquita & Colli 2010
K. calcarata	Amazon	October, March, May, and June	?	?	(5-7)	?	?	?	January-April, and July-October	M	Suriname	Hoogmoed 1973
K. calcarata	Amazon	January-March, and May-September	69.0	81±1.34	5.0 ±0.3 (4-7)	921 ±0.31	0.153	0.181	June-September	?	Rondônia and Pará, northern Brazil	Vitt 1991; Vitt et al. 1995
K. calcarata	Amazon	?	?	?	5.63 ±1.23 (3-9)	921.16 ±149.13	?	?	?	?	Warniabo Creek, Guyana, and Vila Rica, Brazil	Werneck et al. 2009
K. altamazonica	Amazon	January, February, June, August and September	70.0	?	(2-4)	?	?	?	October-December	M	Iquitos, northeastern Peru	Dixon & Soini 1986
K. altamazonica	Amazon	?	?	?	5.45 ±1.11 (3-9)	713.45 ±127.94	?	?	?	?	Loreto, Peru, and Tapirapeco, Venezuela	Werneck et al. 2009

Table 1. *Continued.*

Species	Biome	Reproductive period	Female SVL (mm) at sexual maturity	Female mean size (SVL, mm)	Clutch size	Egg volume (mm^3)	RCMinc	RCMexc	Hatching period	CF	Locality	Reference
K. pelviceps	Amazon	February, March, April, May, August and December	80.0	?	(3-5)	?	?	?	June-December	M	Iquitos, northeastern Peru	Dixon & Soini 1986
K. pelviceps	Amazon	?	80.0	104±2.6	6.5 ±0.3 (5-8)	1028.9 ±61.8	0.22 (0.19-0.21)	0.29 (0.23-0.34)	?	M	Sucumbíos, northeastern Ecuador	Vitt et al. 1995
K. pelviceps	Amazon	?	?	?	5.52 ±0.85 (4-7)	1089.39±200.05	?	?	?	?	Sucumbios, Ecuador	Werneck et al. 2009
K. striata	Amazon	May-July	74.0	83.1±1.1	5.3 ±0.33 (3-9)	602.4 (340.5-867.3)	0.185±0.026 (0.134-0.221)	0.230±0.038 (0.155-0.283)	November-?	M	Boa Vista, Roraima, northern Brazil	Vitt & Carvalho 1992; Vitt et al. 1995
K. striata	Amazon	October, November, and January	?	?	(3-5)	?	?	?	October	?	Suriname	Hoogmoed 1973
K. striata	Amazon	?	?	?	5.84 ±1.72 (3-12)	670.65 ±135.69	?	?	?	?	Southern Rupununi Savanna, Guyana	Werneck et al. 2009
K. striata	Amazon	?	?	?	?	?	?	?	March-August	?	Pará, nothern Brazil	Magnusson 1987
K. borckiana	Amazon	?	?	?	(5-9)	?	?	?	?	?	Suriname	Hoogmoed 1973

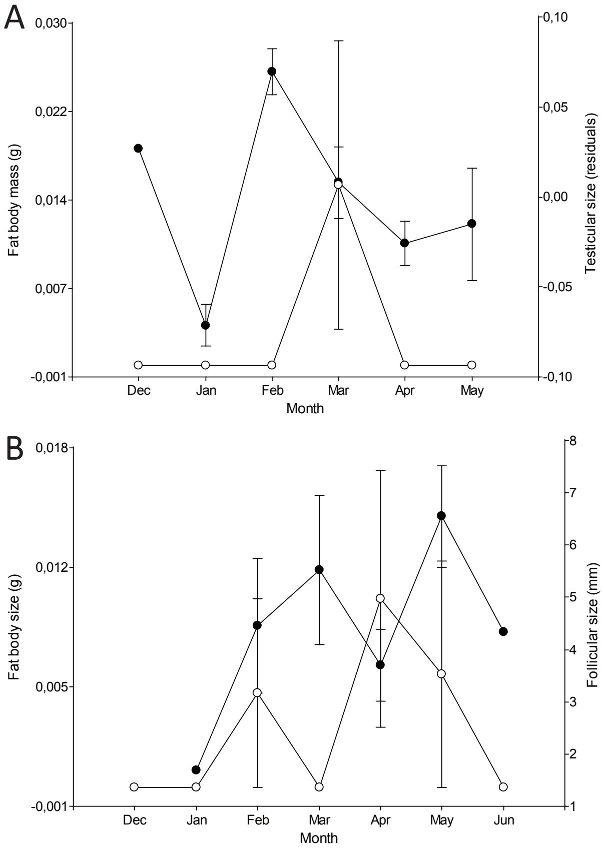

Fig. 8. Fat body cycle of adults *Kentropyx viridistriga*. Monthly fat body mass (open circles) and adjusted testicular size (solid circles, A) or follicular size (solid circles, B) are showed. Bars indicate the standard error.

DISCUSSION

Kentropyx viridistriga from Wet Chaco of Corrientes are active from early summer to late autumn, and show a seasonal and annual reproductive cycle in females and a continuous reproductive cycle in males. Females show two peaks of vitellogenesis, one in the beginning of autumn (March) and another in mid autumn (May), and males exhibited spermatozoa in seminiferous tubules during the entire activity season. The bimodal vitellogenesis and the presence of females with vitellogenic follicles and oviductal eggs or corpora lutea during their activity season suggest multiple clutches. Furthermore, females with enlarged vitellogenic follicles, oviductal eggs or corpora lutea in mid-summer, and an adult female captured at the beginning of their activity season with non-vitellogenic follicles suggest that vitellogenesis starts in early summer. The female collected in June with vitellogenic follicles (4.4 mm), and the two adult specimens observed in activity suggest that the reproductive cycle extends to winter time. In teiids like *Aspidoscelis sexlineatus* (Etheridge et al., 1986), *Teius oculatus* (Blanco & Acosta, 1998), and *Teius teyou* (Cruz et al., 1999), females also start the vitellogenic cycle before brumation. However, since metabolic activities during the brumation period are reduced to a minimum (Vitt & Caldwell, 2009), females probably enter brumation with vitellogenic follicles of medium size, and resume the vitellogenic cycle as soon as they start activity in summer. Moreover, the brumation period as well as cold temperatures are necessary for several reptiles to complete vitellogenesis and ovarian growth (Gavaud, 1983; Whittier & Tokarz, 1992; Duvall et al., 1982).

The autumn reproductive cycle of *K. viridistriga* appears as an adaptive response to a subtropical environment, and has also been described in other high-altitude species in tropical and subtropical Central and South America (Guillette & Casas-Andreu, 1980; Méndez-de la Cruz & Villagrán, 1998; Ramírez-Pinilla, 1991, 1995), as well as in lowland lizards (Mount, 1963; Ballinger, 1973; Guillette & Bearce, 1986). Autumn reproduction allows embryonic development during winter followed by births in spring, giving the young time to grow and store energy before the next winter (Goldberg, 1971; Ramírez-Pinilla et al., 2009). In subtropical and temperate teiids, the breeding season usually occurs in warmer periods (Blanco & Acosta, 1998; Cappellari et al., 2011; Cruz, 1996; Cruz et al., 1999), while in tropical teiids reproduction is linked to precipitation (Magnusson, 1987; Colli, 1991; Ramírez-Bautista et al., 2000). Species of the *Kentropyx calcarata* group are active throughout the year with multiple clutches (Hoogmoed, 1973; Dixon & Soini, 1986; Table 1), while species of the *paulensis* group exhibit a seasonal pattern; the length of the reproductive cycle is shorter in *K. viridistriga* from Corrientes than in other species (e.g., *K. paulensis*, Anjos et al., 2002). The decrease in temperature and photoperiod are likely to exert control on the onset of the brumation period in *K. viridistriga,* limiting their activity and reproductive functions (Milsom et al., 2008). *Kentropyx viridistriga* responds to an environment with marked rainfall, low temperature and short photoperiod in winter by reducing its activity to 7 months. Vitellogenesis occurs during the rainy season, and the first oviposition occurs when relative temperatures are still high.

In *K. viridistriga*, fat body mass of males and females is unlinked to reproductive cycle or winter dormancy. The active foraging mode allows to replenish the energy expended on reproduction by continues feeding (Ramírez-Bautista et al., 2000), and fat accumulation may not be necessary to ensure energetic resources for reproduction (Serrano-Cardozo et al., 2007). However, lipid accumulation probably takes place in the liver or tail to support metabolism during brumation (Derickson, 1976).

Spermatogenesis in Teiidae has been reported to start before males emerge from hibernation (Goldberg, 1976; Etheridge et al., 1986; Blanco & Acosta, 1998; Cruz et al., 1999). Nevertheless, *K. viridistriga* males have spermatozoa in seminiferous tubules and epididymis throughout their activity period, without testicular regression or quiescence. However, the observed changes in testicular size, probably related to hormonal function rather than differences in spermatogenesis, suggest a peak in testosterone production at the end of summer, and a decrease of hormonal activity with temperature and photoperiod. Males of *K. viridistriga* emerge from brumation before females and are immediately ready to copulate, reflecting a protandric pattern described in reptiles from both temperate climates and subtropical zones (Olsson et al., 1999; Jenssen et al., 2001; Cappellari, 2005; Winck & Cechin, 2008). Early-emerging males might benefit by increasing copulation opportunities, and by producing more spermatozoa (Olsson et al., 1999; Jenssen et al., 2001; Winck & Cechin, 2008). Delayed-emerging females can benefit from choosing males with established territories (Jenssen et al., 2001; Winck & Cechin, 2008).

Sexually dimorphic traits like large body size and larger head in males are the result of male agonistic encounters (Anderson & Vitt, 1990; Andersson, 1994). Males of *K. vistrigata* have proportionally larger head sizes and longer tails than females. Although head size dimorphism can be linked to food niche segregation (Presst, 1994; Herrel et al., 1999), *K. viridistriga* males and females do not differ in prey item size (Acosta, personal communication). Larger heads in males are likely the result of intrasexual selection, increasing the ability of males to maintain control on the female through bites during copulation (Anderson & Vitt, 1990; Zaldívar-Rae & Drummond, 2007; Alfonso & Torres, 2012). Moreover, a larger tail could result from male aggressive behavior through tail whipping. Aggressive interactions cause higher caudal autotomy in males, although a similar proportion of caudal autotomy across body sizes in both sexes suggests that this is caused by predators (Bateman & Fleming, 2009; Cromie & Chapple, 2013). Males of *K. viridistriga* are also characterised by spurs on either side of the cloaca, a trait exclusive to the genus *Kentropyx* (Gallagher & Dixon, 1980).

The larger interlimb length of *K. viridistriga* females is likely a result of fecundity selection (Olsson et al., 2002, Cox et al., 2007). The degree of sexual size dimorphism is inversely related to reproductive frequency (Cox et al., 2007), and the multiple clutches of *K. viridistriga* females are consistent with the observed female-biased sexual size dimorphism. Clutch size and egg volume are not significantly different among *Kentropyx* from forest and savanna ecosystems, independently of phylogenetic structure (Werneck et al., 2009). Furthermore, mean relative clutch mass (RCM) of *K. viridistriga* from Corrientes was similar to the RCM documented for other teiids (Vitt & Price, 1982). Although these may be indicative of high phylogenetic inertia in *Kentropyx* for reproductive parameters (Werneck et al., 2009), *K. viridistriga* from the Wet Chaco showed a clutch size and egg size lower than the Pantanal population (Table 1). In addition, comparing species of the three groups, we observed a trend in the *paulensis* group for a smaller clutch size, egg size and female size at maturity (Table 1). Based on molecular and morphological data, Werneck et al. (2009) determined that *K. striata* occupies a basal position in relation to all other species, suggesting that the reproductive parameters in the *paulensis* group are derived. Taken together, *K. viridistriga* from the Wet Chaco of Corrientes shows the shortest activity pattern in the southernmost distribution of the genus, and can be classified into a species with small size, an oviparous mode of reproduction, early sexual maturity and small multiple clutches as described by Tinkle et al. (1970) and Dunham et al. (1988).

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