

**REPRODUCTION OF *TROPIDURUS MONTANUS* RODRIGUES, 1987
(TROPIDURIDAE), A LIZARD FROM A SEASONAL HABITAT OF SOUTH-
EASTERN BRAZIL, AND A COMPARISON WITH OTHER *TROPIDURUS* SPECIES**

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The reproductive and fat body cycles of the lizard *Tropidurus montanus* (Tropiduridae) were studied in a seasonal, open habitat at Minas Gerais State, south-eastern Brazil. Lizards were sampled monthly from June 1996 to June 1997. Reproductive females were found from August to January. The smallest reproductive female was 56.5 mm in body size, and was collected in December. Mean clutch size (± 1 SD), based on counts of eggs or follicles, was 3.48 ± 1.15 , and was significantly related to female body size. Reproductive males were found throughout the year, but their frequency of occurrence varied greatly between months. The smallest reproductive male had a SVL of 60.6 mm, and was collected in August. For both sexes, fat-body mass (adjusted for body length) was greatest during the non-reproductive season.

Key words: lizards, reproduction, seasonality, south-eastern Brazil, *Tropidurus*

INTRODUCTION

A wide variety of reproductive strategies is known within lizards, and a major distinction between temperate and tropical species has been made concerning reproductive patterns (Tinkle *et al.*, 1970). According to this generalization, reproduction of temperate species is seasonal and mainly affected by temperature and photoperiod (Tinkle *et al.*, 1970; Licht, 1971), whereas in tropical lizards reproduction is considered to be aseasonal (Tinkle *et al.*, 1970; Benabib, 1994). However, such a broad generalization differentiating between temperate and tropical species no longer explains the diversity of reproductive patterns found in lizards. This is mainly because reproduction of many tropical species is now known to be related to seasonal changes in temperature, rainfall, humidity or ultraviolet light (Sexton *et al.*, 1971; Magnusson, 1987; Rocha, 1992; Clerke & Alford, 1993; Wiederhecker, 1999). Sherbrooke (1975) went a step further, and grouped the reproductive tactics of tropical lizards into three main categories: (1) continuous reproduction; (2) continuous with variation in reproductive activity; and (3) non-continuous. Vitt & Goldberg (1983) stated that a single reproductive pattern for tropical lizards was, thus far, not evident, and the actual determinants of seasonality in tropical lizards remain unclear (Vitt, 1992).

Evolutionary history has an overriding effect on most lizard life history traits, including reproduction, especially when considering higher taxonomic levels

(Dunham & Miles, 1985; Dunham *et al.*, 1988; Miles & Dunham, 1992). Vitt (1992) analysed the reproductive characteristics of lizards in different Brazilian sites and observed a diversity of reproductive strategies among species within single localities. He argued that if the environment was the main cause of variation, sympatric species would be expected to be more similar in their reproductive characteristics than different populations of the same species, whereas evolutionary history seemed to have a stronger influence. Nevertheless, while variation in reproductive patterns seems to be affected by evolutionary history, within some species of lizards variation exists that might be attributed to the local environment. For example, Colli (1991) and Vitt & Colli (1994) found that for the tropical lizard *Ameiva ameiva* (Teiidae) some life history characteristics differ among different populations, including the relationship between female body size, clutch size and the length of the reproductive season. These differences were mainly attributed to differences in predictability of rainfall, indicating that local environmental factors may also affect reproduction in tropical lizards.

Abdominal fat bodies are important lipid storage organs in lizards and exhibit a seasonal cycle in many species (Derickson, 1976). These cycles tend to be inversely related to reproductive cycles because lipid stored in fat bodies is used for reproduction (Derickson, 1976; Guillette & Casas-Andreu, 1981; Vitt & Cooper, 1985). In females, fat bodies may be used during vitellogenesis, and in males they can be used for sperm production or courtship behaviour (Guillette & Sullivan, 1985; Benabib, 1994). Although recognizing that the relationship between reproduction and fat bodies should also exist in tropical lizards, Magnusson (1987) proposed it would be weaker for tropical species than for temperate ones.

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The South American genus *Tropidurus* comprises mainly heliophilous, insectivorous lizards, living in open habitats, from semi-arid caatinga to seasonal cerrado, and to mesic lowland forests, where they occupy different microhabitats (Rodrigues, 1988; Vitt, 1993). Because these lizards have broad geographic ranges – and as many as four species may occur in sympatry or syntopy – they are ideal models for the study of variation in reproduction of tropical lizards. In general, when in seasonal habitats, these lizards have non-continuous reproduction with most reproduction occurring during the dry-wet season (*T. spinulosus* – Cruz *et al.*, 1997; *T. etheridgei* – Cruz, 1997; Cruz *et al.*, 1998; *T. itambere* – Van Sluys, 1993; *T. nanuzae* – Galdino, 2000; *T. torquatus* – Wiederhecker, 1999; *T. hispidus* – Prieto *et al.*, 1976), or dry season [*T.* (formerly *Platynotus*) *semitaeniatus* – Vitt & Goldberg, 1983]. Possible exceptions may be *T. torquatus*, at a coastal area in Espírito Santo State (south-eastern Brazil) where, despite seasonality in rainfall, females carrying oviductal eggs were found throughout the year (Teixeira & Giovanelli, 1999), and *T. hispidus* (formerly *T. torquatus*), at a seasonal habitat in north-eastern Brazil, which has an extended reproductive season lasting 11 months (Vitt & Goldberg, 1983).

Tropidurus montanus Rodrigues, 1987 is a medium-sized tropidurid endemic to the mountainous region of the Espinhaço mountain range, east of Minas Gerais State, south-eastern Brazil (Rodrigues, 1987). We studied the reproductive cycle of *T. montanus* in a seasonal habitat, specifically addressing the following questions: (1) do male and female *T. montanus* have seasonal or continuous reproduction; (2) to what extent is reproduction correlated with environmental variables such as temperature, rainfall and photoperiod; (3) what is the relationship between female body size and clutch size; and (4) how are fat body cycle and reproduction related? In addition, we compared the reproductive cycle of *T. montanus* with that of other *Tropidurus* species from different habitats.

MATERIAL AND METHODS

STUDY AREA AND CLIMATE

The study was carried out at a site in Serra do Cipó (19° 12'S/43° 27'W, 1260 m above sea level), at the southern portion of the Espinhaço mountain range, Minas Gerais state, eastern Brazil, near a stream called "Chapéu de Sol". The Espinhaço mountain chain ranges parallel to the eastern Brazilian coast, from 20°35'S to 11°11'S. In general, this mountain chain is characterized by quartzitic and arenitic outcrops (Giulietti *et al.*, 1987). At Serra do Cipó, the plant cover is diverse, and above 1000 m there is a predominance of grassy and herbaceous species (mainly Gramineae, Compositae, Melastomataceae, Eriocaulaceae, and Velloziaceae – Giulietti *et al.*, 1987).

The climate is highly seasonal, with warm and wet summers and dry winters (Giulietti *et al.*, 1987). The

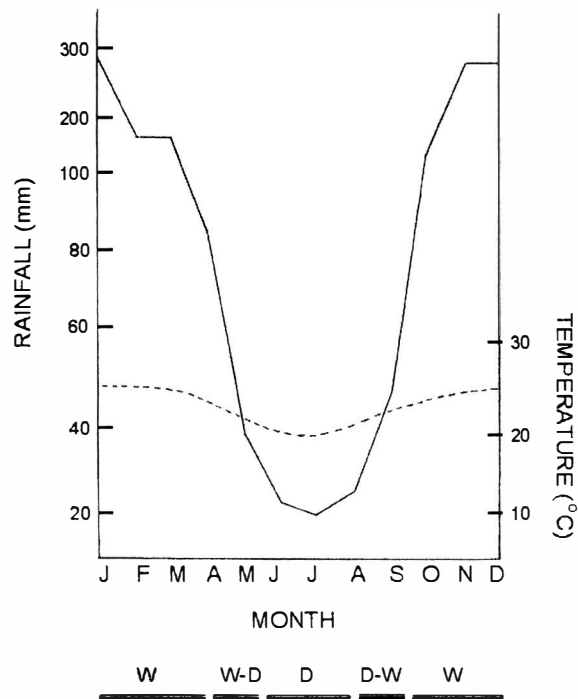


FIG. 1. Mean (1971-1990) monthly rainfall (in mm) and temperature (in °C) for Santana do Riacho, close to Serra do Cipó, Minas Gerais. The continuous line represents rainfall and the dashed line represents temperature. Bars below graph indicate the wet (W), dry (D) and transition (W-D and D-W) seasons.

dry season lasts from May to September and the wet season, from October to April (Fig. 1). Between 1971 and 1990 the mean annual rainfall in the area was 1540 mm and annual mean air temperature was 20.8 °C.

COLLECTING METHODS AND ANALYSIS

We collected lizards ($n=138$ females, 187 males) monthly from June 1996 to June 1997, using a noose or by hand. We measured each lizard's snout-vent length (SVL) to the nearest 0.1 mm, using a vernier caliper. We weighed each lizard with a Pesola spring scale (precision 0.2 or 0.5 g). The lizards were anaesthetized and killed in the field and were subsequently fixed in 10% formalin. Voucher specimens are deposited at the scientific collection of the Ecology Department, UERJ.

We assessed the reproductive status of each female lizard on the basis of vitellogenic follicles, oviductal eggs and/or corpora lutea. Follicles were considered vitellogenic when they were yellow and bigger than 3 mm in diameter (Van Sluys, 1993). We estimated clutch size, based on the number of vitellogenic follicles or oviductal eggs. The simultaneous presence of vitellogenic follicles and oviductal eggs was considered as evidence of the production of at least two clutches by that female in a single reproductive season. When there was any evidence of the production of more than one clutch, we considered only the number of oviductal eggs for the estimation of clutch size of that female. Relative clutch mass (RCM) was determined by dividing clutch

wet mass (preserved) by total mass (fresh clutch + body) (Vitt & Price, 1982).

For males, we measured the width and length of the testes to the nearest 0.1 mm using a digital caliper and estimated their volumes by using the formula for an ellipsoid, ($V = 4/3\pi ab^2$) (Mayhew, 1963; Van Sluys, 1993), where $a = 1/2$ of longest diameter and $b = 1/2$ of the smallest diameter. Left testis and the attached epididymes were removed, dehydrated, embedded in paraffin, sectioned at 5 mm, mounted on slides, and stained with haematoxylin-eosin. Males were considered to be reproductive when they had spermatozoa in either the testes or epididymes. In addition, we measured the height of the germinal epithelium (HGE) and the diameter of the seminiferous tubules (DST) with an ocular micrometer to analyse reproductive activity in the testes. These measurements were taken in 10 different tubules and their means were used for statistical analysis.

Both abdominal fat bodies were removed and weighed on an electronic balance to the nearest 1 mg. The combined mass of fat bodies was log-transformed and subjected to linear regression on SVL; the residuals of this relationship were used as measures of fat body mass adjusted for lizard body size and were used in further statistical analysis.

The relationships between the proportions (arcsine transformed) of reproductive males and females and photoperiod, monthly rainfall and mean monthly temperature averaged over a 20-year period (1971-1990, long term rainfall – LT), and with a one-month time lag (short term rainfall – ST), were explored using linear regression analysis (Zar, 1999). The additive effect of these variables on reproduction was tested using multiple regression.

Testis measures (log-transformed testis volume, HGE and DST) were related to body size and, in the case of a significant relationship, the residuals were used in subsequent statistical analysis. In the figures we present all data, following Magnusson (2000).

RESULTS

Sampled males ranged in SVL from 30.5 to 98.0 mm, and females, from 39.0 to 82.6 mm. Adult males were significantly larger (mean ± SD: 78.1±10.51 mm, $n=129$) than adult females (69.79±6.61 mm, $n=114$; $t=7.28$, $df=241$, $P<0.001$; Fig. 2).

We found reproductive females from August (39%) to January (94%; Fig. 3a). Females with vitellogenic follicles occurred from August to January, and oviductal eggs were found from October to January (Fig. 3a). In February 1997, two females out of eleven (18.2%) contained only corpora lutea; the others showed no evidence of reproductive activity. The smallest reproductive female was 56.5 mm in SVL, and was collected in December. We found four females (9.1%) with vitellogenic follicles and oviductal eggs, simultaneously, and they were collected in November and December, suggesting that at least two clutches may be produced by individual females during a reproductive

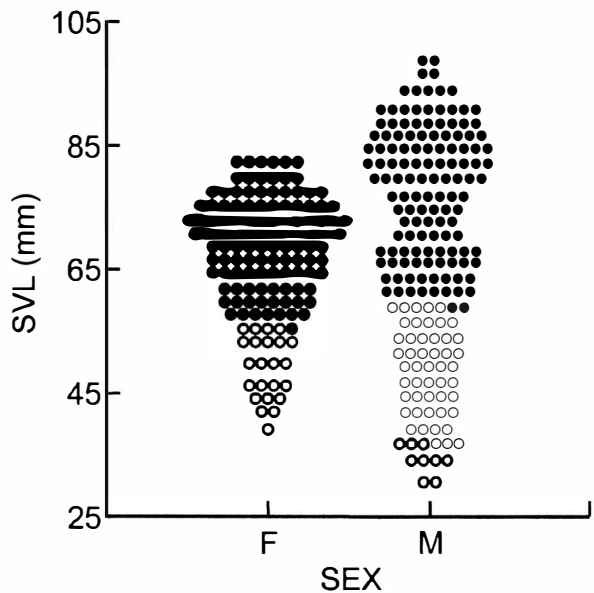


FIG. 2. Size distribution of male and female *Tropidurus montanus* at Serra do Cipó, Minas Gerais. Open circles represent juveniles and closed circles represent adults.

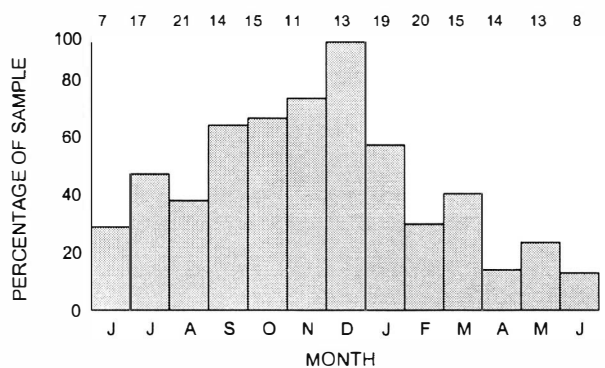
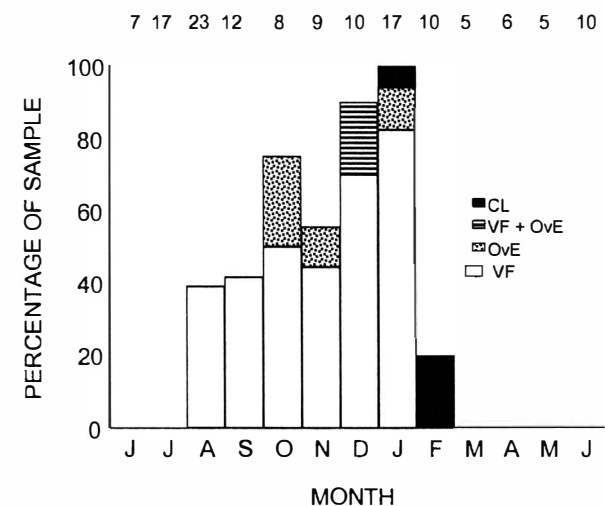


FIG. 3. Monthly percentages of reproductive *Tropidurus montanus* at Serra do Cipó, Minas Gerais, from June 1996 to June 1997: a) females and b) males. Numbers above each bar represent sample size. VF = vitellogenic follicles; OvE = oviductal eggs; CL = corpora lutea; VF + OvE = vitellogenic follicles and oviductal eggs.

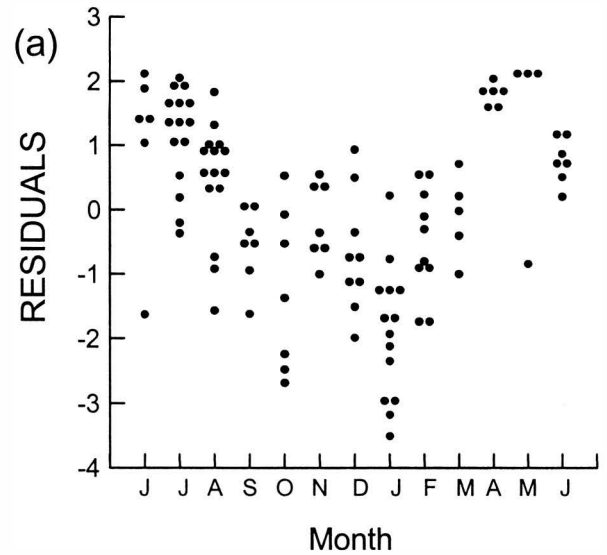
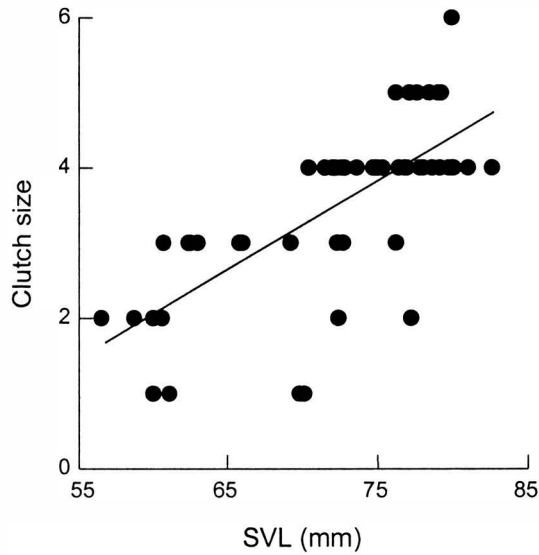


FIG. 4. Relationship between clutch size and female body size (SVL) of *Tropidurus montanus* at Serra do Cipó, Minas Gerais. Numbers beside graph represent sample size.

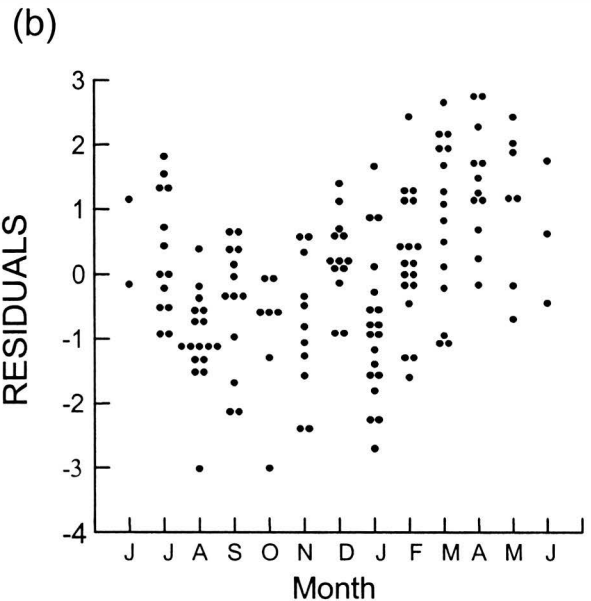
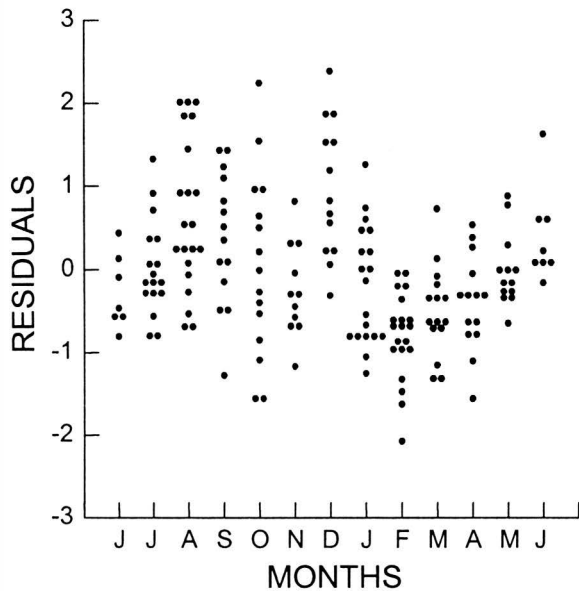


FIG 5. Monthly variation in size-adjusted testes volume in *Tropidurus montanus* at Serra do Cipó, Minas Gerais, from June 1996 to June 1997.

FIG. 6. Variation in size-adjusted abdominal fat-body mass of *Tropidurus montanus* at Serra do Cipó, Minas Gerais, from June 1996 to June 1997: (a) females; (b) males.

TABLE 1. Statistical results of the relationships between photoperiod, long term (LT) rain and temperature (1971-1990), and short term rain and temperature with one month time-lag (ST), and the frequency (arc-sin transformed) of reproductive male and female *Tropidurus montanus* at Serra do Cipó, south-east Brazil.

Environmental variable	Males			Females		
	R^2	F	P	R^2	F	P
Photoperiod	0.53	12.571	0.005	0.54	12.988	0.004
LT rain	0.42	7.909	0.017	0.42	7.930	0.017
LT temperature	0.21	2.880	0.118	0.23	3.206	0.101
ST rain	0.12	1.351	.272	0.17	2.051	0.183
ST temperature	0.06	0.688	0.426	0.05	0.524	0.486

season. Mean \pm SD clutch size (based on counts of follicles or eggs) was 3.48 ± 1.15 (range: 1-6, $n = 52$), and was significantly related to female body size ($R^2 = 0.50$; $F_{1,50} = 50.2$; $P < 0.01$; Fig. 4). The mean relative clutch mass was $0.050 (\pm 0.043, n=20)$.

Reproductive males were found throughout the year, but the proportion varied among months (Fig. 3b). From September to January, the proportion of males in reproductive condition rose and from January the proportion declined. In December, 92.3% ($n=13$) of the males had spermatozoa in either the testis or epididymes (Fig. 3b). The smallest reproductive male had a SVL of 60.6 mm, and was collected in August. In February and April, four (11.8%) large adult males (SVL > 83 mm) had no spermatozoa in either the testis or epididymes.

Size-adjusted testis volume varied during the year, being largest between September and December (Fig. 5), the period with the highest proportion of reproductive males. Size-adjusted DST and HGE varied similarly and testis volume was significantly correlated with both measures (testis volume vs DST: $r=0.92$; testis volume vs HGE: $r=0.91$ and $P < 0.001$, for both correlations). After December, all values of these measures decreased considerably.

The monthly proportions of males and females in reproductive condition were significantly correlated with photoperiod and long-term monthly means of rainfall, but not with monthly means of temperature (Table 1).

For both males and females, size-adjusted fat-body mass varied similarly during the year. Fat bodies of both sexes increased in mass rapidly before the onset of the reproductive season and subsequently decreased during the reproductive season (Fig. 6). The variation in fat body mass appeared to be greater in females than in males.

DISCUSSION

Reproduction in *T. montanus* at Serra do Cipó is seasonal, starting during the middle of the dry season and lasting until the middle of the wet season (February). Females seem to have a more pronounced reproductive cycle than males, and from February to July we found no reproductive females. During every month some males were in reproductive condition (i.e. producing sperm). The proportion of sperm-producing males varied, being higher during the wet season, at the same time when there were reproductive females. The fact that some large adult (mature) lizards had no spermatozoa in either testis or epididymes in the months after the reproductive season (February and April) suggests they were post-reproductive and that there may be a period of time when individual males are reproductively quiescent. The exact significance of the presence of reproductive males during all months of the year is not clear, but may be due to high levels of sexual hormones in the blood. As suggested by Wiederhecker (1999) for *T. torquatus*, this may affect those aggressive behaviours that might be important for territory maintenance.

The time interval between the first female found with vitellogenic follicles (August) and the first female found with oviductal eggs (October) were found suggests that two months are required to produce a clutch.

At the study site, arthropod availability is highly seasonal, being rather greater during the wet season than during the dry season (Kiefer, 1998). Thus, when young lizards hatch, environmental conditions are propitious, with more food enabling them to grow quickly and reach a body size at which they are less vulnerable to predators (Vrcibradic & Rocha, 1998). In addition, because moisture is a critical factor for egg survival (Wiederhecker, 1999), females laying eggs during the wet season may enhance their reproductive success by reducing losses caused by desiccation.

In *T. montanus* fat-body mass increased during the dry season, and the greatest values were recorded during this time. Guillette & Casas-Andreu (1981) stressed the importance of food availability on fat-body mass in tropical lizards, arguing that supplementary feeding increases fat body size. At our study site, Kiefer (1998) found some seasonal variation in arthropod availability, which was lower during the dry season (June to August), but the fat body cycles indicate there is enough food for adults to increase their lipid levels during the dry season. Our data suggest that the seasonal cycle in fat-body mass of *T. montanus* at Serra do Cipó is inversely related to the gonadal cycle of both males and females, as is known for many other lizard species (e.g. Derickson, 1976; Vitt & Cooper, 1985; Benabib, 1994; van Wyk, 1994; Van Sluys, 1998; Vrcibradic & Rocha, 1998). Vitellogenesis starts during the dry season, when food availability is lower, suggesting that females rely heavily on lipid stored in their abdominal fat bodies. However, as the proportion of females producing more than one clutch was low, it is not clear whether they rely on food for the production of this second clutch, as suggested by Benabib (1994) for *Sceloporus variabilis*, and Wiederhecker (1999) for *Tropidurus torquatus*. The lowest values of fat-body mass were observed during the wet season, when food availability is greatest (Kiefer, 1998), suggesting that lipid depletion was due to its utilization for gonad maturation and reproduction. The difference between male and female fat body cycles may reflect a higher cost of reproduction for females (e.g. Vrcibradic & Rocha, 1998 and included references). The dynamics of seasonal energy storage in males have only been reported for a few species, mostly showing that lipid storage in females is greater than in males (van Wyk, 1994). Yolk deposition during egg production is energetically expensive for female lizards (van Wyk, 1994).

Analysing the reproductive cycle of species in the genus *Tropidurus* for which there are data (16 species, 22 populations; Table 2), we observe a few general patterns. For those species that have been studied for a full year, the reproductive cycle is similar to that found for *T. montanus*, i.e. reproductive males were found

TABLE 2. Reproductive characteristics of *Tropidurus* species used for comparisons with *T. montanus* from Serra do Cipó, Minas Gerais; a, mean, range in parentheses; b, ?, not a year-round study.

Species	Locality	Clutch size ^a	Male reproductive cycle ^b	Female reproductive cycle ^b	Habitat	Source
<i>T. torquatus</i>	Brasília, CW Brazil	6.1 (3-10)	year round	6 months	cerrado	Wiederhecker (1999)
<i>T. torquatus</i>	Guriri, SE Brazil	- (2-4)	—	year round	restinga	Teixeira & Giovanelli (1999)
<i>T. itambere</i>	Valinhos, SE Brazil	3.5 (1-8)	year round	5 months	rock outcrops	Van Sluys (1993)
<i>T. montanus</i>	Serra do Cipó, SE Brazil	3.5 (1-6)	year round	6 months	rock outcrops	This study
<i>T. cf. montanus</i>	Alto do Araguaia, CW Brazil	?	?	?	cerrado	Vitt, (1991a)
<i>T. nanuzae</i>	Serra do Cipó, SE Brazil	2.1 (1-3)	year round	9 months	rock outcrops	Galdino (2000)
<i>T. semitaeniatus</i>	Exu, NE Brazil	2	year round	7 months	caatinga	Vitt & Goldberg (1983)
<i>T. hispidus</i>	Exu, NE Brazil	7.4 (3-14)	year round	year round	caatinga	Vitt & Goldberg (1983)
<i>T. hispidus</i>	Venezuela	5.6 (1-8)	7 months	6 months	thorn forest	Prieto <i>et al.</i> (1976)
<i>T. plica</i>	Amazonian Brazil	2.9 (1-5)	?	?	forest	Vitt (1991b)
<i>T. umbra</i>	Amazonian Brazil	1.9 (1-2)	?	?	forest	Vitt <i>et al.</i> (1997)
<i>T. flaviceps</i>	Ecuador	2	?	?	forest	Vitt & Zani (1996)
<i>T. spinulosus</i>	Sierra Grande, Argentina	5.7 (4-8)	year round	4 months	thorn forest	Martori & Aùn (1994)
<i>T. spinulosus</i>	Alto do Araguaia, CW Brazil	4.0 (3-6)	?	?	cerrado	Vitt (1991a)
<i>T. spinulosus</i>	Salta, Argentina	5.0 (3-7)	3 months	3 months	dry chaco	Cruz <i>et al.</i> (1997)
<i>T. etheridgei</i>	Salta, Argentina	6.2 (3-9)	5 months	5 months	dry chaco	Cruz (1997)
<i>T. etheridgei</i>	Alto do Araguaia, CW Brazil	4.9 (3-7)	?	?	cerrado	Vitt (1991a)
<i>T. etheridgei</i>	Salta, Argentina	5.9 (?-9)	5 months	6 months	dry chaco	Cruz <i>et al.</i> (1998)
<i>Tropidurus</i> sp1	Santa Barbara, N Brazil	3.4 (2-5)	?	?	rock outcrops	Vitt (1993)
<i>Tropidurus</i> sp2	Ariquemes, N Brazil	3.5 (2-4)	?	?	rock outcrops	Vitt (1993)
<i>Tropidurus</i> sp3	Santa Cruz, N Brazil	3.8 (1-5)	?	?	rock outcrops	Vitt (1993)
<i>T. cf. oreadicus</i>	Pará, N Brazil	4.2 (2-6)	?	?	rock outcrops	Vitt (1993)
<i>T. itambere</i>	Pirenópolis, CW Brazil	3.6 (1-8)	?	?	rock outcrops	Faria (2001)
<i>T. oreadicus</i>	Pirenópolis, CW Brazil	3.7 (1-6)	?	?	rock outcrops	Faria (2001)

throughout the year but their proportion varied; whereas reproductive females were found only during part of the year (Table 2). *Tropidurus hispidus* from a caatinga habitat (Exu, Pernambuco), and *T. torquatus* from a restinga area (Espírito Santo) are probably exceptions to that pattern, because reproductive individuals were found for most of the year. For most seasonal species, reproduction occurs from the middle of the dry season to the wet season. The similarity of the reproductive patterns found across species in different habitats, ranging from forests to open-habitats, suggests that there is a general pattern of seasonality in reproduction in *Tropidurus* lizards.

Considering the effect of local environmental variables on the reproductive cycle of *Tropidurus* lizards, only a few comments can be made because for only a few species is there any analysis evaluating the effect local environmental factors may have on reproduction. Only the studies of Wiederhecker (1999), Galdino (2000) and Van Sluys (1993) considered the effect of rainfall, temperature and photoperiod on reproduction of *T. torquatus*, *T. nanuzae* and *T. itambere*, respectively. In these species the reproductive cycle was significantly correlated with seasonality in rainfall and/or variation in photoperiod. However, experiments should be carried out to test whether these factors really cause reproductive seasonality, independent of phylogeny. At present, then, it is difficult to clearly understand the role environmental factors might have on reproduction of *Tropidurus* species.

Clutch size for *T. montanus* was significantly related to female body size, which explained about half of the variation in the former. A significant relationship between clutch size and female body size is a pattern in many open-habitat *Tropidurus* species (Vitt & Goldberg, 1983; Vitt, 1993; Van Sluys, 1993; Cruz, 1997; Cruz *et al.*, 1997; Cruz *et al.*, 1998; Wiederhecker, 1999). However, such a correlation has not been demonstrated for some species/populations (*T. semitaeniatus* – Vitt & Goldberg, 1983; *T. spinulosus* and *T. etheridgei* – Vitt, 1991a; two of the undescribed species from Ariquemes and Santa Cruz – Vitt, 1993; *T. flaviceps* – Vitt & Zani, 1996, and *T. nanuzae* – Galdino, 2000). Rand (1982) found that Amazonian lizards tended to have smaller clutches than similar species in open habitats. However, Vitt & Zani (1996) argue that there seems to be no clear pattern in clutch size between species of forested and open areas. When clutch size is affected by female body size, it may indicate that natural selection would favour larger females, because they would tend to produce larger clutches. However, females might also increase their fitness by laying more clutches during each reproductive season. A relatively constant clutch size and the consequent lack of an effect of female body size on clutch size may be advantageous for habitat-specialists such as the forest-dweller *Tropidurus flaviceps* (Vitt & Zani, 1996) and the crevice-dweller *T. semitaeniatus* (Vitt & Goldberg, 1983) or small-sized species (*T. nanuzae*, Galdino, 2000). Only

about 9% of the females that could potentially bear oviductal eggs (those found from October to January, $n=44$) showed signs of producing more than one clutch per reproductive season and this suggests that *T. montanus* females may enhance their reproductive success by growing fast and not by laying multiple clutches.

Relative clutch mass of *T. montanus* at our study site was similar to that of *T. torquatus* at a cerrado site (mean \pm SD: RCM 0.056 \pm 0.138; Wiederhecker, 1999), but smaller than that found for other *Tropidurus* species both in rainforest (0.11 for *T. flaviceps* – Vitt & Zani, 1996; 0.124 for *T. [formerly Plica] plica* – Vitt, 1991b and 0.154 for *T. umbra* – Vitt, Zani & Ávila-Pires, 1997), and in open areas (Vitt, 1993; Cruz *et al.*, 1997). The difference between *T. montanus* and the congener *T. nanuzae* in RCM (larger in *T. montanus*) and the relationship between clutch size and female body size (not significant for *T. nanuzae* – Galdino, 2000) may be due to the small body size of *T. nanuzae* (mean \pm SD female SVL = 51.6 \pm 4.1mm; Kiefer, 1998). Both species are saxicolous and use rock crevices as shelters. The reason for this difference is still open to testing.

Because of the general patterns found, irrespective of habitat, at this point it seems that reproduction in *Tropidurus* lizards is greatly affected by their evolutionary history. Nevertheless, more detailed studies on reproduction of *Tropidurus* species with broad geographic distributions (e.g. *T. torquatus*, *T. hispidus* and *T. itambere*), and sympatric species, might allow a test of the relative influence of phylogeny and local environmental conditions on reproduction of these lizards.

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