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Reproductive and Fat Body Cycles of the Tegu Lizard, *Tupinambis teguixin,* in the Llanos of Venezuela

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Lizards of the genus *Tupinambis* are large and, in places, common teiids of the tropical and subtropical regions of South America (Vanzolini, 1993). While the taxonomy of the genus is being clarified (Avila-Pires, 1995; Fitzgerald et al., 1999), aspects of their ecology, including reproductive patterns, remain largely unknown. Moreover, many thousands of individuals of two species in the genus, *T. teguixin* and *T. rufescens* are killed for their skins every year in southern South America (Norman, 1987; Fitzgerald, 1994a, b) making them important from a conservation viewpoint.

Adult *Tupinambis teguixin,* often called *T. nigropunctatus* (Avila-Pires, 1995) and known as black or common tegu lizards, weigh 1–2 kg and measure up to one m total length. They can be found in a variety of habitats in tropical South America, east of the Andes (Vanzolini, 1993). They are largely omnivorous, although animal prey, including vertebrate eggs and insect larvae, are preponderant in their diet (Herrera, 1980; Mercolli and Yanosky, 1994). *Tupinambis* appear to hibernate in southern South America (Gallardo, 1970) but they are active throughout the year in the tropical north (pers. obs.). In the Chaco of Argentina, a continental, subtropical dry region, Fitzgerald et al. (1993) found that female *T. rufescens* nested in November, at the beginning of the warm, rainy period. Yanosky and Mercolli (1995) found that *T. teguixin* lays eggs in captivity in late October and November (spring), while Beebe (1945) observed that tegus in northern South America nest several times a year within termite mounds. Beebe (1945), Hoogmoed (1973), and Avila-Pires (1995) described their natural history (some of them as *T. nigropunctatus*). In this paper, we report on the reproductive and fat body cycles of tegu lizards in a seasonal tropical area of northern South America. We also present data on the sexual dimorphism in this species.

This study was carried out on Hato El Frío (7°46′N, 68°57′W), an 80,000-ha cattle ranch located in the Venezuelan seasonally flooded savannas or Llanos. The region is characterized by vast expanses of flat grassland interspersed with patches of woodland. The main climatic feature of the Llanos is the alternation of wet (May–October) and dry (November–April) seasons. During the wet season extensive flooding occurs, while in the dry season most ponds dry up and severe water scarcity is typical of February and March.

Monthly samples of tegus were taken from May 1979 to April 1980. Lizards were collected with a .22 cal. rifle, or trapped in Tomahawk live traps (15 × 15 × 47 cm) mostly along elevated dirt roads throughout the ranch. Each lizard was weighed to the nearest 50 g and its snout-vent length (SVL) recorded to the nearest mm. Only adults of at least 250 mm SVL were used in the analyses (Yanosky and Mercolli, 1991). Each animal was preserved in 10% formalin. Both gonads and abdominal fat bodies were carefully excised and weighed to the nearest 0.01 g. For presentation purposes, gonad and fat body masses were divided by body mass, while ANCOVA was used for statistical comparisons. Statistical tests followed Sokal and Rohlf (1981) and were performed using MINITAB ver. 7.2 (Ryan et al., 1985) and SYSTAT ver. 7.0 (SYSTAT, 1997).

A total of 65 male and 55 female tegus were collected. There was clear sexual dimorphism in size, with males averaging 1263 ± 371 g (N = 58) and females 991 ± 263 g (N = 46; t = 4.20, df = 102, $P <$ 0.0001). Sexual dimorphism was also marked in SVL (males: $\bar{x}$ = 329.4 ± 27.8 mm, N = 64; females: $\bar{x}$ = 310.8 ± 22.4 mm, N = 55; t = 3.96, df = 117, $P <$ 0.0001; note that sample sizes in the analyses vary since difficulties in the field did not allow all data to be recorded for all animals).

Fig. 1 shows how gonadal-somatic indices (GSI: testes mass/body mass) of males increased steadily from the mid-wet season (July) until the beginning of the dry (November), while the females' GSI (ovaries mass/body mass) started peaking later in the wet season (September) reaching a maximum in December. The differences in the monthly values of gonad masses for both males and females are significant (ANCOVA comparing mean gonad masses across months using body mass as covariate: Males, F = 6.68, df = 9,1,44, $P < 0.01$; Females, F = 3.93, df = 10,1,24, $P < 0.01$). In both November and December, one female was found with oviductal eggs, while in January (mid-dry season), two out of six females (body masses not available) were found with 17 and 11 oviductal eggs, weighing 45.2 g and 172.2 g in total, respectively. From January onwards, ovary masses fell to their lowest levels (Fig. 1). These results indicate that egg-laying occurred some time between January and February, i.e., during the middle of the dry season. In fact, on 10 February 1981, a clutch of tegu eggs was found within a tree-borne termite mound, 1.13 m above ground. It contained 15 eggs, only five of which were intact, while the other 10 were rotten. Intact eggs weighed a mean 31.0 ± 2.2 g and measured 45.0 ± 0.5 mm in length.

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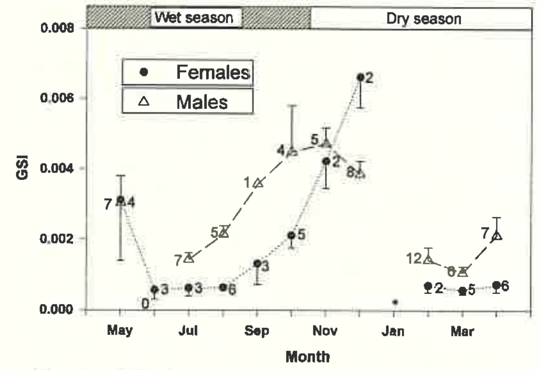

FIG. 1. GSI (Gonad Somatic Index), for tegu lizards collected between May 1979 and April 1980. Female with oviductal eggs are not included in the graphs (see text). Numbers to the left of symbols are male sample size; to the right are females. Bars are standard errors. *No body masses are available for January.

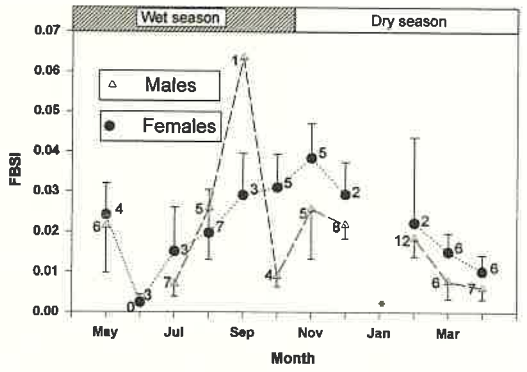

FIG. 2. FBSI (Fat Body Somatic Index), for tegu lizards collected between May 1979 and April 1980. Numbers to the left of symbols are male sample size; to the right are females. Bars are standard errors. *No body masses are available for January.

The females' fat body-somatic indices (FBSI) seem to show a pattern of lipid storage, increasing from the mid wet season (July) until the first dry month (November), while decreasing steadily after that (Fig. 2). The males' FBSI varied widely but no clear pattern was discernible. The monthly means of fat body masses of males are significantly different while the females' differences approach significance (ANCOVA comparing mean fat body masses across months using body mass as covariate: Males, F = 3.43, df = 9,1,44, $P < 0.01$; Females, F = 2.07, df = 10,1,24, $P <$ 0.07).

The pattern described here reflects a clear reproductive cycle represented by an increase in female gonad masses during the wet season with mating and egg-laying apparently occurring in the early to mid-dry season. The males' cycle is one or two months ahead of the females'. In a wetter, less seasonal region in northern South America, Beebe (1945) found "breeding tegus" in April, May, June, and August. In a subtropical region in Argentina, Yanosky and Mercolli (1995) recorded captive female *T. teguixin* laying in late October and November, which is the beginning of the wet spring.

Such reproductive seasonality is not uncommon in the tropics. For instance, Magnusson (1987), who studied the reproductive cycle of the teiids *Ameiva ameiva, Cnemidophorus lemniscatus,* and *Kentropyx striatus* in a seasonal savanna in Brazil, found that all three species reproduce seasonally with most egg-laying occurring in the wet season. Similarly, Colli (1991) found oviductal eggs in *Ameiva ameiva* in a seasonal wooded savanna of Brazil in the last month of the wet season. Rodriguez-Ramirez and Lewis (1991) found a similar pattern for *Cnemidophorus* in Puerto Rico. Cruz et al. (1999) found that a related teiid, *Teius teyou,* from a subtropical region in Argentina (23° South) with markedly seasonal precipitation, reproduced once a year during the wet months. Wikramanayake and Dryden (1988) made the important point that the reproductive pattern of tropical lizards in a seasonal region may be related to their size: a small lizard should lay in the wet season, while a larger animal, having a longer incubation period, could lay in the dry season and have the young born in the wet season. The latter appears to be the case for tegus in the Llanos: laying in the mid-dry season (January-February) with a long incubation period (64 d in artificial incubators according to Yanosky and Mercolli, 1995 but perhaps more than five months according to Avila-Pires, 1995, citing Köhler, 1989) would lead to hatching in the early to mid-wet season. This would certainly be advantageous to the young since the increase in resource availability and vegetation cover would provide them with food and protection from predators. Simmons (1975) found a similar pattern for the relatively large teiid *Ameiva petersii* in a seasonal region of Ecuador. On the other hand, a lack of reproductive seasonality has been reported for the teiid *Cnemidophorus lemniscatus* in northeastern Venezuela (León and Cova, 1973) and *Mabuya striata* in Malawi (Central Africa) (Patterson, 1990), both in seasonal tropical study sites.

The fat body cycle of tegus in the Llanos precedes the reproductive cycle, at least in females, suggesting that fat is being used for egg production (Derickson, 1976). Despite their varied diet (Herrera, 1980; Mercolli and Yanosky, 1994), female tegus appear to take advantage of resources available in the wet season to accumulate reserves for egg production in the dry season. A previous study in the same location showed that field metabolic rate declined significantly at the height of the dry season (March) (Green et al., 1997). Males, by not requiring fat for gamete production, have a more erratic pattern of lipid storage.

Virtually nothing is known at present about the laying behavior of female tegus, except that their eggs are laid in termite mounds, at least in tropical, northern South America (Beebe, 1945; Avila-Pires, 1995 and references therein; Cristina Ramo, pers. comm.; this study). The habit of laying in termite mounds has been reported for no less than 11 lizard species and three snakes (Riley et al., 1985). By laying their eggs in a chamber with constant temperature and humidity, female tegus could have a more predictable incubation time, contributing to the strong seasonality observed, while providing the eggs with protection from predators.

The clutch sizes observed in this study (11–17) are close to those found by Beebe (1945: 4–12) in northern South America but much lower to those reported by authors in Argentina (Serié, 1932: 54 buried eggs) and Southern Brazil (Milstead, 1961: 32 oviductal eggs). However, the former value could be a product of multiple laying, a fact observed in Venezuela (A. Arteaga, pers. comm.). In captivity, Yanosky and Mercolli (1991) found clutches ranging from 24 to 49 ($\bar{x}$ = 30, N = 7). Eggs in southern South America were also somewhat smaller (42 vs. 45 mm in length) and lighter (18.7 g at laying, increasing to 25.6 g after seven weeks, vs. 31.0 g; Yanosky and Mercolli, 1991, 1995). Further, Donadio and Gallardo (1984) noted that clutch size decreases in this species as one approaches the tropics. This suggest that *T. teguixin* in the more temperate southern South America has a markedly different reproductive strategy with a larger number of smaller eggs laid. Perhaps the greater survivorship provided by the habit of laying in termite mounds in the tropical north has favored the reproductive strategy of laying larger and fewer eggs.

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The Pattern of Testicular Activity in the Gecko *Hemidactylus brooki* from India

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Most studies on gekkonid reproductive cycles have described ovarian cycles, age at maturity in females, frequency of reproduction, period of gestation (in viviparous species), and clutch size (e.g., Church, 1962; King, 1977; Pianka and Huey, 1978; Vitt, 1986; Selcer, 1990; Cree and Guillette, 1995). However, information on testicular activity in males is less well documented. Lizards in general exhibit prenuptial spermatogenesis and therefore both female and male gonadal cycles are temporally synchronized. The present study describes the pattern of male reproductive cycle vis-a-vis, changes in spermatogenetic and Leydig cell activity in the common gecko, *Hemidactylus brooki*, for which the ovarian cycle was described recently (Shanbhag et al., 1998).

Specimens of *Hemidactylus brooki* were hand-collected once every two weeks from September 1992–August 1993 in Dharwad, Karnataka State, India (15°27′N, 75°03′E). The monthly mean temperature and rainfall during the study period is given in Fig. 1. A total of 221 male lizards with a mean of 54.12 mm ± 0.47 snout vent length (SVL) and body mass 3.74 g ± 0.11 were used in this study. A day after the collection of lizards, they were autopsied after recording SVL (mm) and body mass (g). The weight (mg) of both the testes was recorded. The testis and epididymis were fixed in Bouin's fluid, embedded in paraffin, sectioned at 6 μm, and stained with hematoxylin-eosin.

In histological sections of the testis, the diameters of the testis, seminiferous tubules, and Leydig cell nucleus were measured as described by Sharma and Shanbhag (1991). Based on the occurrence and density of spermatogenetic cells, the testicular activity was categorized into Four stages: Stage I - with spermato-

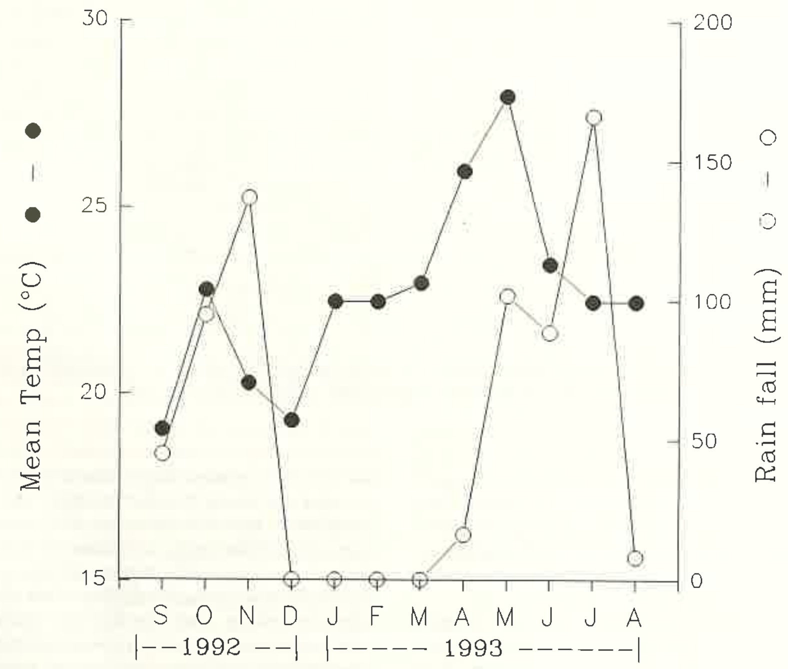

Fig. 1. Monthly mean temperature and rainfall in the study area.