The Reproductive Cycle and the Size at Maturity of *Tupinambis rufescens* (Sauria: Teiidae) in the Dry Chaco of Argentina

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ABSTRACT. — The reproductive patterns of *Tupinambis rufescens* have not been described. The present study had three objectives: (1) to describe the reproductive and fat body cycles of *T. rufescens* from our study site in the dry chaco of Argentina; (2) to elucidate and analyze the distribution of sizes at which female *T. rufescens* reach sexual maturity; and (3) to discuss the conservation implications of the reproductive cycle of *T. rufescens*.

Oviductal width increased significantly after females reached 320 mm SVL, and we presumed the increase was due to stretching of the oviducts in females that had been gravid. Seventy-eight percent of the females >319 mm snout–vent length (SVL) and 84.3% >349 mm SVL possessed oviducts >3.5 mm wide, our criterion for indicating a female had reproduced, while only 6.9% of the females <320 mm SVL had oviducts wider than 3.5 mm. Additionally, all the oviducts >3.5 mm wide were convoluted, while all the narrower oviducts were straight or striated. The reproductive and fat body cycles of *T. rufescens* at our study site were characteristic of lizards from seasonal environments, and appeared closely tied to the onset of the rainy season and increasing spring temperatures. Mature females exhibited significantly longer ovaries in November than in other months, and nesting was observed in November and December. The average clutch size was 21.4, and the smallest female we found with eggs was 330 mm SVL. Testis mass was significantly greater in November than in other months, and declined slightly throughout the activity season. Some gonadal development in males presumably occurred while the lizards were inactive during winter. Fat body volume was tightly linked to the gonadal cycle of both males and females. Females apparently allocated fat stores to developing eggs, while males probably used fat stores for spermatogenesis or for meeting the energetic demands of mate seeking.

Large numbers of *Tupinambis* are exploited for their skins, and this study provides life history information needed to develop scientifically-based management plans, for example, the size distribution of reproductive females, the timing of reproduction, and clutch size. Based on our analyses, management strategies aimed at harvesting adults and subadults could be evaluated because the proportions of the harvest comprised of adults can be reliably determined. We recommend that strategies aimed at classifying harvests according to adults and subadults use 350 mm SVL as a cut-off point for mature females.

RESUMEN. Los patrones reproductivos de *Tupinambis rufescens* no han sido descritos. El presente estudio tuvo tres objetivos: (1) describir los ciclos reproductivos y de cuerpos grasos de *T. rufescens* de nuestro sitio de estudio en el chaco semiárido de Argentina; (2) determinar y analizar la distribución de tamaños a los cuales las hembras de *T. rufescens* llegan a la madurez sexual; y (3) discutir las implicaciones de manejo que tienen ciclos reproductivos de *T. rufescens*.

El ancho del oviducto aumentó significativamente en hembras >320 mm largo hocico-ano (LHA), supuestamente debido al estiramiento de los oviductos en hembras que fueron grávidas. Setenta y ocho porciento de las hembras >319 mm LHA y 84.3% >349 mm LHA tuvieron oviductos >3.5 mm, nuestro criterio para indicar que una hembra se ha reproducido, mientras solo 6.8% de las hembras <320 mm LHA tuvieron oviductos >3.5 mm. Los ciclos reproductivos y de cuerpos grasos de *T. rufescens* en nuestro sitio de estudio fueron tipicos de lagartos de ambientes estacionales, correlacionados con el comienzo de la época lluviosa y al aumento de las temperaturas durante la primavera. Las hembras maduras mostraron ovarios significativamente mas largos en noviembre que en los otros meses, y la nidificación fue mayor en noviembre y diciembre. El tamaño de postura promedio fue 21.4 y la hembra mas pequeña que encontramos con huevos medió 330 mm LHA. El peso testicular fue significativamente mayor en noviembre, y desminuyó durante diciembre hasta marzo. Aparentemente ocurrió desarrollo gonadal en machos durante el periodo de inactividad de los lagartos en el invierno. El volumen de cuerpos grasos se encuentra estrechamente vinculado al ciclo gonadal de machos y hembras. Las hembras aparentemente asignaron las reservas grasas al desarrollo de los huevos, mientras los machos probablemente usaron la grasa para espermiogenesis o para alcanzar las demandas energéticas de buscar pareja.

Grandes números de *Tupinambis* son explotados debido a su piel, y este estudio provee información necesaria para desarrollar modelos de manejo racional, por ejemplo la distribución de tamaño de hembras reproductivas, el periodo de reproducción y el tamaño de postura. Recomendamos que estratégias de manejo con el objeto de cosechar adultos y subadultos usan 350 mm LHA como limite para clasificar hembras maduras.

Although a large body of literature exists on the reproductive cycles of both temperate and tropical lizards (Duvall et al., 1982), the reproductive cycle of the South American teiid lizard *Tupinambis rufescens* has not been described. Seasonal reproduction is a common pattern observed in lizards, but different hypotheses have been put forth to explain the onset of reproduction in tropical and temperate forms (Fitch, 1970; Duvall et al., 1982). Increasing temperatures have been hypothesized as the proximate trigger for reproduction in temperate forms, while increasing rainfall is presumably the most common proximate cue for reproduction in lizards from the seasonal tropics. These patterns are far from definite however, and interesting exceptions to these generalizations have been documented for both temperate and tropical lizards (Vitt and Goldberg, 1983; Saint Girons, 1984; Vitt, 1986; Guillette and Casas-Andreu, 1987). In this regard, we were interested in how the reproductive cycle of *T. rufescens* compares to that of other lizard species from temperate, seasonal tropical, or subtropical environments.

Fat stores are associated with gonadal and ovarian follicle development in many lizards (Hahn and Tinkle, 1965; Fitch, 1970; Derickson, 1976; Fox, 1977), but Magnusson (1987) concluded that seasonal changes in fat stores of three Amazonian teiids were not closely linked to the species' reproductive cycles. Similarly, changes in the volume of fat bodies of female *Ameiva ameiva* in Amazonian Ecuador were not associated with ovarian follicle development (Simmons, 1975). One objective of this study was to describe the relationship between fat body cycles and the reproductive cycle of *T. rufescens*. *Tupinambis* accumulate fat in their tails as well as in abdominal fat bodies, and we tested the hypothesis that the circumference of the tail would track the reproductive cycle. If fat stores in the tail tracked the reproductive cycle, then monitoring tail circumferences of samples of individuals would be an easy and useful technique for assaying the reproductive condition of live individuals.

Age and size are poorly correlated in *T. rufescens* (Quintana, 1991) and, as Zug and Rand (1987) suggested for *Iguana iguana*, size may be more important than age in determining when individuals are able to reproduce. Not all females reach maturity at the same size, and the minimum recorded size of reproduction may be of limited value in understanding demographic processes if relatively few females reach maturity near the minimum size. Of greater interest and application is the variation in size at first reproduction. Herein, we elucidate and analyze the distribution of sizes at which female *T. rufescens* reach sexual maturity.

Descriptions of reproductive patterns in *Tupinambis* are important for practical reasons. About two million individuals of *T. rufescens* and *T. teguixin* are exploited annually for their skins (Hemley, 1984; Norman, 1987; Luxmoore et al., 1988; Fitzgerald et al., 1991), and the government of Argentina is developing management strategies in an attempt to insure the conservation and rational use of *Tupinambis* species. The size at maturity, clutch size, and breeding phenology are life history traits that have direct bearing on population growth (Dunham et al., 1988), and measurements of these traits need to be incorporated into management models.

METHODS

Field work was carried out in the vicinity of Joaquin V. Gonzalez, Salta, Argentina (25°S latitude; 64°30'W longitude), on the property of a forestry and charcoal operation, Salta Forestal, S.A. and a large ranch, Campos del Norte, during November through March in 1988–1989. The region was characterized by distinct rainy and dry seasons, with rains typically beginning in November and continuing through the warm months until March. Very little, and often no rain falls between May and September. The average annual rainfall during the 54 year period between 1935 and 1988 and 553 mm, and the wettest year was 1987, when a total of 957 mm of rain fell. Average maximum monthly temperatures between 1935 and 1988 were always >38 C, and were >44.5 C between October and February. Although daily maximum temperatures can be high, frosts can occur between May and September. The landscape of the area was a mosaic of botanically complex thorn forest influenced by grazing, farming, and logging (Saravia Toledo, 1988). The vegetation at these study sites has been well-described elsewhere (Bucher, 1982; Saravia Toledo, 1988). *Tupinambis rufescens* was the only *Tupinambis* species at the study site.

Specimens of *T. rufescens* were collected by hunters, who saved the skinned carcasses in buckets of 10% formalhyde solution. We vis-

ited the hunters on a regular basis to take the carcasses they had stored and to replenish the formaldehyde solution. Although the animals had been skinned, we were still able to measure snout–vent length (SVL) from the tip of the rostrum to the cloacal slit with a flexible tape to the nearest 1.0 mm. We also measured the circumference of the base of the tail (TC), which was skinned. Length, width, mass, and volume were measured for testes, ovaries, and fat bodies, as was the width of the oviducts. Volumes were determined by water displacement in a graduated cylinder to the nearest 1.0 ml, linear measurements were measured with a vernier caliper to the nearest 0.1 mm, and mass was measured to the nearest 0.1 g on a triple beam balance. To minimize observer induced variance, only one of us (FBC) made the measurements. These variables were examined graphically, and four were finally chosen for statistical analyses: testis mass (TM), ovary length (LO), oviductal width (OW), and fat body volume (FBV). We classified the condition of the oviducts (CO) according to three categories: smooth, striated, or convoluted. Smooth oviducts were straight, without visible signs of thickening or stretching. Striated oviducts were straight, but with obvious transverse striations along the entire oviduct. Convoluted oviducts were convoluted along their entire length with thickened walls. The oviducts were classified and measured separately at different times, on separate data sheets, and in random order. Data from the left gonad or fat body was used for analyses, except in a few cases where the left tract was missing or damaged.

The samples were divided into six SVL groups for some ANOVAs: Group I <260 mm; Group II = 260–289 mm; Group III = 290–319 mm; Group IV = 320–349 mm; Group V = 350–379; and Group VI >380 mm. The data were square-root transformed when necessary to homogenize group variances and ensure they conformed to the assumptions of the model being applied. For some analyses, the effects of SVL were removed with ANCOVAs when slopes among groups were homogenous at the $P > 0.05$ alpha level. Student Newman-Keuls multiple comparisons tests of sample means followed ANOVAs, and comparisons of least-square means followed ANCOVAs when appropriate (SAS Institute, 1985; Pimentel and Smith, 1990).

RESULTS AND DISCUSSION

Characteristics of the Population.—*Tupinambis rufescens* exhibits sexual size dimorphism, with males attaining larger sizes than females (Quintana, 1991). In the total sample, males averaged 347.9 mm SVL (N = 158, SD = 69.93), compared to 326.3 mm SVL for females (N = 138, SD = 51.09). Only 5.1% (7) of the females were >400 mm SVL, compared to 19.6% (31) of the males (Fig. 1).

Significantly more males then females were collected in November than in other months, and they were larger than males taken in other months (Sex ratio analysis: N = 38, χ^2 = 11.61, $P < 0.01$; Size analysis: N = 158, df = 4,153, F = 6.96, $P < 0.0001$). This pattern apparently resulted from increased vulnerability of large male *T. rufescens* to hunters during the spring breeding period, perhaps due to increased activity of males seeking mates (Fitzgerald et al., 1991).

Reproductive Size of Females and Clutch Size.—The mean length of females with eggs was 358 mm SVL (N = 10, SD = 25.62) and the smallest was 330 mm SVL, smaller than the minimum size of 350 mm SVL reported by Quintana (1991). The mean clutch size was 21.4 (N = 10, SD = 4.95), close to the average reported by O. E. Donadio (pers. comm.) from J. V. Gonzalez.

Even within our small sample, clutch size was correlated with SVL. When we removed one outlier from the data set the relationship was statistically significant (N = 7, df = 5, Spearman's R = 0.7500, t = 2.535, P = 0.0516), although with the outlier included it was not (N = 8, df = 6, Spearman's R = 0.5714, T = 1.7056, P = 0.1369). It is likely that a stronger pattern will emerge when larger sample sizes are available.

These data provided a baseline, but we were interested in determining the proportions of females of different sizes that had reproduced. To approach this question, we examined the relationship between OW, CO, and SVL. We hypothesized that immature females should exhibit narrower, straighter oviducts compared to females that had reproduced, because the oviducts of females that had contained eggs should be wider and convoluted from being stretched and due to physiological changes of the oviduct. Permanent changes in oviductal characteristics after puberty have been documented in at least one other lizard species; once female *Uma scoparia* developed convoluted oviducts, they remained so throughout life (Mayhew, 1966).

Results confirmed that OW was wider in large females. To illustrate the discontinuity in OW according to SVL, we plotted the running mean and variance of OW against the running mean of SVL (Fig. 2A). To make the plot we ranked the sample by SVL from low to high, and calculated the mean and variance for the smallest 10 individuals, then for individuals 2 to 11, 3 to 12, 4 to 13, . . . (n − 10) to n. Oviductal width was consistently small for individuals <320 mm
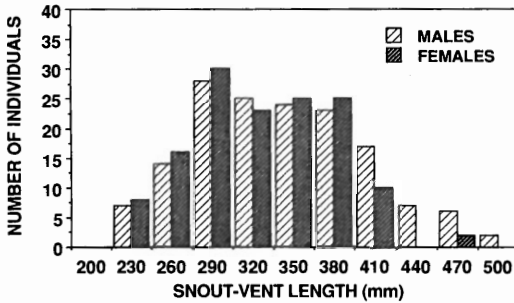
FIG. 1. Size frequency distributions for male and female *Tupinambis rufescens* collected by hunters during 1988–1989.

FIG. 2. (A) Running mean and variance of OW vs. running mean of SVL; (B) scattergram of OW vs. SVL, plotted according to the condition of the oviducts.

SVL, but increased abruptly in larger individuals (Fig. 2). Both measures, especially the variance, fluctuated more in females >319 mm SVL, probably because of additional variation associated with the reproductive cycle of mature females (see below).

The width of the oviducts varied significantly according to the six size groups (N = 136, df = 5,130, F = 28.00, P < 0.0001). Multiple comparisons tests at the 0.05 confidence level reflected the increase in OW in individuals >319 mm SVL; OW among Groups I, II, and III did not differ statistically, but was significantly narrower than in groups IV, V, and VI. Groups IV, V, and VI were not distinguished by the comparisons.

There was a direct correspondence between OW and CO (Fig. 2B). All the convoluted oviducts were >3.5 mm, whereas none of the smooth or striated oviducts were >3.3 mm. Smooth and striated oviducts ranged in width from 0.5 to 3.0 mm and from 1.0 to 3.3 mm, respectively.

We presumed the increase in OW was due to stretching of the oviducts in mature females that had been gravid, and thus considered the discontinuity in OW at 3.5 mm (midway between 1.9 and 5.1, the nearest raw means in the distinct size groups) a good indicator that a given female had reproduced. Based on that criterion, 78.2% of the females in this population >319 mm SVL, and 84.3% of those >349 mm SVL, had reproduced. Four females <320 mm SVL (6.9%) had oviducts >3.5 mm, and presumably matured at smaller than average sizes. They measured 260, 287, 290, and 310 mm SVL, respectively. Apparently, female *T. rufescens* at our study site rarely reproduced before reaching 300 mm SVL.

Several explanations can account for the observation that some large females had small oviducts (Fig. 2B). Some individuals may not have reached maturity even though they were >319 mm SVL, and others may have grown to repro-
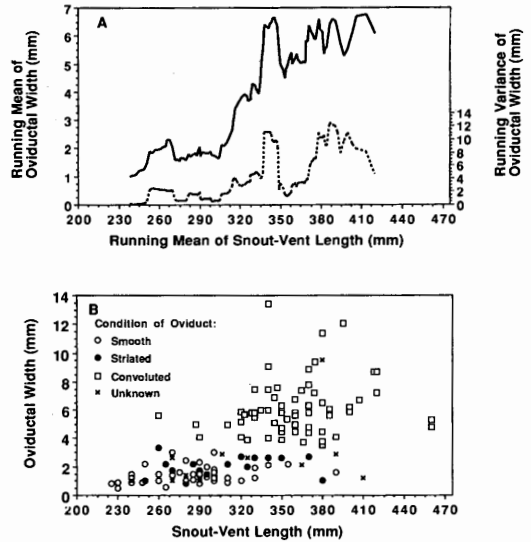
ductive size after the breeding season. Seven of the nine individuals in group IV (320–349 mm SVL) with OW <3.5 mm were collected in January through March, for example, and based on available growth rates, would have been close to or <320 mm SVL during the breeding season (Fitzgerald et al., 1991; Quintana, 1991). Thus it seems likely some of them were virgins, or had never been gravid, when collected. Similarly, four of 28 females in Class V (350–379 mm SVL) had OW <3.5 mm, three of which were also collected in February and March. Finally, it is possible a few females in the sample were sterile, and their oviducts remained small throughout life.

Part of the variation in OW, especially for females >319 mm SVL, was due to their reproductive cycle. Oviducts were significantly wider in November and December than in January through March for individuals >319 mm SVL (ANCOVA: N = 78, df = 4,72, F = 4.27, P = 0.0037; homogeneity of slopes: df = 4,68, F = 0.97, P = 0.4314; Fig. 3A). Variation in OW by sample month for females <320 mm SVL was not significant at the 0.05 level, and the variation did not exhibit a seasonal pattern (the single individual in November was not included in the analysis; ANCOVA: N = 57, df = 3,52, F = 2.38, P = 0.0804; homogeneity of slopes: df = 3,49, F = 0.90, P = 0.4466). Even in March, the adjusted mean OW of females >319 mm SVL was 4.45 mm (SE of adjusted mean = 0.73), evidence that OW does not shrink to within the range of OW of most non-reproductive individuals by the end of the activity season. It is
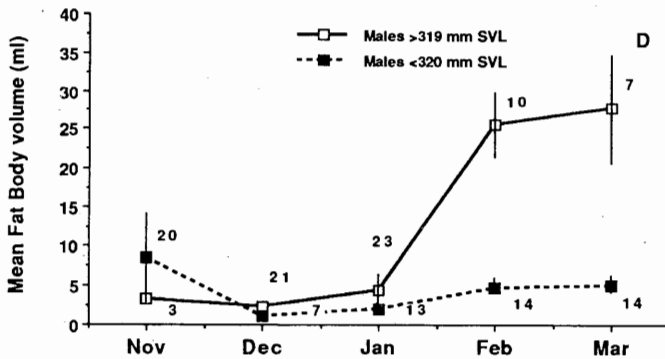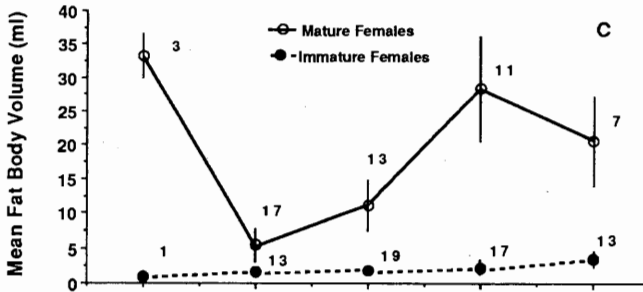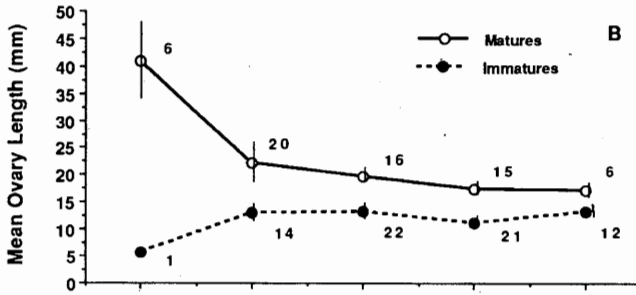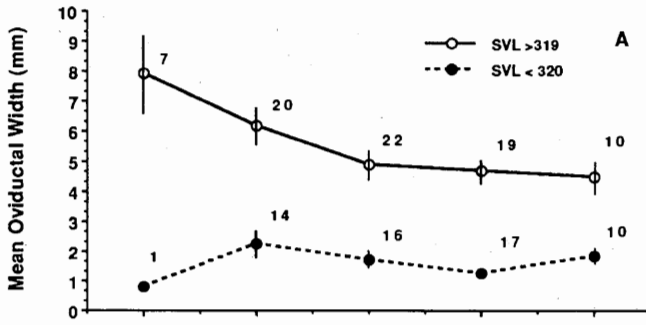
impossible to determine from our data, however, if females' oviducts continue to shrink until the next reproductive period, and to what degree they remain stretched after a female's first clutch.

Female Reproductive Cycle.—The female ovarian cycle was reflected by seasonal changes in LO. Based on the above analyses, we assumed all those females with OW >3.5 mm were mature, and analyzed LO according to immature and mature categories. Mature females exhibited significantly longer ovaries in November than in other months, and LO was not distinct throughout the rest of the season (ANCOVA: $N = 63$, df $= 4,57$, F $= 6.47$, $P < 0.0002$; homogeneity of slopes: df $= 4,53$, F $= 1.71$, $P = 0.1611$; Fig. 3B). There was no significant trend in LO according to sample months for immature females (one individual from November was not included in the analysis. ANCOVA: $N = 69$, df $= 3,64$, F $= 0.987$, $P = 0.6941$; homogeneity of slopes: df $= 3,61$, F $= 1.385$, $P = 0.2549$). Gonadogenesis apparently peaked in November for females, followed by nesting in November and December. Reports from hunters also led us to believe that most females had already nested by early December.

Male Reproductive Cycle.—The data set for males was analyzed according to large and small size classes: individuals >319 mm SVL and those <320 mm SVL (Groups I–III and IV–VI). The seasonal pattern in testis mass was highly cyclical for both large and small males: The mean testis mass in November for large males was 3.45 g ($N = 20$, SD $= 1.48$), and it decreased to 1.20 g ($N = 21$, SD $= 1.53$) in December. Mean TM decreased further through March, when it was only 0.30 g ($N = 7$, SD $= 0.13$). The mean TM for small males in November was 1.25 g ($N = 3$, SD $= 1.18$) and in March it was 0.22 g ($N = 13$, SD $= 0.24$). This variation was distinguished statistically for both large and small males. Testis mass was significantly heavier in November than in the other months, and multiple comparisons did not distinguish TM in December through March (ANOVA for large males: $N = 91$, df $= 4,86$, F $= 29.1795$, $P < 0.00001$; ANOVA for small males: $N = 56$, df $= 4,51$, F $= 10.5635$, $P < 0.00001$). Because the first males collected in spring already had enlarged testes, some gonadal development in *T. rufescens*

probably occurred during the period of inactivity between April and October. This pattern has been documented in a variety of temperate lizard species (Fitch, 1970; Schrank and Ballinger, 1973; Goldberg, 1976; Fox, 1977; Trauth, 1979; Saint Girons, 1984; Abts, 1988).

Fat Body Cycles.—Fat body cycles were tightly linked to the reproductive cycle of both males and females. Fat body volumes varied significantly for mature (OW >3.49 mm) and immature females (OW <3.5 mm) and for large and small males (>319 and <320 mm SVL, respectively), but the pattern was different (Fig. 3C, D) (ANCOVA for mature females: $N = 51$, df $= 4,45$, F $= 4.29$, $P = 0.0050$; homogeneity of slopes: df $= 4,41$, F $= 0.90$, $P = 0.4756$). The adjusted, mean FBVs for mature females in November, February, and March were significantly greater than in December and January, but were not distinct from each other. Fat body volume of mature females decreased rapidly during November and was at its lowest monthly average by December. Immature females had the largest average FBV in March, which was significantly greater than in December, January, and February (ANOVA for immature females [the single individual from November was not included]: $N = 62$, df $= 3,61$, F $= 4.3782$, $P = 0.00769$). Large males, in contrast, had significantly smaller fat bodies in November, December and January than in February and March (Fig. 3D; ANOVA for males >319 mm SVL: $N = 81$, df $= 4,76$, F $= <0.00001$). Small males had the largest mean FBV in November and the smallest FBV in December. The means in November, January, February and March were not distinguishable statistically, however, and overlapped with the mean FBV in December (ANOVA for males <320 mm SVL: $N = 51$, df $= 4,50$, F $= 4.376$, $P = 0.00452$).

There was no statistically significant variation in circumference of the tail (TC) according to month for either large or small males (ANCOVA for large males: $N = 99$, df $= 4,93$, F $= 1.588$, $P = 0.1827$; homogeneity of slopes: df $= 4,89$, F $= 0.366$, $P = 0.8336$; ANCOVA for small males: $N = 56$, df $= 3,51$, F $= 1.132$, $P = 0.3452$; homogeneity of slopes: df $= 3,48$, F $= 0.594$, $P = 0.6260$). Circumference of the tail did vary statistically according to month for mature females. The adjusted mean TC increased grad-

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FIG. 3. Reproductive variables of *Tupinambis rufescens* plotted by sample month. Values are raw means, vertical lines indicate plus or minus 1 standard error, and numbers are sample sizes. (A) Oviduct width according to sample month for females >319 and <320 mm SVL; (B) Length of the ovary according to sample month for mature (OW >3.5 mm) and immature (OW <3.5 mm) females; (C) Fat body volume according to sample month for mature and immature females; (D) Fat body volume according to sample month for large and small males.

ually throughout the season, but the means were not distinguished by the multiple comparisons procedure (ANCOVA for mature females: $N = 64$, df $= 4,58$, F $= 5.028$, $P = 0.0016$; homogeneity of slopes: df $= 4,54$, F $= 0.429$, $P = 0.7895$). Circumference of the tail did not vary statistically according to sample month for immature females (ANOVA for immature females [the single individual from November was not included]: $N = 70$, df $= 3,66$; F $= 0.5592$, $P = 0.6478$). Summarizing, although there was important variation in TC according to sample month for mature females, the hypothesis that TC would track the reproductive condition of the lizards was not supported by these analyses.

Female *T. rufescens*, like many temperate zone lizards, apparently allocated energy stored in fat bodies to developing eggs prior to nesting (Hahn and Tinkle, 1965; Derickson, 1976). The role of fat use by males was difficult to discern, however, because the first males collected in November already exhibited reduced fat bodies. Male FBV was strongly inversely correlated with testis mass, indicating the males may also have allocated fat stores to testicular development and spermatogenesis (Derickson, 1976; Trauth, 1979; Abts, 1988). On the other hand, males are more active than females during the breeding season and are known to compete for mates (Fitzgerald et al., 1991). Hence, fat body stores may have been used more for supplying the energetic demands of mate seeking behaviors than for spermatogenesis.

The reproductive cycle of *T. rufescens* at our study site was characteristic of lizards from seasonal and subtropical environments (Saint Girons, 1984). Fat body cycles were apparently closely linked to gametogenesis, possibly even from males, in contrast to findings from a variety of tropical species (Vitt and Goldberg, 1983; Magnusson, 1987; Wikramanayake and Dryden, 1988). It would be interesting to compare these results to populations of *T. rufescens* at the latitudinal extremes of its range, and to Amazonian Tupinambis, where one may expect FBV to be less closely linked to gonadogenesis.

The onset of reproduction in *T. rufescens* appeared closely tied to the beginning of the rainy season and increasing spring temperatures. But increasing temperatures coincided with the rainy season in the arid chaco, so it was not possible to determine from our data which environmental factor might be the most important for cueing the onset of reproduction. Selection for hatchling growth and survival may also influence when females nest (Stamps and Tanaka, 1981; Snell and Tracy, 1985), further confounding our ability to draw firm conclusions regarding the proximate cues for reproduction in *T. rufescens* in the dry chaco. Research into the trade-offs between reproductive energetics of adults, the chances of survival of hatchlings, and how both are limited by seasonality in the extreme chaco environment would be fruitful.

IMPLICATIONS FOR MANAGEMENT

This study provides a good base for understanding three life history traits of *T. rufescens* that are needed to develop scientifically based management plans; the size distribution of reproducing females, the timing of reproduction, and clutch size. At our study site, an oviductal width >3.5 mm was a good indicator that a given female had reached maturity and reproduced. Additionally, only oviducts >3.5 mm wide were convoluted. Fewer than 7% of the females <320 mm SVL were sexually mature, while 78% of those >319 mm SVL, and nearly 85% of the females >349 mm SVL at our study site had probably laid eggs during their lives. This kind of information is very important for management strategies designed to selectively harvest adults and subadults, because the proportions of the harvest corresponding to adults can be reliably estimated. We recommend that management strategies aimed at classifying harvests according to adults and subadults use 350 mm SVL as a cut-off point for mature females. We warn however that our results are based on only one sample from one locality. Variation in size at maturity may exist over the broad geographic range of *T. rufescens*, and the proportion of females that are mature at a SVL >350 mm SVL at other localities might be smaller or larger than what we found.

Quintana (1991) calculated a growth model with data from wild and captive samples of *T. rufescens*, and based on his equation, it is likely that most *Tupinambis rufescens* in the wild grow to >320 mm SVL by their third birthday. As Quintana (1991) suggested, most females should be ready to reproduce after their fourth winter. Our preliminary data on a closely related species, *T. teguixin*, indicate similar growth rates (Fitzgerald et al., 1991).

Tupinambis rufescens breeds almost exclusively in the spring months of November and December, as evidenced by the advanced reproductive cycles in both sexes when they emerged from hibernation. Harvesting Tupinambis in these months could interfere with normal breeding and nesting behaviors, and ramifications of harvesting and other activities during the breeding season should be considered. Seasonally-based harvest controls may not be feasible, however, given the traditional system of exploitation (Fitzgerald et al., 1991).

Many important questions regarding *Tupinambis* reproductive biology remain that have bearing on the development of life tables and

sustained use models. Longitudinal studies of individual females are required to answer definitively whether or not females reproduce every year. Moreover, it is possible that geographic variation exists in the periodicity of nesting, due to different environmental and biotic influences on *Tupinambis* energetics (Abts, 1988). Females in "favorable" habitats may nest every year, while those in less optimal habitats may be energetically limited in some years and not reproduce. Clutch size probably also varies geographically (O. E. Donadio, pers. comm.). Hence, geographic and temporal variation in reproductive effort would have important effects on local population dynamics. Clearly, these factors should be studied and incorporated into management strategies. Finally, important differences in reproductive biology, especially clutch size, may exist between *T. rufescens* and *T. teguixin*. These questions present formidable research tasks, but because the national and provincial wildlife agencies of Argentina are implementing management plans, and so many captive breeding facilities are coming into operation, data bases may soon become available. Still, many studies over many years will required to construct detailed regional fecundity schedules for each *Tupinambis* species.

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