

Reproductive biology of the false coral snake *Oxyrhopus guibei* (Colubridae) from southeastern Brazil

Lígia Pizzatto¹, Otavio A.V. Marques²

¹ Departamento de Zoologia, Universidade Estadual de Campinas, CP 6109, 13083-970, Campinas, SP, Brazil
e-mail: ligia_oceanica@yahoo.com

² Laboratório de Herpetologia, Instituto Butantan, Av. Vital Brazil, 1500, 05503-900, São Paulo, SP, Brazil
Corresponding author; e-mail: otaviomarques@butantan.gov.br

Abstract. The reproductive biology of the false coral snake, *Oxyrhopus guibei*, was studied through dissection of 496 specimens, combined with observations on captive individuals. Males mature with smaller body size than females, females attain much larger body size, and male-male combat is not expected. Clutch size ranged from 3 to 20, and was correlated with female length. Reproductive cycles in both males and females seem to be continuous, with vitellogenesis and spermatogenesis occurring throughout the year. Reproductive activity in both sexes decreased at the end of the rainy season possibly due to previous intense reproductive activity in more favorable climatic conditions. The smaller number of individuals collected at the end of the rainy season apparently occurs due to the decrease of reproductive activity of this snake.

Introduction

The reproductive biology of tropical snakes is still largely unknown (Fitch, 1982; Seigel and Ford, 1987) and available data are based mostly on observation of captive specimens (e.g. Laporta-Ferreira et al., 1986; Pontes and Di-Bernardo, 1988) and community studies (e.g. Duellman, 1978; Vitt and Vangilder, 1983; Dixon and Soini, 1986). This kind of data is inadequate to characterize reproductive cycles (Fitch, 1982; Marques, 1998). Efforts are being made recently to detail reproductive biology of tropical species (Jordão, 1996; Marques, 1996a,b, 1998; Almeida-Santos and Salomão, 1997; Bizerra, 1998; Fowler et al., 1998; Marques and Puerto, 1998). Even so, these studies are insufficient to generalize on reproductive patterns in tropical snakes due to the high species richness in the tropics.

The false coral snake *Oxyrhopus guibei*, a common species in southeastern Brazil, occurs in forest edges and open areas (Sazima and Abe, 1991; Sazima and Manzani, 1995). It belongs in the monophyletic tribe Pseudoboini that includes seven genera (Zaher, 1994)

of medium-sized snakes, which generally have a "coral-snake" color pattern. *Oxyrhopus guibei* is predominately nocturnal, terrestrial and feeds on rodents and lizards (Sazima and Abe, 1991; Sazima and Haddad, 1992; Andrade and Silvano, 1996), but almost nothing is recorded on its reproductive biology. The present study provides information on size at maturity, sexual dimorphism in size, reproductive cycles in both sexes, fecundity and seasonal activity, and size of newborns.

Material and methods

A total of 496 specimens was examined from the collections of the Instituto Butantan (IB) and the Museu de História Natural da Universidade Estadual de Campinas (ZUEC). The studied specimens came from São Paulo state (19°46'N, 25°16'S, 44°09'E, 53°08'W) southeastern Brazil. This area is covered mainly by open formation, disturbed and cultivated areas. The climate of the area is seasonal with warm and rainy season (October to March) and dry season (April to September) (Nimer, 1989). Mean annual temperature varies between 15 and 24 °C and annual rainfall varies from 1200 to 2100 mm (Nimer, 1989).

The following data were taken from each dissected specimen: (1) snout-vent length (SVL) - to the nearest 1 mm; (2) sex; (3) reproductive condition, recorded as mature or immature (females were considered mature when the diameter of their ovarian follicles was greater than 10 mm or if they had oviductal eggs; males were considered mature if the testes were large and turgid or if the deferent ducts were opaque and convoluted, indicating the presence of sperm - see Shine, 1977a, b); (4) diameter of the largest ovarian follicles or eggs in females (to the nearest 0.1 mm); (5) largest and smallest diameters of testes (testicular volume --- TV --- was estimated using the ellipsoid volume formula $TV = 4/3ab^2$ where a = largest radius, b = smallest radius --- see James and Shine, 1985); (6) deferent duct diameter close to cloaca; (7) presence of prey in the gut.

Data on the period of egg-laying were obtained from gravid females detected by palpation and maintained in captivity. The eggs were incubated in moist vermiculite at room temperature (19.3-31.9 °C). After oviposition, the number of eggs and clutch mass (to the nearest 0.1 g) were recorded. Length and width of eggs was measured to the nearest 0.5 mm. Females were measured and weighed after egg-laying. Clutch size was estimated from number of eggs counted in preserved specimens, laid by captive snakes collected gravid in the wild and records from clutches at IB and ZUEC. The snout-vent length (SVL) and body mass were recorded for neonates. Maximal SVL for newborn individuals was estimated based on the growth of 11 neonates in captivity before the first feeding. All these measurements were made until 72 h after egg-laying and hatching, to be included in the relative clutch mass (RCM --- clutch mass/mother body mass after egg-laying) estimate (Seigel and Fitch, 1984; Seigel et al., 1986; Seigel and Ford, 1987; Ford and Seigel, 1989). Snout-vent length for newborn individuals in field was recorded from eggs received at the reception of the Laboratório de Herpetologia (IB) on hatching time. Degree of sexual size dimorphism (SSD) was 1 --- mean adult SVL of the larger sex/mean adult SVL of the smaller sex (see Shine, 1994).

Analysis on follicle/eggs diameter, residual volume of testes and diameter of deferent duct and seasonal abundance of snakes was made using data divided into four periods: onset rainy season (October-December), end of rainy season (January-March), onset of dry season (April-June) and end of dry season (July-September). As testes volume and deferent duct diameter were correlated with SVL, its residuals were used to indicate spermatogenic activity and sperm release respectively (see Volsøe, 1944; Shine, 1977b). Seasonal occurrence of vitellogenesis and eggs were analysed comparing proportions (number of females with vitellogenic follicles or eggs/number of collected females in the period) by a chi-squared test (Zar, 1999). As we examined specimens collected in many years we limited data on the seasonal abundance from snakes collected each month from 1997 to 1999. These data were obtained from reception of the Laboratório de Herpetologia (IB) where all snakes received were recorded (cf. Marques et al., 2001).

Results

Body size. The smallest mature female had 632 mm SVL and the smallest male had 388 mm SVL (however eight immature males measured 390-510 mm SVL). Mature females ($\bar{x} = 819 \pm 97$ mm, range 632-1080 mm, $n = 211$) were significantly larger than mature males ($\bar{x} = 599 \pm 86$ mm, range 388-780 mm, $n = 160$) ($t = -22.7$, $df = 369$, $P < 0.0001$).

The degree of sexual size dimorphism (SSD) was 0.37.

Female reproductive cycle. Enlarged follicles and oviductal eggs were present throughout the year but they were not equally distributed through the periods (fig. 1, $X^2 = 43.18$, $df = 3$, $P < 0.00001$). Females with vitellogenic follicles or oviductal eggs were more abundant from the end of the dry season and the onset of the rainy season than in the other periods (fig. 1, $X^2 = 35.59$, $df = 1$, $P < 0.00001$). Eggs were more abundant at the onset of the rainy season (fig. 1, $X^2 = 4.48$, $df = 1$, $P < 0.034$). Egg-laying in captive snakes ($n = 30$) occurred from August to April (fig. 1). Newborn individuals were collected in the field from January to July (fig. 1). Additionally, specimens with SVL < 230 mm were most often received at the Instituto Butantan from April to July, with a peak in April (fig. 2). One isolated captive female laid eggs in October 1999, October 2000, January 2001 and died in March 2001. Dissection of this individual revealed oviductal eggs. One-tenth of *O. guibei*

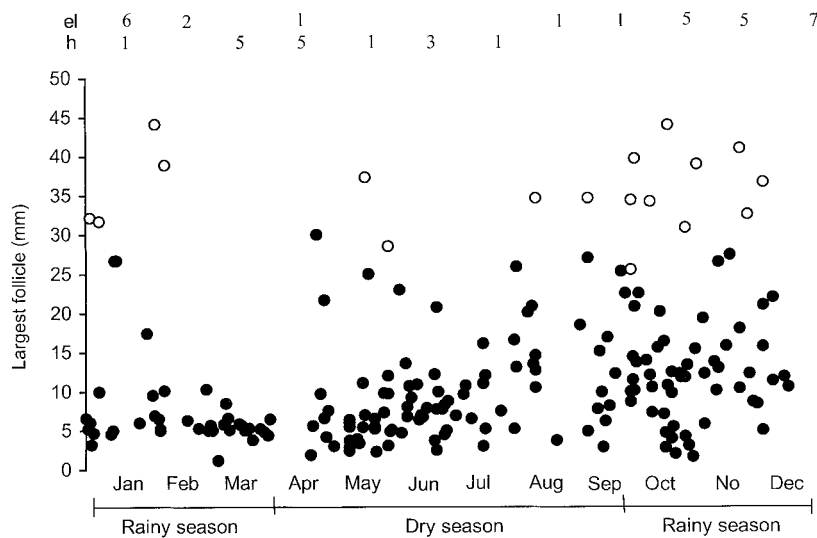


Figure 1. Seasonal variation in the diameter of the largest ovarian follicle in adult females of *Oxyrhopus guibei* (SVL > 632 mm, $n = 203$) from southeastern Brazil. Solid circles = ovarian follicle; open circles = oviductal eggs (both from wild snakes); el = number of egg-laying from females collected gravid or just after egg-laying; h = number of hatchlings (from eggs laid and incubated in captivity or eggs collected at hatchling time).

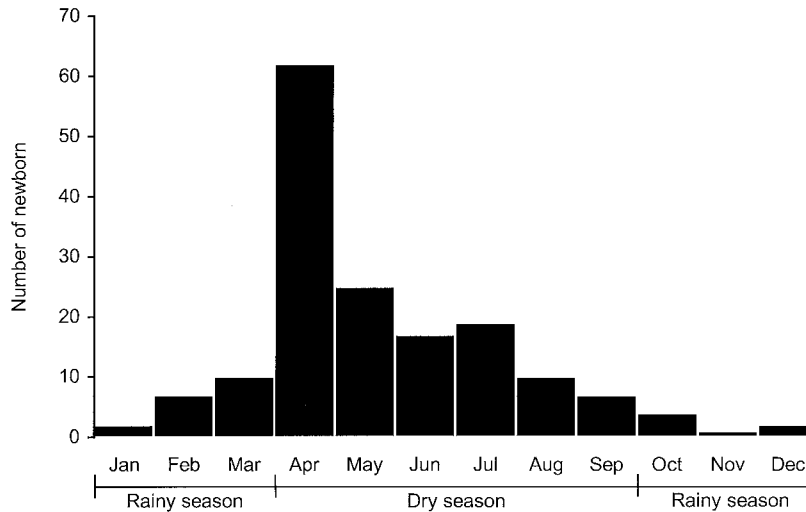


Figure 2. Seasonal abundance of newborns (SVL < 230 mm) of *Oxyrhopus guibei* based on individuals received at the Instituto Butantan between 1997 and 1999.

females contained vestiges of prey in their gut, but none of these presented oviductal eggs. Captive females only accepted food after egg-laying.

Fecundity. Clutch size averaged 10.9 eggs ($s = 3.6$, range 3-20, $n = 47$). Clutch size was positively and significantly related with female body length (fig. 3; $r = 0.46$; $P = 0.00325$; $n = 39$). Clutch mass was not affected by female mass ($r = 0.34$; $P = 0.149$; $n = 19$) although clutch mass was positively correlated with clutch size ($r^2 = 0.5$; $P = 0.0007$, $n = 19$). Relative clutch mass was 0.34 ± 0.13 g ($n = 19$ clutches). Egg length averaged 29.5 mm ($s = 3.8$, range 16.6-47.6 mm, $n = 178$ fertile eggs from 19 clutches) and egg width averaged 15.6 mm ($s = 1.6$ mm, range 10.7-26.0, $n = 178$ fertile eggs from 19 clutches). Clutch size was inversely correlated with mean egg size (fig. 4; $y = 24.54e^{1.84/x}$, $r^2 = 0.76$, $n = 178$ fertile eggs from 19 clutches). The largest mean egg size (45 mm) was from a very small clutch ($n = 3$; fig. 4).

Newborn individuals. A total of 41 (18.6%) of 220 eggs (20 clutches) laid by captive females — collected gravid in wild — was atresic. The period of egg incubation in captivity ranged 57-94 days ($\bar{x} = 83.6$, $s = 11.3$, $n = 47$ newborns from 11 clutches). About 35% of all fertile eggs did not hatch due to fungal contamination or dehydration. Neonates born in captivity averaged 194 mm SVL (range 137-230 mm, $s = 14.1$, $n = 70$) and 3.8 g (range 2.9-4.9 g, $s = 0.5$, $n = 63$). Snout-vent length ($\bar{x} = 193.3 \pm 7.7$ mm, range 173-205 mm, $n = 31$) and body mass ($\bar{x} = 3.8 \pm 0.7$ g, range 2.1-4.6 g, $n = 15$) of newborn individuals hatched in nature did not differ from these hatching in captivity (size: $t = -0.25$, $df = 99$, $P = 0.79$; mass: $t = 0.05$, $df = 76$, $P = 0.96$). Growth rate before first feeding (about one month after hatching) for 11 newborn individuals in captivity averaged 0.16

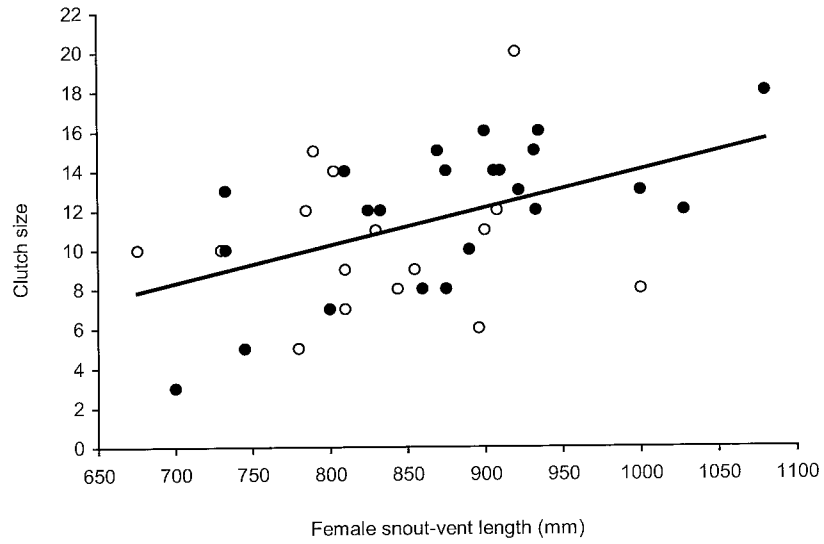


Figure 3. Relationship between female snout-vent length and clutch size in *Oxyrhopus guibei* from southeastern Brazil ($r = 0.46$; $P = 0.00325$; $n = 39$). Open circles = data from preserved snakes, solid circles = data from captive snakes.

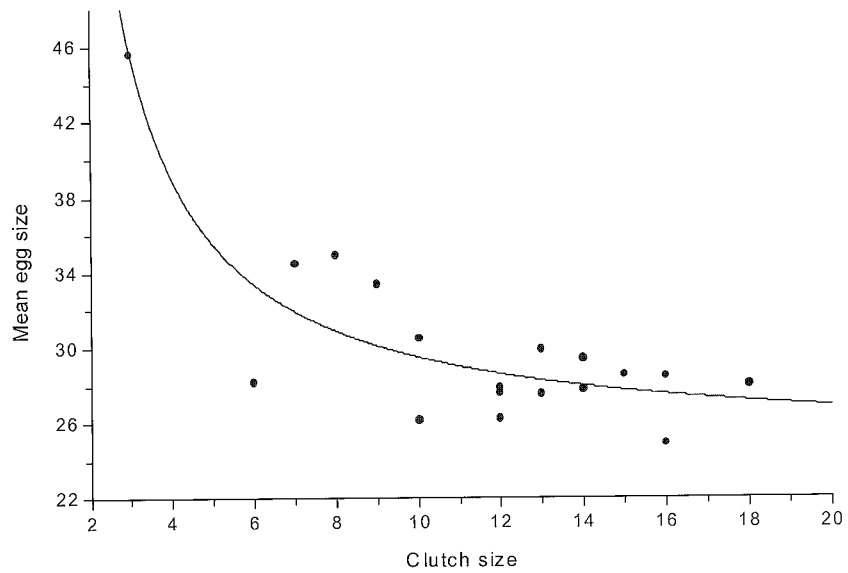


Figure 4. Relationship between clutch size and mean of the largest diameter of eggs in *Oxyrhopus guibei* from southeastern Brazil ($y = 24.54e^{1.84/x}$, $r^2 = 0.76$, $n = 178$ fertile eggs from 19 clutches).

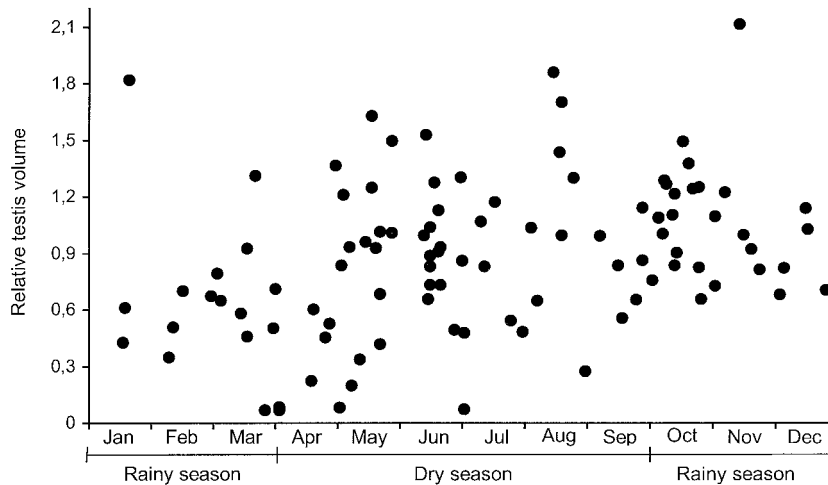


Figure 5. Relative testis volume in mature males of *Oxyrhopus guibei* throughout the year. Testis volume was smaller from February to April than from May to January (Mann-Whitney Test: $Z_{adj} = -4.35$, $P = 0.000013$, $n = 102$).

(range 0.11-0.19 $s = 0.028$). Thus, 230 mm is here considered as the maximal SVL for newborns.

Male cycle. Sperm were found in the deferent ducts of the smallest male with ducts opaque and convoluted and they were absent when ducts were translucent and flat. Males with small testes had small deferent ducts too ($r^2 = 0.48$, $P < 0.0001$, $n = 104$). Testis volume did not vary throughout the year ($H = 0.04$, $P = 0.99$, $df = 3$, $n = 102$, fig. 5). The same pattern was observed for the deferent duct diameter ($H = 0.020$, $P = 0.99$, $df = 3$, $n = 113$).

Seasonal abundance. Both adult males and females were collected during all months of the year. However, they were not equally distributed through the periods ($X^2 = 13.03$, $P = 0.0046$, $df = 3$ for females and $X^2 = 13.00$, $P = 0.0046$, $df = 3$ for males). Adult snakes were less abundant at the end of the rainy season ($X^2 = 9.68$, $P = 0.0019$, $df = 1$ for females and $X^2 = 7.38$, $P = 0.0066$, $df = 1$ for males) and more abundant at the onset of the dry season ($X^2 = 5.204$, $P = 0.0225$, $df = 1$ for females and $X^2 = 8.68$, $P = 0.0032$, $df = 1$ for males).

Discussion

Males mature smaller than females, as in other medium-sized and oviparous colubrid species in temperate regions (see review in Parker and Plummer, 1987). Females larger than males, as here recorded for *O. guibei*, is the most common situation among snakes, and is

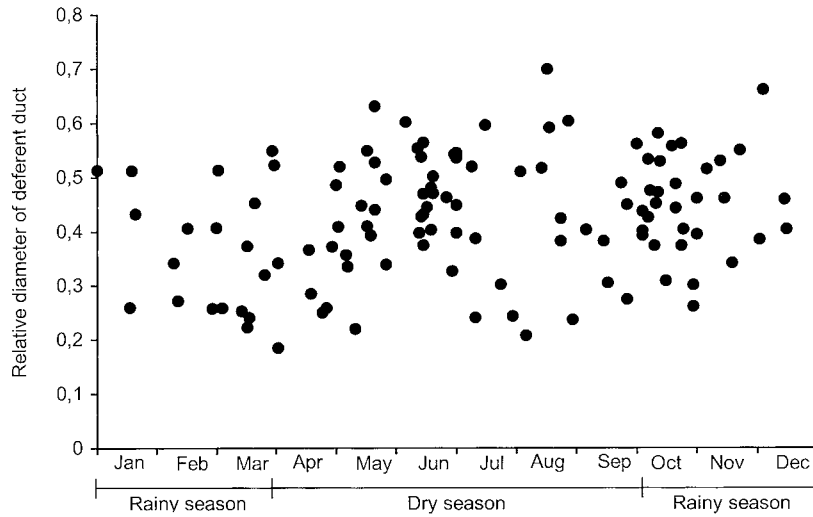


Figure 6. Diameter of the deferent duct in mature males of *Oxyrhopus guibei* throughout the year. It was smaller from February to April than from May to January (Mann-Whitney Test: $Z_{adj} = -4.63$, $P = 0.000004$, $n = 114$).

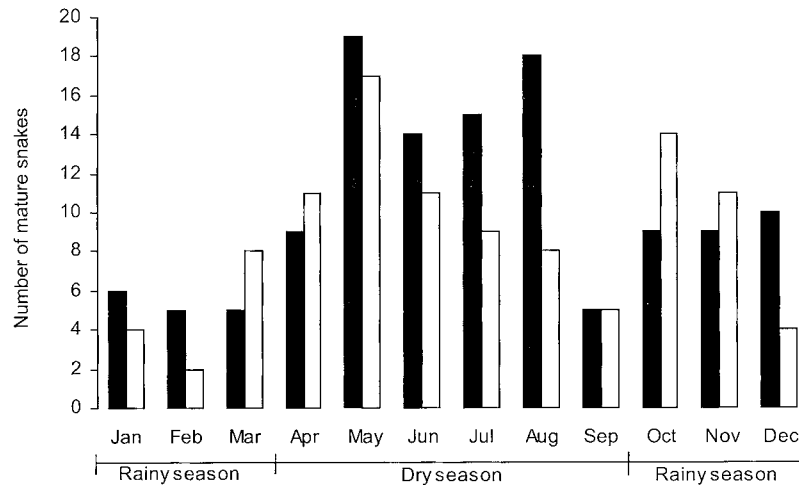


Figure 7. Seasonal abundance of adult males (white bars, $n = 104$) and adult females (black bars, $n = 124$) of *Oxyrhopus guibei* based on individuals received at the Instituto Butantan between 1997 and 1999.

recorded for about two-thirds of the studied species (Shine, 1993). As in other species, the large body size confers a considerable selective advantage for females of *O. guibei*, because fecundity is size-dependent. Combat ritual in colubrid snakes was recorded only for species with $SSD < 0.25$ (see Shine, 1994), thus it is probable that this behavior does

not occur in males of *O. guibei*. Besides, it seems that there are two possible strategies in *O. guibei* reproduction: females can lay many small eggs or just a few and large eggs.

The continuous reproductive cycle of *O. guibei* is similar to cycles of some other neotropical snakes (Fitch, 1970, 1982; Seigel and Ford, 1987; Jordão, 1996; Marques, 1996b, 1998). There is no evidence that *O. guibei* lays multiple clutches in the wild, therefore the continuous cycle may result from asynchronous reproduction (Seigel and Ford, 1987). Multiple clutches in captivity indicate that females can store sperm; sperm was found stored in the infundibulum of a few females dissected just after killed (L. Pizzatto, pers. obs.) which confirms sperm storage (Fox, 1956; Halpert et al., 1982; Aldridge, 1992). Although *O. guibei* reproduces continually, there is a larger number of reproductive females from the end of dry season and the onset of rainy season and most oviposition occurs during the onset of the rainy season. This may be advantageous since egg-laying occurs mainly in the middle of the rainy season, and thus most eggs will be incubated during the warmer and wetter months. Egg-laying in warmer periods can be profitable for embryonic development (Vinegar, 1977). Moreover, hatching of juveniles occurs most frequently at the end of rainy season and onset of the dry season. The diet of juveniles of *O. guibei* is based on small lizards (Andrade and Silvano, 1996; Sazima and Haddad, 1992), and small lizards (SVL < 50 mm) also are frequent at the end of the rainy season in open areas in southeastern Brazil (Van Sluys, 1993; R.J. Sawaya, pers. com). Thus, prey is available for the juveniles of *O. guibei* at hatching. The gap recorded in secondary vitellogenesis (mid-February — April) occurs just after the egg-laying peak. Thus, it is possible that more females are regaining their energetic reserves expended during the previous reproductive period. However, spermatogenesis seems to occur throughout the year but only histological analysis can reveal a refined measure of it.

Mating was not observed in *O. guibei*. However, it is possible to occur during the first half of the dry season where there is an increase in male and female activity. If so, this snake presents a pre-nuptial reproductive cycle (Saint-Girons, 1982; Garstka et al., 1982). Snake collection by common people is higher during the day than at night (pers. obs.), obviously reflecting daytime working activity. Basking time (a diurnal activity) in non-gravid snake females is shorter than in gravid ones (Shine, 1980a). Additionally, non-gravid snakes likely are more agile and faster than gravid ones and therefore are less collected (see Shine, 1980a for lizards). Thus, the decrease in number of *O. guibei* females at the second half of the rainy season may be explained by a collecting bias.

Reproduction may influence energy budget, decreasing total intake of energy (feeding) or using energy that otherwise would be available for body growth. Females of *O. guibei* practically abstain from feeding while carrying oviductal eggs and this seems to be common for many reptiles, mainly in snakes (Shine, 1977a, 1980a, b). Gravid females are expected to be slower than non-gravid ones and, in species that are active foragers, this may reflect a reduction in the ability of capturing prey (Shine, 1980a).

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