REPRODUCTION OF THE RUFOUS-BEAKED SNAKE, *RHAMPHIOPHIS OXYRHYNCHUS* (COLUBRIDAE, LAMPHROPHIINAE)

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INTRODUCTION

Data are generally lacking for most aspects of the reproductive biology of an African rearfanged snake, the Rufous-Beaked Snake (*Rhamphiophis oxyrhynchus*). Oviposition has been reported to occur in the wild during December-January (Sweeney 1959, 1961, Branch 1988, Marais 1992) and August (Loveridge 1928). Pitman (1974) found a gravid female on 27 October and reported the duration of incubation as about "3 months". Clutch size has been recorded as between six (Sweeney 1961) and eighteen (Marais 1992) eggs.

The only details report covering a clutch incubated to term and producing viable hatchlings was that of a female *Rhamphiophis oxyrhynchus rostratus* at the National Zoological Park (NZP, Washington, D.C.) by Walsh and Davis (1978). Subsequently, additional clutches have been recorded at the NZP. Data concerning these clutches, eggs, and hatchlings, as well as courtship and mating, the period between copulation and oviposition, incubation period, and female reproductive output are presented below.

METHODS AND MATERIALS

Two female *Rhamphiophis oxyrhynchus rostratus* produced 27 clutches containing a total of 314 eggs during an 18-year period (June 1976-March 1994) at the NZP. The first female (no. 301586) was wild hatched in South Africa and was received 9 June 1976. A second female (no. 303644) was a daughter of female 301586 that hatched at the NZP on 4 June 1983.

Three males were involved in all but one of the 27 recorded clutches (female 301586 laid a clutch of nine infertile eggs on 16 June 1976 during quarantine before being placed on display with a male). Male (no. 301215) was wild-hatched in South Africa and was obtained 11 March 1976. The second male (no. 303645) was an offspring of male 301215 and female 301586 hatched at the NZP on 6 June 1983, and a clutch sibling of female 303644. The third male (no. 304943) was a backcross offspring of male 301215 and female 303644 that hatched at the NZP on 2 July 1986.

The various pairings (one male with one female) of *R. oxyrhynchus* were housed on exhibition in a glass-fronted 84 x 63 x 100 cm ventilated cage. The floor of the cage was covered with 10 cm of peagravel, and a hollow log provided shelter for the snakes. Plastic plants simulated a natural habitat. Temperature in the exhibit cage was

maintained with a heat lamp and fluctuated about 6.0°C between day and night, averaging 26.7°C diurnally and 21.0°C nocturnally. Extreme temperatures recorded were 32.2°C and 17.0°C. Overhead skylights provided a natural photoperiod. An ultraviolet light was suspended above the screened top of the cage. The cage was misted with water daily, and a bowl of drinking water was constantly available for the snakes. Diet generally included one mouse (*Mus musculus*) per snake per week.

Females used their snout to rake out and make a depression in the peagravel, typically under the hollow log, in which they deposited eggs. The date of oviposition was recorded for each egg, and the eggs were carefully removed from the cage, weighed, and measured for length and width to the nearest 0.1 mm with a dial calipers. Total egg mass was recorded for each clutch. Selected eggs were then placed either in a 60 x 60 x 30 cm styrofoam box or in 4.4 litre (gallon) jars on sphagnum moss. Eggs were positioned on 4 cm of potting soil in 15 x 10.5 x 17.5 cm plastic containers, and then incubated at 28.0-29.0°C on a 30-cm layer of peagravel covering two lengths of subterranean 125 W heat tape.

Periodically the eggs were candled to determine fertility and monitor embryonic development. Collapse of the eggs, indicating water loss was noted; shell collapse is a normal event during incubation. The hatching date of each egg was recorded, and, within hours of emergence from the egg, the neonate body mass and total length (TBL) of each hatchling were recorded. Egg and hatchling weights were recorded on a triple beam balance. the snout-vent length (SVL), tail length (TL), head length (HL), and head width (HW) were also recorded for a litter of 15 hatchlings after preservation.

Egg, hatchling, and female body size measurements were compared descriptively, as well as with linear regressions. Assumptions for the regressions were analyzed graphically (Cleveland 1993). All regression results are stated with the independent variable given first. A few two-sample t-tests were also employed. All regressions and t-tests were performed using the SAS system (SAS Institute, Inc. 1990). The level of alpha was 0.05 for all statistical tests.

RESULTS AND DISCUSSION

COURTSHIP, MATING AND OVIPOSITION

Both courtship and mating behaviours by *Rhamphiophis oxyrhynchus* have been observed at the NZP. Reproductively ready males repeatedly pursued females. Courtship involved swaying the head and anterior neck from side to side in a jerky manner while peering about by both sexes, and much tongue flicking by the male. During copulation, the bodies of both sexes were usually stretched out on the floor of the cage with the male lying on the female's back.. His head was placed on top of her's, and their bodies pulsated in a jerky manner every few seconds. The male's tail was loosely wrapped around that of the female, with their cloacal vents in contact and one hemipenis inserted into the female's cloaca. The two copulations observed lasted from 20 minutes to 2-3 hours. Periods of inactivity alternated with periods of intense activity, and after separating the snakes usually retreated into the cover of the hollow log.

Three matings were observed in 1977 on 15 February, 22 March, and 19 April. Courtship activity also was recorded on 28 March 1982. A clutch of seven eggs (five fertile, two infertile) was laid on 21 April 1977. If these eggs were fertilized on 15 February, the interval between copulation and oviposition was 65 days, but, if fertilization occurred on 22 March the interval was only 30 days. After the courtship activity on 28 March 1982, a clutch of 10 eggs (not incubated) was laid 29 days later on 26 April. A second clutch

Rufous Beaked Snake, *Rhamphiophis oxyrhynchus*

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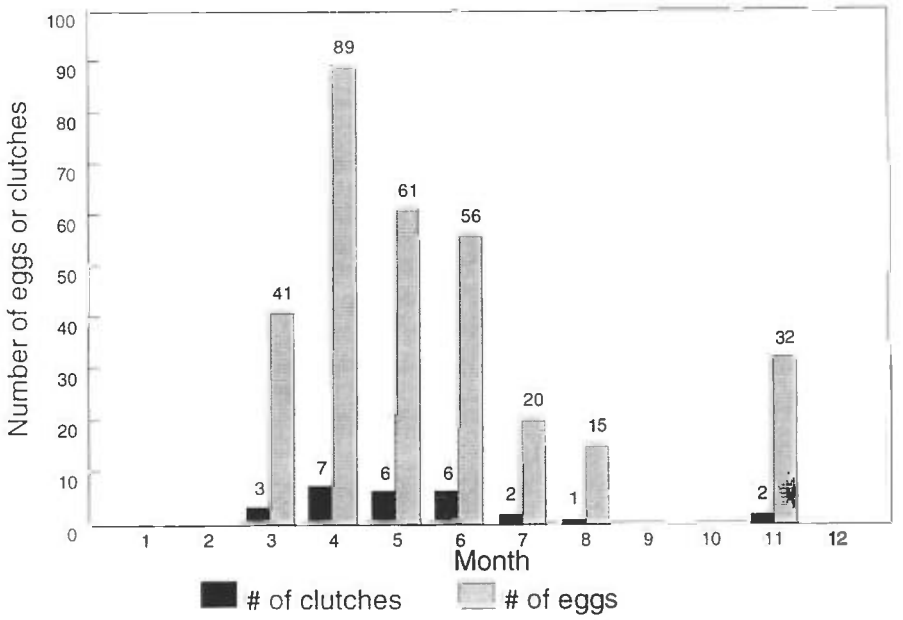

Fig. 1. Number of clutches and total eggs produced by *Rhamphiophis oxyrhynchus* per month

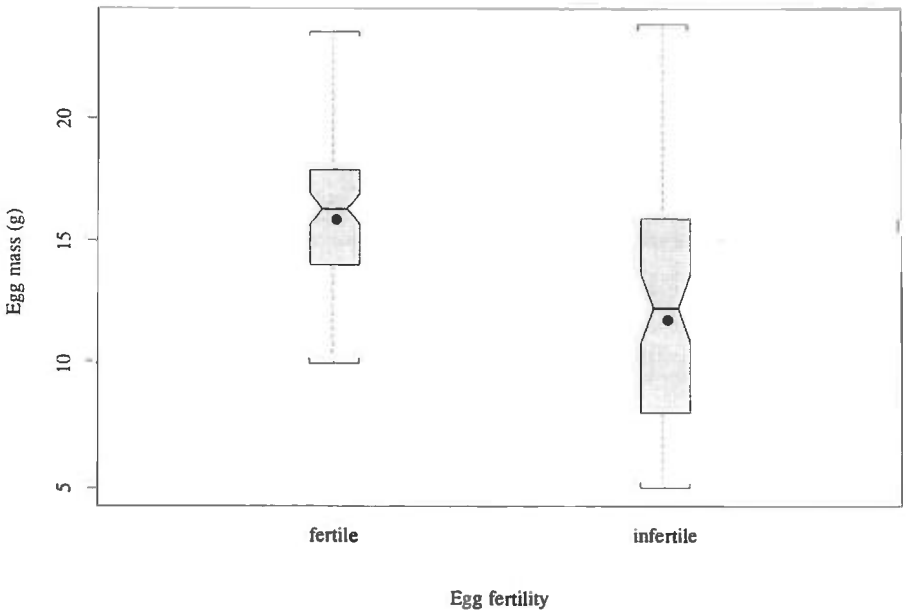

Fig. 2. Comparison of egg mass in fertile and infertile eggs of *Rhamphiophis oxyrhynchus.*

composed of 9 eggs (laid 12-13 June 1982) was oviposited 76-77 days after the 28 March courtship behaviour was noted. If the above clutches were produced from the observed reproductive activities, an average interval between copulation and oviposition would be 55.4 days (29-77 days); however, unobserved matings may have occurred. It is also possible that the clutch laid 12-13 June may indicate sperm storage ability by female *Rhamphiophis oxyrhynchus.*

Clutches were laid from March through August and in November, with most oviposition in April (7 clutches), May (6 clutches) and June (6 clutches) (Fig. 1). Multiple clutches were laid in some years. Female 303644 produced four clutches totalling 62 eggs within an eleven-month period: 16 April 1989 (18 eggs), 12 June 1989 (14 eggs), 14 November 1989 (15 eggs), and 5 March 1990 (15 eggs). She also laid three clutches (43 eggs) in another seven month period: 7 November 1986 (17 eggs), 13 April 1987 (15 eggs), and 29 May 1990 (11 eggs). In each series there was a decrease in the number of eggs laid after an initial large clutch. An average of 54.7 days (48.5-68.0) elapsed between ovipositions by female 301586 during the years she laid more than one clutch. Duration between ovipositions by female 303644 averaged 125.4 days (44-217)), but several of these clutches were laid at mean intervals of only 50.5 days (44-57). Disregarding the two longest intervals between ovipositions by female 303644, the mean duration between the laying of clutches by both females was 53.5 days. Based on these durations, we believe a period of 50-55 days between clutches to be normal. This closely matches the 55.4 days between copulation and oviposition calculated above.

Mean clutch size and clutch mass were significantly different between females 301586 and 303644 (t-test, $p<.001$). Difference in the clutch masses oviposited by the two females is explained by the fewer eggs per clutch by female 301586, mean = 8.5 (6-11), versus a mean of 15.0 eggs (11-18) for female 303644. The discrepancy between the numbers of eggs per clutch is not easily explained.

Shine and Seigel (1996) showed that clutch size differs more in snake species with relatively variable adult female body lengths, and that there is a high rate of increase in clutch size with increasing female length. The two factors act to magnify the extent of clutch size variability brought about by differences in maternal body sizes. Unfortunately, lengths of the two females were not recorded, so no body length/clutch size relationships could be determined. (The literature also is devoid of such data for this species, but a record exists. Field notes accompanying a female in the reptile collection of the United States Museum of Natural History [USNM 206944] collected 27 December 1977 in Tanzania state that she had a TBL of 133 cm [SVL 91.5 cm], was very fat, especially in the area of the oviducts, and contained "16 (?)" eggs, each approximately 32 x 10 mm). In addition, although the age of female 303644 was known since she had been hatched at NZP, that of the wild caught 301586 was unknown, so no age/clutch size comparisons could be made between the two females; however, the relationship of clutch size to female age was not significant in female 303644.

Clutch size and mass in oviparous snakes are known to differ with variance in available resources (Seigel and Fitch 1985, Ford and Seigel 1989b, Seigel and Ford 1991). Since both female *Rhamphiophis* were maintained under the same habitat conditions and feeding regime, resource variance can not explain the difference in clutch sizes between the two individuals.

Most likely the difference in mean clutch size between the two females is simply an indication of the normal variance (phenotypic plasticity, Seigel and Ford 1991) in fecundity within *Rhamphiophis oxyrhynchus.*

REPRODUCTIVE CAPACITY

An idea of reproductive capacity can be determined by examining the individual egg output of the two female *Rhamphiophis*. Female 301586 lived until 20 March 1985 and laid 14 clutches, totalling 119 eggs during her confinement at the NZP, 13 clutches were sired by male 301215 (110 eggs). Forty-four young hatched from these eggs, including female 303644, who, herself, laid 13 additional clutches between 1985 and her death on 26 May 1994 (195 eggs, 44 hatchlings). Three of these clutches were sired by male 301215 (48 eggs); nine clutches were fathered by her F_1 litter mate 303645 (131 eggs), and one clutch of 16 eggs was sired by male 304943. Combined mean clutch size for the two females was 11.6 eggs (6-18) (see above).

EGGS

Mean measurements for eggs were: length 46.5 mm (28.6-71.0, n = 270), width 22.2 mm (14.1-29.1, n = 263), mass 14.8 g (5.0-23.7, n = 270), and clutch mass 171.16 g (62.8-321.8, n = 25). Mean egg mass vs. mean egg length, and clutch mass vs. mean egg length were not significant, but mean egg mass vs. mean egg width ($p<.0001$, $R^2 = 0.69$), clutch mass vs. mean egg mass ($p<0.0002$, $R^2 = 0.48$), and clutch mass/mean egg width ($p<.0001$, $R^2 = 0.67$) were. In addition, female age vs. mean egg width was significant ($p<.01$, $R^2 = 0.54$).. Ford and Seigel (1989a) found that when adjusted for female length increasing clutch size in snakes is negatively correlated with egg length and usually egg mass.

No significant differences were found between the lengths and widths of 90 fertile eggs and 61 infertile eggs (condition of most eggs not recorded); but the masses of fertile and infertile eggs were significantly different (t-test, $p<0.02$; Fig. 2). The average mass of fertile eggs was 16.6 g (12.7-21.7), whereas that of infertile eggs was 12.3 g (6.9-16.3).

HATCHLINGS

In contrast to the plain tan dorsal body colouration of adults, hatchlings were darker brown with light flecks. They had the following mensural characteristics: mean TBL 35.0 cm (28.0-41.2, n = 60), mean SVL 26.9 cm (24.6-29.4, n = 15), mean TL 10.3 cm (8.6-11.9, n = 15), mean HL 1.5 cm (1.3-1.7, n = 15), mean HW 0.7 cm (0.6-0.8, n = 15), and mean mass 11.7 g (6.2-14.5, n = 45). Both SVL ($p<0.001$) and TL ($p<0.0358$) were significantly related to TBL.

The relationships of hatchling TBL to female age and clutch mass, and hatchling mass to female age and clutch size were not significant. However, hatchling TBL was significantly related to clutch mass ($p<0.04$, $R^2 = 0.52$), as was also hatchling mass ($p<0.04$, $R^2 = 0.47$). Heaviest clutches produce the largest offspring.

Reproductive biology of most lamprophine snakes is unknown. Comparative studies similar to this would be very helpful in determining management programs and proper captive husbandry. Especially needed are reproductive data on the other species of *Rhamphiophis*, and on wild populations of *R. oxyrhynchus*.

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