Female Reproduction in an Arkansas Population of Rough Green Snakes (*Opheodrys aestivus*)

MICHAEL V. PLUMMER

INTRODUCTION

Because of the kinship between lizards and snakes the tendency when reviewing certain aspects of snake ecology is to compare them to lizards (e.g., Fitch 1970; Turner 1977). However, while lizards ". . . may well become paradigmatic for ecology as a whole" (Schoener 1977), such is hardly true for snakes. Indeed the nocturnality, secretiveness, great vagility, and frequent periods of inactivity of most snakes make them less of an ideal subject than the conspicuous, mostly diurnal lizards. Reviews of reproductive ecology in lizards and snakes (Fitch 1970; Turner 1977) clearly reveal the need for more information on the latter.

Although highly cryptic, *Opheodrys aestivus* is a non-secretive, diurnal arboreal snake that is abundant, has low vagility, and is easily collected (Plummer 1981). Consequently, some of the attributes of lizards that contribute to successful study also make this snake species a favorable subject. *Opheodrys aestivus* ranges from southern New Jersey to southern Florida, west to eastern Kansas and Texas, and south to southern Tamaulipas, Mexico (Conant 1975). In this paper I report on female reproduction from a population in the central part of the species' range.

METHODS

Female *O. aestivus* (N = 167) were collected May 1977–October 1979 from a population at Bald Knob Lake in White County, Arkansas. Snout–vent length (SVL) and body weight were measured. Cloacal smears were made on 43 snakes during April–October 1979 and were examined for sperm under $100\times$ magnification. One hundred and twenty-seven snakes were preserved and autopsied for reproductive condition. Forty gravid snakes, collected 14 June–14 July 1979, were returned to the field after their clutches were deposited in the laboratory. Observations were made on snakes in the field which were not collected. Autopsy included counting and measuring with vernier calipers or an ocular micrometer, ovarian follicles, corpora lutea, and oviducal eggs. The diameter of the oviducts was measured at their approximate midpoint. Coelomic fat bodies were removed, blotted, and weighed to the nearest .01 g. Percent body fat (fat (g)/body wgt. (g) $\times$ 100) was used to control for size-induced variation in fat body weight. In the laboratory snakes were housed in a 1.1 W $\times$ 4.9 L $\times$ 2.8 H m cage. A thin layer of moist wood shavings was maintained on the floor. Ten 30 $\times$ 30 cm plywood boards were placed on the floor under which clutches were deposited. The cage was maintained at 28 $\pm$ 2°C and on a 14L:10D photoperiod. Crickets and water were provided *ad libitum*. On the day of oviposition females and eggs were measured, weighed, the eggs were individually marked with a felt-tipped pen, and each egg was incubated individually on top of a thin layer of moist vermiculite in a small glass jar at 28°C. Some eggs were sacrificed immediately following oviposition in order to stage the embryo according to Zehr (1962). On the day of emergence from the egg hatchlings were weighed, measured (SVL) and sexed. They were returned to the field at a later date. Data are reported as mean $\pm$ 1 SE.

RESULTS

Sexual Maturity and Mating.—The presence of oviducal eggs, corpora lutea, enlarged ova, or convoluted oviducts indicated sexual maturity. Most snakes mature between 36–40 cm SVL (Table 1). The largest immature was 45.0 cm whereas the smallest mature measured 33.5 cm. Immature snakes had straight, narrow (0.5–1.5 mm), ribbon-like oviducts and follicles <3.0 mm in diameter with greater interfollicular distance than mature snakes.

Sperm were present in most mature females in spring but were not detected in other parts of the year (Table 2) indicating that mating is limited to spring. No sperm was found in any females <35.0 cm SVL.

Ovarian Cycle.—In adults follicles measuring 1–5 mm in greatest diameter were present in

TABLE 1. *Opheodrys aestivus*: size at sexual maturity of females.

SVL (cm)	N	No. mature (%)
>45	50	50 (100)
41–45	47	46 (97.9)
36–40	30	29 (96.7)
31–35	16	2 (12.5)
<31	19	0 (0)

TABLE 2. *Opheodrys aestivus*: Presence of cloacal sperm in females (>35.0 cm SVL) at different times of the year.

Period	Snakes (N)	Snakes (N) with cloacal sperm (%)
Apr–May	10	8[1] (80.0)
Jun–Aug	16	2[2] (12.5)
Sep–Oct	17	0 (0)

[1] Spermatozoa extremely abundant.

[2] Only 3 spermatozoa detected in 2 samples from each of 2 snakes collected in June.

ovaries throughout the sampling period (Fig. 1). Follicles measuring 1–3 mm proliferate in post-reproductive females in July and August and increase in size to a maximum 5 mm by October. Two snakes collected in mid-February had a mean of 9 follicles measuring 1–3 mm and 9.5 follicles measuring 3–5 mm. The February data are similar to the September–October data and indicate that very little follicular activity occurs over winter. Vitellogenesis resumes in spring. Rapid yolking and enlargement to approximately 15–25 mm occur in May and oviducal eggs are present from late May to early July.

In 8 pre-ovulatory females which contained enlarged (>12 mm) follicles the mean number in the left and right ovaries was $2.6 \pm .26$ and $3.6 \pm .38$, respectively. Fourteen of 23 post-ovulatory females (60.1%) had a disparity in the corresponding number of corpora lutea and oviducal eggs on each side. In 10 snakes extrauterine transfer of ova involved only 1 ovum and in 2 snakes movement of 2 ova was involved. A significantly greater number of ova moved from the left ovary to the right oviduct than vice versa ($\chi^2 = 7.14$, $P < .01$). Reciprocal transfers, of course, could not be detected. The average number of oviducal eggs in the left and right oviducts was $2.2 \pm .15$ and $4.1 \pm .23$, respectively. It appears that the right oviduct, which is longer than the left, receives more ova because of greater ova production by the right ovary and because of greater extrauterine transfer from the left ovary.

Oviposition dates in the laboratory from females collected 14 June–14 July 1979 were 1–7 July (N = 11); 8–15 July (N = 18); 16–23 July (N = 11). Oviposition in 1978 apparently occurred earlier (Table 3) or perhaps laboratory stress caused a delay in oviposition in 1979. Snakes collected in 1979 seemed to be delayed in follicular enlargement and ovulation as determined by palpation.

Body fat (Fig. 1, Table 4) is the greatest in early

spring and late fall and least in June. Two February females averaged 8.3 (range = 5.3–11.4). These data indicate that fat is not depleted in overwintering snakes. However, the significant reduction of fat during secondary vitellogenesis and ovulation from late May to June ($t = 9.27$; $P < .001$) suggests that energy needed for these processes is derived from fat reserves. Although the pattern of fat cycling resembles that in juveniles (Table 4), an abrupt significant decrease in fat is not evident. Additionally, mature females have more fat overall than do juveniles ($t = 3.17$, $P < .01$).

Clutch Size.—The number of eggs in a clutch was determined by counting the eggs actually deposited (42 snakes), by counting oviducal eggs (28 snakes), or by counting enlarged (>12 mm) ova (8 snakes). Clutch size in 77 snakes was $6.1 \pm .21$ (range 3–10). Estimates of clutch size by these methods are subject to some error. Enlarged, atretic follicles (N = 4) were present in the ovaries of 3 snakes which had oviducal eggs. Additionally, 11 unfertilized, unshelled ova were deposited singly and separate from clutches among the 40 laboratory snakes. The relative number of enlarged follicles that do not terminate as a part of an actual clutch, therefore, appears to be small. This fact along with the fact that only 8 of 77 clutch size estimates were based solely upon number of enlarged ova probably has not biased the clutch size estimate greatly. Clutch size averaged $6.3 \pm .59$ eggs based on number of enlarged follicles which is not significantly different from the total estimate ($t = .20$; $P > .50$).

No evidence was seen which indicated that more than 1 clutch was produced in a given year.

Incubation and Hatching.—Of 180 eggs laid and incubated in the laboratory, 161 (89.4%) were fertile. One hundred forty-five (90.0%) of the fertile eggs hatched. Of 19 infertile eggs, 18 (94.7%)
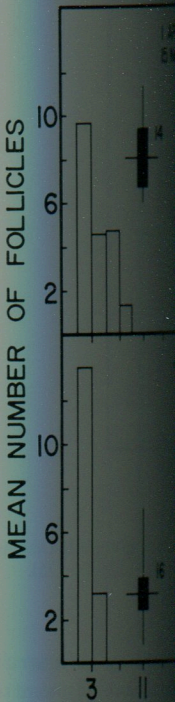

FIG. 1. *Opheodrys aestivus* [...] different times of the year. The [...] delimit 95% confidence limits. [...]

were either partially or tot[...] totally shelled eggs the mod[...] (Zehr 1962) at oviposition wa[...] 21–27). The range of stages [...] 7 eggs was 25–26. For parti[...] those that were inviable at o[...] sition (determined by the [...] and growth of mold) the mo[...] 14–19; N = 10). Statistics r[...] given in Table 5.

Incubation ranged 36–43 [...]

TABLE 3. *Opheodrys* [...] (>35.0 cm SVL) determined to h[...] in the field during various times [...]

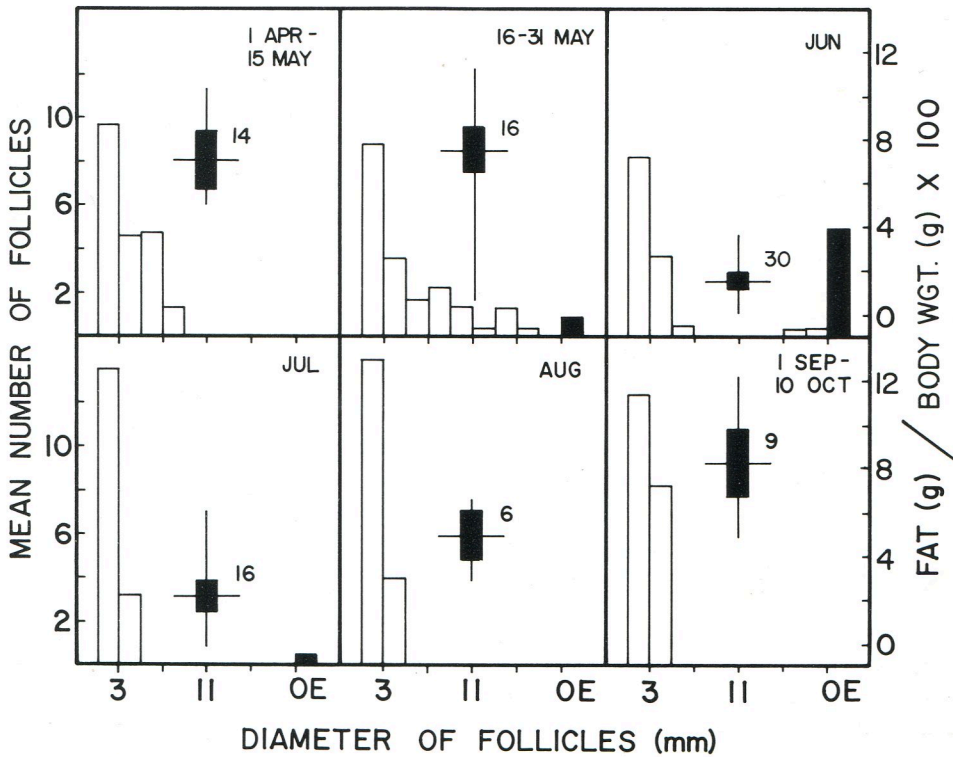| Period	Snakes (N)
5–20 Jun	39
22–30 Jun	32
2–7 Jul	29
12–31 Jul	50

FIG. 1. *Opheodrys aestivus*: Number of various sized follicles and amount of body fat in mature females at different times of the year. The horizontal lines of the dicegrams are means; vertical lines are ranges; rectangles delimit 95% confidence limits. OE = oviducal eggs.

were either partially or totally unshelled. For totally shelled eggs the modal embryonic stage (Zehr 1962) at oviposition was 25 (N = 37, range 21–27). The range of stages in a single clutch of 7 eggs was 25–26. For partially shelled eggs or those that were inviable at or soon after oviposition (determined by the rapid loss of tonicity and growth of mold) the mode was 18 (range = 14–19; N = 10). Statistics relating to egg size are given in Table 5.

Incubation ranged 36–43 days and averaged

39.2 ± .12 (N = 142). Hatching occurred 9–30 August in the laboratory. Hatchlings were seen in the field on 31 August and on 10 September in 1978.

Statistics relating to hatchling size are summarized in Table 5. Of 141 hatchlings, 67 (47.5%) were males. Sex ratio is not significantly different from 1:1 ($\chi^2 = .35$; $P > .50$). Male hatchlings weigh about the same as females (1.37 ± .023,

TABLE 3. *Opheodrys aestivus*: Number of snakes (>35.0 cm SVL) determined to be gravid by palpation in the field during various times in 1978.

Period	Snakes (N)	No. gravid (%)
5–20 Jun	39	39 (100)
22–30 Jun	32	20 (62.5)
2–7 Jul	29	11 (37.9)
12–31 Jul	50	0 (0)

TABLE 4. *Opheodrys aestivus*: Percent body fat of juvenile females and adult females. Data are $\bar{x} \pm 1$ SE (N) fat (g)/body weight (g) × 100.

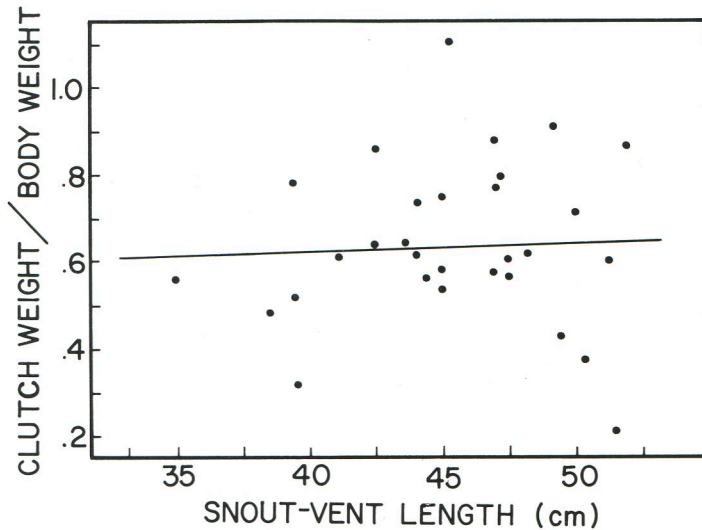| Period	Juvenile	Adult
Apr–15 May	4.1 ± 1.17 (5)	7.2 ± .62 (14)
16–31 May	1.7 ± .11 (2)	7.9 ± .57 (16)
Jun	2.1 ± .49 (9)	1.9 ± .20 (30)
Jul	2.3 ± .34 (9)	2.3 ± .38 (16)
Aug	2.4 ± .54 (7)	5.1 ± .57 (6)
Sep–Oct	3.2 ± .42 (6)	8.6 ± .77 (9)

FIG. 2. *Opheodrys aestivus*: The relationship of clutch weight/post-reproductive body weight and snout–vent length for snakes collected in 1979. The regression equation is $\hat{Y} = .001X + .588$ ($r = .024$, $P > .75$).

1.36 ± 0.23 g; $t = .01$, $P > .90$) and have about the same SVL ($13.9 \pm .10$, $14.0 \pm .10$ cm; $t = .02$, $P > .90$).

Reproductive Effort.—Reproductive effort of a female is that organism's total investment in a current act of reproduction (Pianka 1976). In snakes reproductive effort has been crudely estimated using the ratio of clutch weight to non-reproductive female weight (C/B) (Clark 1970; Fitch 1975; Pianka and Parker 1975; Shine 1977). Because in *O. aestivus* there is no parental care (egg brooding or oviducal retention) most of the reproductive investment should be contained in the egg itself and therefore the ratio C/B should be representative of reproductive effort (but see Vitt and Congdon 1978). The risks involved in transporting the enlarged ova and eggs in the maternal body are assumed to be negligible. In *O. aestivus* C/B averages .64 and does not change with body size (Fig. 2). Less than .06% of the variation in C/B is explained by body size. Larger

snakes produce both larger eggs and larger clutches (Fig. 3). There is a possible trend toward smaller eggs with increasing clutch size (Fig. 4) although there is great variation ($r^2 = 1.7\%$) and the regression is not significant. Larger eggs produce significantly larger hatchlings (Fig. 5).

DISCUSSION

Opheodrys aestivus appears to have a typical female reproductive cycle for a temperate oviparous snake. From the limited data available for a comparison of geographic variation in reproductive attributes, other reports appear to conform with this population. In southern Louisiana Tinkle (1960) and in Illinois Morris (1982) found similar results in *O. aestivus* with regard to size at sexual maturity, the ovarian cycle, and reproductive potential. Apparently, mating is limited to spring in this population although fall mating may occur in other populations (Richmond 1956).

TABLE 5. *Opheodrys aestivus*: Egg and hatchling statistics. All data are expressed as $\bar{x} \pm 1$ SE (N); range.

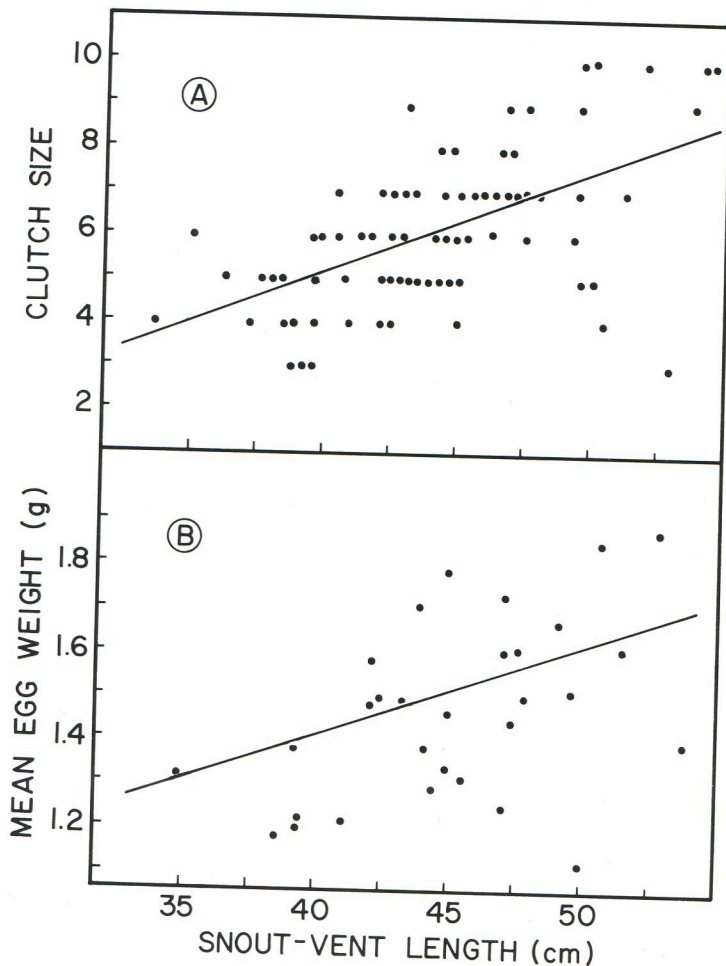|	Wgt. (g)	Max. width (cm)	Max. length (cm)	SVL (cm)
Shelled eggs	$1.62 \pm .015$ (190);	$9.9 \pm .04$ (190);	$24.8 \pm .23$ (190);	—
	1.17–2.26	8.4–11.9	16.2–34.2	—
Hatchlings	$1.37 \pm .016$ (144);	—	—	$13.9 \pm .07$ (144);
	.82–1.76	—	—	10.7–16.1

FIG. 3. *Opheodrys aestivus*: A. The relationship of clutch size and snout–vent length. The regression equation is $\hat{Y} = .23X - 4.1$ ($r = .58$, $P < .001$). B. The relationship of egg weight and snout–vent length. The regression equation is $\hat{Y} = .02X + .61$ ($r = .46$, $P < .05$).

McCauley (1945) observed mating behavior on 18 May of a captive male *O. aestivus* directed toward a female *O. vernalis*. The data on egg and hatchling size, clutch size, and dates of oviposition and hatching of several anecdotal reports (Conant 1938; Conant and Downs 1940; McCauley 1945; Curtis 1950; Guidry 1953; Carpenter 1958; Sabath and Worthington 1959; Smith 1961; Anderson 1965; Webb 1970; Mount 1975; Morris 1982; and others summarized in Wright and Wright 1957) generally are similar to the present report. The greatest differences are in time of oviposition and in incubation time. Since the timing of these probably is dependent upon phenological events and temperature, respectively, it is not surprising that they are so variable. The extremely wide variation in oviposition dates (17 June–28 August) and subsequent hatching in southeastern Texas (Guidry 1953) suggests the possibility of multiple clutching.

Seemingly, enlargement of follicles to the 5 mm stage occurs throughout the activity season and could be described as primary vitellogenesis (*sensu* Aldridge 1979). The rapid enlargement from the 5 mm follicle to ovulatory size is confined to late April and May and may be described as secondary vitellogenesis (*sensu* Aldridge 1979).
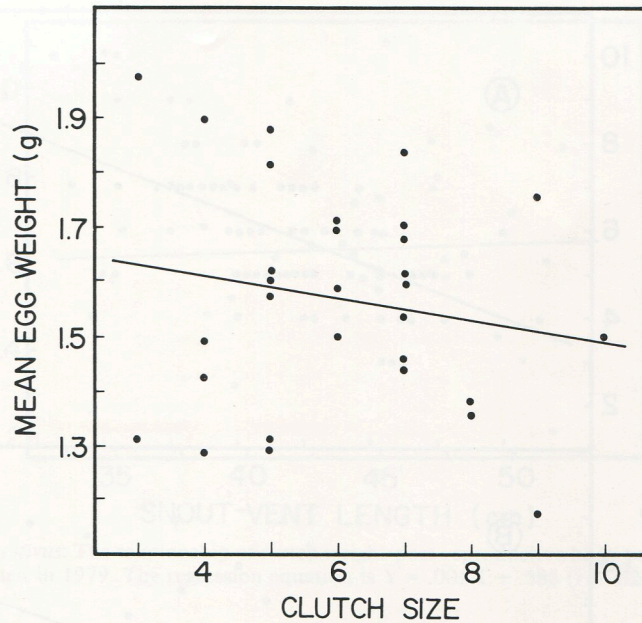
FIG. 4. *Opheodrys aestivus*: The relationship of egg weight and clutch size. The regression equation is $\hat{Y} = -.014X + 1.65$ ($r = -.13$, $P < .50$).

Aldridge (1979) described Type I secondary vitellogenesis in which rapid yolking of ova is confined to spring and Type II secondary vitellogenesis in which rapid yolking begins in late summer and fall, becomes dormant in winter, and resumes in spring. He classified *O. aestivus* as having a Type II pattern based upon Tinkle (1960). My interpretation of Tinkle (1960) is that of a Type I pattern, as is that of the present study. Although not mentioned by Aldridge, I suspect that intraspecific vitellogenic patterns might vary geographically.

Differential production of ova by left and right ovaries and extrauterine transfer of ova are probably simple consequences of space limitations. Shine (1977) stated that it is difficult to see how extrauterine transfer would affect clutch size and embryonic survivorship and therefore would be of doubtful selective importance. However, because in snakes the right oviduct is longer than the left, production of ova by the left ovary beyond that which the left oviduct can accommodate probably would result in greater follicular atresia were it not for differential extrauterine transfer to the right oviduct.

The decision to stage the embryos at oviposition was prompted by the data of Blanchard (1933) for *O. vernalis*, who found incubation to vary from 4 to 23 days. This species is a possible example in the evolutionary transition from oviparity to viviparity (Packard *et al.* 1977) with a relatively short incubation period and a presumably wide range in the degree of embryonic development at oviposition. *Opheodrys aestivus*, however, has little variation in embryonic development at oviposition and has an incubation period similar to many other oviparous colubrids (Fitch 1970).

Determination of oviposition dates in the field by palpation assumes that each mature female breeds annually. This apparently is the case as all 39 females palped 5–20 June in 1978 were gravid (Table 3), all 40 mature females collected for the laboratory oviposited in 1979, and all 125 females autopsied April–July (1977–1979) were in breeding condition or had evidences of recent oviposition. The annual ovarian cycle is correlated with an annual fat cycle which presumably provides much of the energy needed for reproduction. Energy, in the form of stored fat reserves or as an outcome of foraging success, has been implicated as the major factor in the control of
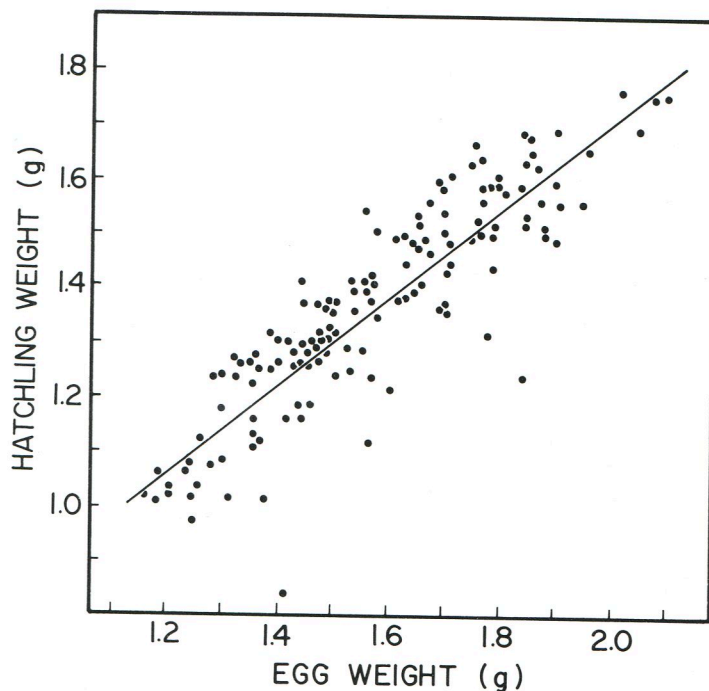
Fig. 5. *Opheodrys aestivus*: The relationship of hatchling weight and egg weight. The regression equation is $\hat{Y} = .79X + .115$ ($r = .85$, $P < .001$).

frequency of female reproduction in several snakes (summarized in Wharton 1966; Gibbons 1972).

Production of equal numbers of male and female hatchlings of similar size and weight is in accordance with Fisher's sex ratio theory and is the usual situation in snakes (Shine and Bull 1977).

Because metabolism decreases with body weight in snakes (Galvao *et al.* 1965) proportionally more energy may be available for reproduction. The risks involved when time and energy are allocated to reproduction may decrease survivorship and therefore the expectation of future progeny (reproductive value). Therefore, a younger snake with a higher expectation of future progeny might be expected to devote less time and energy to reproduction than an older snake which has less expectation (Pianka and Parker 1975; Pianka 1976). Tests of this hypothesis in snakes have shown diverse results. In *Carphophis vermis* (Clark 1970) C/B increases with body size (=age). In *Diadophis punctatus* (Fitch 1975), *Masticophis taeniatus* (Pianka and Parker 1975),

and *O. aestivus* (present study) C/B remains constant with body size. In *Notechis scutatus* and *Pseudechis porphyriacus* (Shine 1977) C/B decreases with body size. Pianka and Parker (1975) and Pianka (1976) suggested that correlations between reproductive effort and reproductive value might be greater in multiple-brooded species than in single-brooded species where proximal factors such as resource availability might have a greater effect. In all of the above studies the snakes were single-brooded. However, in a study of annual reproductive variation in *O. aestivus* (Plummer 1983) it was shown that C/B and other reproductive attributes did not vary between years in which snakes stored greatly different quantities of lipids. Even if reproductive effort remains constant with age (as in *O. aestivus*), the absolute energy allocated to reproduction actually increases. The increased energy available in *O. aestivus* is reflected in the production of larger eggs and larger clutch sizes (Fig. 3). Fecundity in snakes is often related to body size (Fitch 1970; Shine 1977; Aldridge 1979; present study). Shine (1978) found that in about 66% of species (including *O.*

aestivus) females attain a larger body size than males. Shine suggested that one reason for this disparity was that selection has favored large body sizes in the females because of greater fecundity. Another reason for increased body size might be that larger snakes produce larger eggs which produce larger hatchlings (Fig. 5). In general, larger hatchlings should enjoy higher survivorship and be better competitors (Pianka 1976). In the lizard *Sceloporus undulatus* (Ferguson and Bohlen 1978) larger hatchlings from late broods enjoy greater survivorship than do smaller hatchlings, but larger hatchlings from early broods have survivorship similar to smaller hatchlings. Although to my knowledge there are no comparable data for snakes, if female fitness was increased by producing larger eggs then selection should favor either larger parental body size or decreased clutch sizes (Pianka 1976).

Smith and Fretwell (1974), Pianka (1976), and Stewart (1979) discuss models which predict that with a constant reproductive effort, an increased female size may result in either larger clutches or larger sized eggs. These models assume a negative correlation between clutch size and egg weight. In *O. aestivus* there is no statistical relationship between clutch size and egg weight (Fig. 4). Although the correlation between SVL and egg size is not strong ($r = .46$), it appears that in this population correlates of female body size are selection for increased clutch size as well as for increased egg size.

Summary

Various aspects of female reproduction in *Opheodrys aestivus* were examined by specimen autopsy and from the study of living snakes in the field and in the laboratory. These snakes mature at 36–40 cm SVL and breed annually thereafter. Ovarian follicles measuring 1–5 mm in diameter are present in mature snakes throughout the year. Rapid yolking of follicles occurs in the spring and ovulation begins in late May. Extra-uterine transfer of ova is common. One clutch is produced per year ($\bar{x} = 6.1$ eggs). Coelomic fat bodies cycle annually and presumably provide energy for vitellogenesis and ovulation. Oviposition occurs in late June and July. Ninety percent of the eggs laid were fertile and 90% of fertile eggs hatched in the laboratory. At oviposition the modal embryonic stage (Zehr 1962) was 25 (range 21–27). Incubation averaged 39 days. The sex ratio of hatchlings was not significantly different from 1:1. Male and female hatchlings are similar in length and weight. Reproductive effort ($\bar{x} = .64$) did not change with body size. Larger females produce both larger clutches and larger eggs. Larger eggs produce larger hatchlings.

Acknowledgments

Literature Cited

ALDRIDGE, R. D.
1979. Female reproductive cycles of the snakes *Arizona elegans* and *Crotalus viridus*. Herpetologica, 35:256–261.

ANDERSON, P.
1965. The Reptiles of Missouri. Univ. Missouri Press, 330 p.

BLANCHARD, F. N.
1933. Eggs and young of the smooth green snake, *Liopeltis vernalis* (Harlan). Papers Michigan Acad. Sci., Arts, Letters, 17:493–508.

CARPENTER, C. C.
1958. Reproduction, young, eggs and food of Oklahoma snakes. Herpetologica, 14:113–115.

CLARK, D. R.
1970. Age-specific "reproductive effort" in the worm snake *Carphophis vermis* (Kennicott). Trans. Kansas Acad. Sci., 73:20–24.

CONANT, R.
1938. The Reptiles of Ohio. Amer. Mid. Nat., 20:1–200.

CONANT, R.
1975. A field guide to reptiles and amphibians of eastern and central North America. 2nd ed. Houghton Mifflin Co., 429 p.

CONANT, R. and DOWNS, A., JR.
1940. Miscellaneous notes on the eggs and young of reptiles. Zoologica, 25:33–48.

CURTIS, L.
1950. A case of twin hatching in the rough green snake. Copeia, 1950:232.

FERGUSON, G. W. and BOHLEN, C. H.
1978. Demographic analysis: a tool for the study of natural selection of behavioral traits. *In* Greenberg, N. and MacLean, P. D. (eds.), Behavior and Neurology of Lizards. NIMH. DHEW Publ. No. 77-491.

FITCH, H. S.
1970. Reproductive cycles in lizards and snakes. Univ. Kansas, Mus. Nat. Hist., Misc. Publ., 52:1–247.
1975. A demographic study of the ringneck snake (*Diadophis punctatus*) in Kansas. Univ. Kansas, Mus. Nat. Hist., Misc. Publ., 62:1–53.

GALVAO, P. E., TARASANTCHI, J. and GUERTZENSTEIN, P.
1965. Heat production of tropical snakes in relationship to body weight and body surface. Am. J. Physiol., 209:501–506.

GIBBONS, J. W.
1972. Reproduction, growth and sexual dimorphism in the canebrake rattlesnake (*Crotalus horridus atricaudatus*). Copeia, 1972:222–227.

GUIDRY, E. V.
1953. Herpetological notes from Southeastern Texas. Herpetologica, 9:49–56.

MCCAULEY, R. H., JR.
1945. The Reptiles of Maryland and the District of Columbia. Hagerstown, Maryland, 194 p.

MORRIS, MICHAEL A.
1982. Activity, reproduction, and growth of *Opheodrys aestivus* in Illinois (Serpentes: Colubridae). Nat. Hist. Misc., 214:1–11.

MOUNT, R. H.
1975. The Reptiles and Amphibians of Alabama. Auburn Univ. Agric. Exp. Station, 347 p.

PACKARD, G. C., TRACY, C. R. and ROTH, J. J.
1977. The physiological ecology of reptilian eggs and embryos, and the evolution of viviparity within the class Reptilia. Biol. Rev., 52:71–105.

PIANKA, E. R.
1976. Natural selection of optimal reproductive tactics. Am. Zool., 16:775–784.

PIANKA, E. R. and PARKER, W. S.
1975. Age-specific reproductive tactics. Amer. Nat., 109:453–464.

PLUMMER, M. V.
1981. Habitat utilization, diet and movements of a temperate arboreal snake (*Opheodrys aestivus*). J. Herpetol., 15:425–432.
1983. Annual variation in stored lipids and reproduction in green snakes (*Opheodrys aestivus*). Copeia, 1983:741–745.

RICHMOND, N. D.
1956. Autumn mating of the rough green snake. Herpetologica, 12:325.

SABATH, M. and WORTHINGTON, R.
1959. Eggs and young of certain Texas reptiles. Herpetologica, 15:31–32.

SCHOENER, T. W.
1977. Competition and the niche. *In* Gans, C. and Tinkle, D. W. (eds.), Biology of the Reptilia. Academic Press, pp. 370.

SHINE, R.
1977. Reproduction in Australian elapid snakes II. Female reproductive cycles. Aust. J. Zool., 25:655–666.
1978. Sexual size dimorphism and male combat in snakes. Oecologia, 33:269–277.

SHINE, R. and BULL, J. J.
1977. Skewed sex ratios in snakes. Copeia, 1977: 228–234.

SMITH, C. C. and FRETWELL, S. D.
1974. The optimal balance between size and number of offspring. Am. Nat., 108:499–506.

SMITH, P. W.
1961. Amphibians and Reptiles of Illinois. Bull. Illinois Nat. Hist. Survey, 28:1–298.

STEWART, J. R.
1979. The balance between number and size of young in the live bearing lizard *Gerrhonotus coeruleus*. Herpetologica, 35:342–350.

TINKLE, D. W.
1960. A population of *Opheodrys aestivus* (Reptilia: Squamata). Copeia, 1960:29–34.

TURNER, F. B.
1977. The dynamics of populations of squamates, crocodilians, and rhynchocephalians. Pp. 157–264. *In* Gans, C. and Tinkle, D. W. (eds.), Biology of the Reptilia. Academic Press.

VITT, L. J. and CONGDON, J. D.
1978. Body shape, reproductive effort, and relative clutch mass in lizards: Resolution of a paradox. Amer. Nat. 112:595–608.

WEBB, R. G.
1970. Reptiles of Oklahoma. Univ. Oklahoma Press, 370 p.

WHARTON, C. H.
1966. Reproduction and growth in the cottonmouth *Agkistrodon piscivorus* Lacepede, of Cedar Keys, Florida. Copeia, 1966:149–161.

WRIGHT, A. H. and WRIGHT, A. A.
1957. Handbook of Snakes. Vol. I. Comstock Publ., 564 p.

ZEHR, D. R.
1962. Stages in the normal development of the common garter snake, *Thamnophis sirtalis sirtalis*. Copeia, 1962:322–329.