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Annual Variation in Stored Lipids and Reproduction in Green Snakes (*Opheodrys aestivus*)

MICHAEL V. PLUMMER

The amount of body fat is negatively correlated with reproductive activity in *Opheodrys aestivus* as it is in a number of snakes. Based on experimental evidence from lizards, significant reductions in stored body fat preceding vitellogenesis should adversely affect reproductive output. Comparisons are made between reproductive output in *O. aestivus* following a climatically normal year and following an extremely hot and dry year when stored body fat was reduced by approximately 70%. No significant differences were seen in any reproductive parameter between the two years. It is suggested that spring foraging success provided the energy needed for vitellogenesis despite the reduced fat stores.

MOBILIZATION of fat stores for vitellogenetic activity is important for a number of reptilian species (Derickson, 1976). In lizards lipids may be stored subcutaneously or in abdominal fat bodies. However, it is the latter that are the more labile and therefore more immediately subject to storage or utilization (Derickson, 1974). The amount of lipid in fat bodies approximates the amount in egg clutches (Hahn and Tinkle, 1965). Experimental excision of abdominal fat bodies results in a lower rate of yolk deposition, a greater incidence of follicular atresia and delayed or inhibited follicular growth (Hahn and Tinkle, 1965; Smith, 1968). The adaptive significance of fat bodies in lizards appears to be associated with follicular development during periods of low activity or in early season clutches when feeding conditions are below optimum (Smith, 1968; Hahn and Tinkle, 1965). A test of this hypothesis in a natural population of *Urosaurus ornatus* (Ballinger, 1977) demonstrated that reduced fat storage prior to reproduction resulted in a significant decrease in clutch size and clutch frequency. Low fat storage was attributed to reduced food availability due to low precipitation levels (Ballinger, 1977).

Although experimental evidence is lacking, several studies of snakes have shown inverse relationships between vitellogenetic activity and fat body weight as occurs in lizards (Volsøe, 1944; St. Girons, 1957; Tinkle, 1962; Wharton, 1966; Gibbons, 1972; Parker and Brown, 1980; Jackson and Franz, 1981; Plummer, in press). Shine (1977) stated that fat was mobilized for follicular development in several species of Australian snakes. It seems reasonable, therefore, to assume that fat bodies in snakes affect re-

production. Cale and Gibbons (1972) showed that fat body weight was a good indicator of total lipid in snakes and suggested that this relationship was independent of species. In central Arkansas female *Opheodrys aestivus* produce a single clutch annually and typically enter and exit hibernation with about 8% body fat (by weight) stored in the abdominal fat bodies (Plummer, in press). In 1980 after an extremely hot and dry summer, these snakes entered hibernation with about 2% body fat. The subsequent 1981 reproductive output is reported in this paper.

METHODS

The methods duplicated those of an earlier study (Plummer, in press). Female *O. aestivus* were collected at Bald Knob Lake in White County, Arkansas and brought to the laboratory. Body weights, snout-vent lengths (SVL) and fat body weights were measured on 29 freshly-killed specimens collected at various times from 1979-1981. Twenty-nine gravid snakes, collected 18 June-14 July 1981, were housed 1-2 weeks in a large cage until clutches were obtained. Crickets and water were provided ad libitum. Temperature was maintained at 28 ± 2 C and photoperiod at 14L:10D. As soon after oviposition as possible (maximum ca 3 h), females and their respective eggs were measured and weighed and the eggs were individually marked with a felt-tipped pen. Each egg was incubated individually at 28 C on top of a thin layer of vermiculite with water added (1:1 by wgt.) in a small glass jar. On the day of emergence from the egg, hatchlings were weighed, measured (SVL) and sexed.

Statistical procedures follow Sokal and Rohlf

TABLE 1. MEAN MONTHLY MAXIMUM TEMPERATURE AND TOTAL MONTHLY PRECIPITATION (MM) AT THE STRAWBERRY SUBSTATION OF THE UNIVERSITY OF ARKANSAS AGRICULTURAL EXPERIMENT STATION, CA 4.5 KM NE BALD KNOB LAKE.

	10-year means (1968-1977)		1978		1979		1980		1981	
	Max. temp.	Total precip.	Max. temp.	Total precip.	Max. temp.	Total precip.	Max. temp.	Total precip.	Max. temp.	Total precip.
Mar.	15.9	173	14.2	91	15.4	127	13.3	147	17.2	107
Apr.	21.9	124	24.1	81	20.6	264	21.7	168	26.1	76
May	26.0	107	25.1	160	24.0	229	27.0	137	25.5	262
Jun.	30.1	99	31.2	142	29.3	86	31.9	25	31.4	150
Jul.	32.2	117	33.4	66	31.1	147	39.1	0.5	33.4	97
Aug.	31.1	89	32.3	107	29.4	135	37.1	0.3	31.6	79
Sept.	27.6	130	28.4	97	26.6	109	32.4	145	27.7	33
Oct.	22.8	102	23.4	53	23.6	81	23.1	97	21.2	174

(1969). Weights of abdominal fat bodies are expressed as FBW = fat body wgt. (g)/total body wgt. (g) \times 100. A female fatness index (FI = body wgt. (g)/SVL (cm)) is used to express general degree of health in post-ovipository snakes (Ballinger, 1977). Because the 1979 and 1981 SVL's of the females were not statistically different ($P > 0.90$), body sizes and clutch parameters were compared by *t*-tests.

RESULTS

If one assumes that the 10-year means of the various climatic variables from the years 1968-1977 represent a "normal" year, then 1978 was a normal year climatically but 1980 deviated significantly from the norm (Table 1). Specifically, the months June-Sept. in 1980 were much hotter and drier than normal. Only 0.8 mm of precipitation fell from 19 June to 4 Sept., compared to a normal ca 260 mm for this period, and only 25 mm fell from 4 to 15 Sept. Thereafter, precipitation was nearly normal. During this dry period air temperatures soared to rec-

ord levels, especially maximum daily temperatures. Days when temperatures reached at least 38 C in July-Sept. numbered 42 as compared to an average 1.1 for a normal year. On six days from 1 to 15 Sept. temperatures reached 38 C compared to a normal zero days, but thereafter air temperatures moderated to normal levels coincident with the return of normal precipitation.

In 1978 *O. aestivus* exited hibernation with 7.2% body fat following a climatically normal 1977 (Table 2). FBW's decreased to a low of 1.9% in June coincident with oviposition but then increased steadily to 8.6% in Sept.-Oct. (Table 2). Climatically, 1979 was normal and the single FBW available suggests that snakes entering hibernation in that year had normal FBW's. Oviposition normally occurs from late June through July (Plummer, in press). Coincident with post-ovipository females in 1980 was the severely hot and dry weather. In 1980 females entered hibernation with <25% of the fat that they had in the previous two years (Table 2). FBW's were still greatly reduced in spring

TABLE 2. FAT BODY CYCLING IN MATURE *O. aestivus* IN FOUR DIFFERENT YEARS. Data from 1978 are from Plummer (in press). Data are fat body wet weight/total body weight \times 100 and are expressed as mean \pm 1 SE (N).

Period	1978	1979	1980	1981
Apr.-15 May	7.2 \pm 0.62 (14)	9.6 \pm 1.9 (2)	—	2.58 \pm 0.34 (2)
16-31 May	7.9 \pm 0.57 (16)	—	—	2.26 \pm 0.48 (6)
Jun.	1.9 \pm 0.20 (30)	—	—	1.09 (1)
Jul.	2.3 \pm 0.38 (16)	—	—	—
Aug.	5.1 \pm 0.57 (6)	—	—	—
Sept.-Oct.	8.6 \pm 0.77 (9)	10.5 (1)	2.1 \pm 0.33 (9)	5.7 \pm 0.50 (8)

1981 up until the time of ovulation which normally occurs in late May through June (Plummer, in press). FBW's were greatly elevated in Sept.–Oct. 1981 compared to preovulatory levels but were not as great as in previous years.

The eight snakes collected in April–May 1981 (SVL = $47.2 \pm .92$ cm) were not statistically different in SVL from those that were collected later in the year and which oviposited in the laboratory (SVL = $45.3 \pm .82$ cm; $P > 0.20$; t -test). These eight snakes all had yolking follicles (3–5 mm diameter in the April–15 May sample and 7–22 mm in the 16–31 May sample). The FBW for the April–May 1981 snakes ($2.34 \text{ g} \pm 0.36 \text{ g}$) was not statistically different from that of the fall 1980 snakes (2.1 ± 0.33 ; $P > 0.50$; t -test). These data suggest that the small sample in spring 1981 was reproductive and was representative of the population as a whole.

No significant differences were seen in various snake and clutch variables in 1979 as compared to 1981 (Table 3). Correlations between several variables in 1981 (1979) were: SVL-Clutch size = 0.49 (0.57); SVL-Clutch wt./body wt. = -0.36 (0.02); SVL-Egg wt. = 0.56 (0.46); Clutch size-Egg wt. = 0.19 (0.13). There were no significant differences between any of the correlation coefficient pairs of the 2 years ($P > 0.10$; tests of homogeneity among correlation coefficients; Sokal and Rohlf, 1969).

DISCUSSION

From a low of ca 2% fat in June 1978, female *O. aestivus* increased FBW's to ca 8% in Sept. However, FBW's did not increase after June 1980 because Sept. 1980 samples had values similar to that of June. Caterpillars, spiders, grasshoppers and crickets, and odonates constitute more than 85% of the diet of *O. aestivus* at Bald Knob Lake (Plummer, 1981). Presumably, the low FBW's in 1980 resulted from the reduced food availability from July–Sept. due to the extremely low precipitation and high air temperatures. Strong relationships between insect biomass and precipitation in temperate latitudes have been shown by Derickson (1976) and Ballinger (1977); Janzen and Schoener (1968) found the same results for tropical latitudes. In Texas Dunham (1978) found a positive correlation between individual foraging success of lizards and prey abundance which itself was positively correlated with annual precipitation.

If, in fact, low stored fat does adversely affect

TABLE 3. COMPARISON OF VARIOUS SNAKE AND CLUTCH VARIABLES IN 1979 AND 1981. Data are mean \pm 1 SE (range). There are no differences between years which are significantly different (at least $P > 0.50$ except for P.O. wt. in which $P > 0.10$).

Year	SVL (cm)	Post-ovipository wt. (g)	Fatness index	Clutch size	Clutch wt. (g)	Clutch wt./body wt.	Egg wt. (g)	Hatching wt. (g)
1979 (N = 30)	45.4 ± 0.80 (35.0–54.0)	15.2 ± 0.76 (9.2–28.3)	0.33 ± 0.012 (0.20–0.53)	6.0 ± 0.33 (3–10)	9.41 ± 0.52 (3.92–15.82)	0.64 ± 0.034 (0.21–1.11)	1.62 ± 0.015 (1.17–2.26)	1.37 ± 0.016 (0.82–1.76)
1981 (N = 29)	45.3 ± 0.82 (39.0–54.5)	17.0 ± 0.81 (11.0–27.0)	0.37 ± 0.012 (0.26–0.50)	6.0 ± 0.21 (4–8)	9.62 ± 0.42 (5.71–15.28)	0.58 ± 0.026 (0.30–0.99)	1.59 ± 0.016 (1.05–2.07)	1.33 ± 0.021 (0.75–1.65)

reproduction in *O. aestivus*, there are several possible outcomes resulting from low fat levels. First, reproduction could be delayed until the following year as occurs in some populations of viviparous viperids (St. Girons, 1957; Tinkle, 1962). However, in 1981 all mature female *O. aestivus* appeared gravid in the field during June and all mature females brought to the laboratory produced clutches just as occurred in 1978–79 (Plummer, in press). Secondly, snakes could produce fewer numbers of eggs or produce smaller eggs which would result in smaller hatchlings (Plummer, in press). However, there were no statistical differences in clutch size, egg size or hatchling size in 1981 compared to those in 1978–79. Thirdly, vitellogenesis and ovulation could be delayed until fat stores were increased by feeding. Smith (1968) described feeding in female *Ameiva* spp. which had undergone fat body excision as "voracious." In 1981, however, *O. aestivus* oviposited on a schedule similar to that in 1978–79. Fourthly, somatic tissue (subcutaneous lipids or other) could be mobilized to synthesize yolk. However, post-ovipository body weights of the 1981 females were not statistically different from those of 1979 females.

Because none of the above options were implemented it could be argued that stored fat had no effect upon reproduction. In light of the observed inverse relationship between FBW and reproductive activity in *O. aestivus* (Plummer, in press) and of the experimental data on lizards establishing a direct relationship between fat and reproductive activity (Hahn and Tinkle, 1965; Smith, 1968), it seems more reasonable to argue that another factor substituted for the reduced fat stores in 1981. The most likely candidate is that of spring foraging success. Rainfall and temperature in spring 1981 were at normal levels. Correlates of these climatic factors would be greater insect biomass (Janzen and Schoener, 1968; Derickson, 1976; Ballinger, 1977; Dunham, 1978) and better individual foraging success (Dunham, 1978). Supporting evidence comes from the fact that FBW's of *O. aestivus* more than doubled from May–Sept. 1981. Much of the energy derived from spring foraging probably would be used normally for somatic growth. However, more could be diverted (as presumably in 1981) to follicular growth when little fat has been stored from the previous year. Fat bodies themselves are not essential to reproduction in late season (second and third) clutches of *Uta stansburiana* when feeding op-

portunities are optimum (Hahn and Tinkle, 1965). Even in early season (first) clutches fat body depletion during vitellogenesis is greatly lowered if the lizards are generously fed in the laboratory (Hahn and Tinkle, 1965).

The foregoing discussion assumes that the 2.3% FBW in April–May of 1981 was too low by itself to support an average clutch. Some insight into this assumption may be gained by comparing amounts of fat body lipid with clutch lipid. Using Hahn and Tinkle's (1965) estimate of 19.4% lipid (wet wgt.) in shelled oviductal eggs of the lizard *Uta stansburiana*, total lipid in an average *Ophedrys* clutch in 1981 was 0.194×9.62 (wgt. of avg. clutch) = 1.87 g. An average 25 g snake with ca 2.3% FBW in spring should have ca 0.58 g of fat. Of this amount ca 90% is ether-alcohol extractable lipid (Hahn and Tinkle, 1965) or ca 0.52 g. Therefore, in 1981 fat bodies in April–May accounted for only 28% of the total egg clutch lipid. Similar calculations for normal (1978–1979) years assuming 7.6% spring FBW yield 1.71 g of lipid for an average snake and 1.83 g in an average clutch. Therefore, in a more climatically normal year, FBW and egg clutch lipid are roughly equivalent. Because the 1978 June sample had shelled oviductal eggs and fat bodies averaging 0.48 g, it appears that not all the fat body lipid is mobilized for vitellogenesis even in a normal year and that foraging normally makes some contribution.

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Rapid Development of the Clonal State in Successive Gynogenetic Generations of Carp (*Cyprinus carpio*)

ANDRÁS NAGY, ZSUZSA MONOSTORY AND VILMOS CSÁNYI

Rapid development of the clonal state in the successive gynogenetic carp generations was demonstrated using tissue transplantation. The higher the number of gynogenetic generations, the longer were the survival times of the allografts. In the fourth gynogenetic generation, the lack of allograft rejection or pigment cell destruction within the test period clearly shows the high level of isogenity in this generation.

By altering the paternal contribution in goldfish, we showed the sensitivity of tissue transplantation to genetic diversity in a population.

IN lower vertebrates gynogenesis may serve as an extremely useful genetic tool for producing clones or inbred strains (Nace, 1968; Streisinger et al., 1981), for mutant isolation (G. Streisinger, pers. comm.), for establishment of unisex female populations (Stanley and Sneed, 1973; Nagy et al., 1978), and for direct genetic analysis (Nace et al., 1970; Nagy et al., 1979).