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Abstract

Female reproductive characteristics of 17 genera of Arkansas snakes (27 species and subspecies) were examined. Most of the snakes (n = 495) were collected over a 10-year span (1984-1993). Methods used to estimate clutch and/or litter size were as follows: 1) counts of previtellogenic ovarian follicles, 2) counts of vitellogenic ovarian follicles, 3) counts of oviductal eggs or embryos, 4) counts of corpora luteal scars, and 5) counts of neonates from egg clutches or litters. In several species, Method 1 tended to overestimate clutch size as determined by Method 2 by as much as 100% (e.g., in *Diadophis punctatus, Elaphe obsoleta,* and *Lampropeltis getula*), whereas these methods produced similar counts in *Virginia striatula* and *Thamnophis proximus*. The largest clutch size as estimated by Method 1 was 79 ova in a 744 mm in snout-vent length (SVL) individual of *Thamnophis sirtalis*; the smallest clutch size as recorded by this method was in *Carphophis vermis* (2 ova; 182 mm in SVL). Method 2 reduces the total egg count by one third over Method 1 in most species, and this count was very similar to the estimates obtained by Method 3, the most reliable way to estimate clutch or litter size (without actually having counts from egg clutches or litters). The presence of atretic ovarian follicles accounts for discrepancies found between clutch size estimates using Methods 1 and 2 as compared to Method 3. Comparisons of clutch sizes in Arkansas specimens to those recorded for snake species in neighboring states revealed similar sizes in 13 species; counts were larger in 8 species from Arkansas and smaller in only one species.

Introduction

Baseline reproductive data have been compiled for many wide-ranging North American snake species (Wright and Wright, 1957; Fitch, 1970, 1985; Seigel and Ford, 1987; Ernst and Barbour, 1989; Ford et al., 1990). There remain, however, large geographic regions in the United States that lack such life history data. Geographic variation in snake reproductive traits does exist (Fitch, 1985), but seasonal and annual variation in reproductive traits within and between populations of a species are less well documented. Some species, such as *Storeria occipitomaculata*, show little latitudinal population variation in female reproductive traits between Michigan and South Carolina (Semlitsch and Moran, 1984), whereas Fitch (1985) found that 60% of 25 snake species in the United States showed a northward increase in clutch/litter size.

Few detailed studies on snake reproductive biology have been conducted on snake populations within the state of Arkansas (Plummer, 1983, 1984, 1992; Trauth, 1991; Robinette and Trauth, 1992) when compared with surrounding states [see snake accounts for Kansas (Collins, 1993), Oklahoma (Carpenter and Krupa, 1989), Louisiana (Dundee and Rossman, 1989), Missouri (Anderson, 1965; Johnson, 1987), and Texas (Dixon, 1987). In 1984 a statewide field survey of Arkansas snakes was initiated by one of us (SET) to attain large samples in an effort to establish baseline life history data on snake populations dwelling within the state. Herein, we report on reproduction in 27 species and subspecies representing 17 genera (and two families) of Arkansas snakes by an analysis of museum specimens. We hope our effort will stimulate more intensive studies of geographic and temporal variation on snake reproductive parameters within the state.

Materials and Methods

Reproductive data were derived via gross dissection of 495 preserved females comprised within two snake families (Colubridae and Viperidae) and 27 species and subspecies; this equates to approximately 66% of the known species and subspecies of snakes currently found in Arkansas. Nomenclature followed Conant and Collins (1991). Most snakes were collected from habitats throughout Arkansas between 1984 and 1993; voucher specimens are deposited in the Arkansas State University herpetology museum. Additional Arkansas specimens were borrowed from the Milwaukee Public Museum. Among the variables recorded from each specimen were the following: 1) snout-vent length (SVL), 2) number and size (greatest length = diameter, in some cases) of previtellogenic ovarian follicles (**POF**), 3) number and size (greatest length) of vitellogenic ovarian follicles (**VOF**), 4) number of oviductal eggs and/or oviductal embryos

(OE/OEM), and 5) number of corpora lutea (CL). In most specimens, at least 10 (if present) of the largest ovarian follicles per specimen were counted and measured. Immature ova less than 2 and 3 mm in small and large snakes, respectively, were not counted. In several instances, egg clutches deposited in captivity or collected in nature as well as litters born to females held in confinement provided additional data on clutches. Estimation of clutch or litter size can be based upon a combination of the above methods; however, follicular atresia is common to all size classes during vitellogenesis in snakes (Aldridge, 1979; Fitch, 1985). Thus, the most reliable technique is to use only greatly enlarged VOF (in most cases, > 5 mm in length in small snakes, > 10 mm in intermediate-sized snakes, and > 20 mm in large snakes) when incorporating counts of developing ova. For the purpose of contrasting variation in reproductive potential based on breeding condition within and among species, all methods were employed to some extent. Along with female clutch characteristics mentioned above, we report on other pertinent life history information; the data are from mostly spring and summer samples. Figures 1-9 detail the relationships among date of collection, female SVL, female fecundity (= clutch/litter size; see Ballinger 1978), and stage of reproduction on 21 species, in some instances, reporductive data from injured or abnormal females were omitted from Figs. 1-9, but were included elsewhere. In each species summary (discussed below), we have compiled the data into groups based upon the species; size, mode of reproduction (oviparous = egg layers vs viviparous = livebearers), and family (Colubridae or Viperidae). Colubrids are either oviparous or viviparous, whereas all viperids in Arkansas are viviparous: In all species we state which method (or combination of methods) was used to determine fecundity; mean values for clutch size data as well as for other parameters are, in most instances, accompanied by ± 2 SE (standard error), range, and sample size. Unless stated otherwise, all lengths are in mm.

Results and Discussion

Small Oviparous Colubrid Species.--Four relatively small secretive species were examined in this category. Each deposits one clutch of eggs from late May to mid-June. Hatching occurs around 50 to 60 days following oviposition. In the western worm snake (*Carphophis vermis*), clutch size averaged 3.4 ± 0.5 (2-5; n = 17) using only VOF (> 3 mm in length). This mean was similar to the value reported by Fitch (1985–data from Clark, 1970) for Kansas (3.3; n = 47; value derived by combining VOF and early OE). No females contained OE, and we discovered no egg clutches. Mean adult SVL of reproductive females in Arkansas was 222.6 ± 22.3 mm (186-263; n = 17), whereas 216 mm in SVL was the smallest adult female in Kansas (Clark, 1970). This species produces from 1 - 6 eggs in Missouri (Johnson, 1987). By mid-April in Arkansas, most adult females possessed VOF averaging 9.4 mm ± 1.45 (6.6-13.0; n = 11), although one female with two VOF ($\bar{x}$ = 12.5 mm) was collected on 18 March 1980. Aldridge and Metter (1973) indicated that vitellogenesis begins in ova prior to hibernation in October in Missouri.

In Arkansas clutch size of the northern scarlet snake (*Cemophora coccinea copei*) averaged 4.3 (4-11; n = 3) and was derived using VOF and OE. Developing ovarian follicles averaged 7.9 and 19.7 in two females (336 and 355 mm in SVL, respectively) collected on 20 May 1987 and 26 June 1989, and the one female (289 mm in SVL) possessing OE was collected on 14 June 1989. The largest specimen, a postreproductive female (382 mm in SVL), was taken from Dallas County on 27 July 1991. No egg clutches were discovered during the present study; however, eggs (as well as adults) have been found in sandy and/or red clay soils (Sutton and McDaniel, 1979; Trauth, 1982). Ford et al. (1990) reported a single clutch of six eggs laid by a captive female on 27 June 1988.

Clutch size in the prairie ringneck snake (*Diadophis punctatus arnyi*) was determined as follows: 1) by using POF, clutch size averaged 5.3 (4-8; n = 7), 2) by using VOF, the mean was 3.8 (2-5; n = 8), and 3) with OE, the mean was 4.0 (3 and 5; n = 2). By combining the latter two methods, clutch size averaged 3.8 ± 0.6 (2-5; n = 10). Fitch (1985) reported an average of 3.9 (1-10; n = 300) in northeastern Kansas using the first two methods, whereas Johnson (1987) stated that in Missouri this species may produce from one to ten eggs. Vitellogenesis in Arkansas specimens occurred rapidly after ova reach a length of around 7.0 mm. By mid-April most adult females possessed VOF averaging at least 9.0 mm in length; OE first appeared in mid-May. One female (282 mm in SVL) contained enlarged ova averaging 13.9 mm in length on 5 June 1980. Fitch (1975) provided the most detailed study on female reproduction for this subspecies.

The smallest snake species found in Arkansas is the flathead snake (*Tantilla gracilis*); adult females averaged 161.1 ± 14.0 mm in SVL (133-180; n = 16). This species emerges from hibernation as early as late March in Arkansas and, at that time, has previtellogenic ova averaging less than 3.0 mm (Fig. 1). Mean clutch size, using all methods, was 4.9 ± 1.3 (2-12; n = 16) and using VOF and OE, was 3.1 ± 0.7 (2-4; n = 7). Clutch size as reported by Force (1935) and Carpenter (1958) in Oklahoma populations is generally 2-3 eggs; in Kansas, 1-3 eggs (Fitch, 1985); in Missouri, 1-4 eggs (Johnson, 1987), and in Texas, 2-3 eggs (Cobb, 1990).

Medium-sized Oviparous Colubrid Species.--Two snake species examined during this study fall into this category;

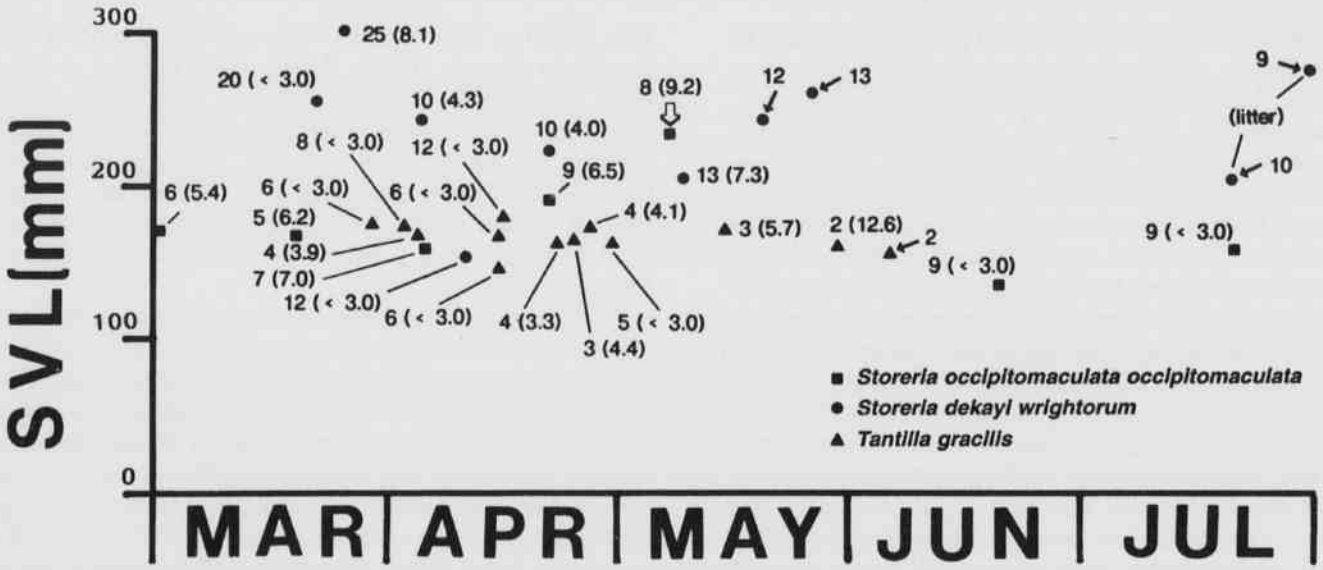

Fig. 1. Relationship between female body size (SVL) and reproductive condition in samples of three Arkansas snakes (*Storeria occipitomaculata occipitomaculata*. *S. dekayi wrightorum*. and *Tantilla gracilis*) according to month. Numerals (outside parentheses) = total number of ovarian follicles, oviductal eggs/embryos (designated with arrows), or neonates (of litters) for each snake. Other numerals (inside parentheses) = average length of ovarian follicles or designate size of previtellogenic follicles (open arrow = average length of oviductal eggs).

both are found throughout most of Arkansas. Clutch characteristics for the eastern hognose snake (*Heterodon platirhinos*) are shown in Fig. 2. Clutch size averaged 22.2 (20-44; n = 4), 25.2 ± 6.1 (15-44; n = 11), and 20.5 (15 and 26; n = 2) using **POF**, **VOF**, and **OE**, respectively. Using only **VOF** and **OE**, the average was 24.5 ± 5.4 (15-44; n = 13). Regression analysis revealed a significant positive correlation (r = 0.75; n = 13; $P < 0.01$) between clutch size (CS) using **VOF** and **OE** and SVL. The regression equation (CS = 30.7895 + 0.0850SVL) predicts that for an increase of 12 mm in SVL, a concomitant increase of one in clutch size would be observed. Enlarged ova were present in adult females in early March; the smallest female (531 mm in SVL) with advanced **VOF** was captured on 16 May 1993. Oviductal eggs were found in one female in early May. Females with a SVL of less than 500 mm were considered immature; this was also true for populations studied by Platt (1969). In addition, Platt (1969) summarized the literature on clutch size and reported a mean of 22.3 eggs (4-61; n = 59). Ford et al. (1990) reported on a clutch of 30 eggs laid by a captive female (660 mm in SVL) on 18 June 1988.

Figure 3 summarizes clutch characteristics on nine individuals of the Louisiana milk snake (*Lampropeltis triangulum syspila*). Vitellogenesis begins in early April in females greater than 325 mm in SVL. Clutch size was derived from counts of **POF**, **VOF**, and **OE**; the average was 8.0 ± 3.2 (4-13; n = 7). The largest vitellogenic ova observed in this subspecies averaged 23.2 mm in length in an early June specimen measuring 730 mm SVL. One female collected on 26 June 1976 contained **OE**; no egg clutches were discovered in this subspecies. Williams (1988) stated that nine clutches from Missouri averaged 5.2 eggs (4-7) and were deposited between 18 June and 22 July; however, Anderson (1965) reported from 6 to 12 eggs per clutch in Missouri. Fitch (1970) reported an average clutch size of 10.2 for 20 clutches (for all subspecies), but in his summary on reproduction on this subspecies (Fitch, 1985), he gives an average clutch size of 6.3 for northeastern Kansas.

Large Oviparous Colubrid Species.--This group of seven large-bodied snakes includes several of the longest and fastest snakes that occur in Arkansas; each species lays a single clutch of eggs per reproductive season. There are few documented records of the Great Plains rat snake (*Elaphe guttata emoryi*) from Arkansas; only a single adult female (of 10 animals) contained 12 **POV** on 4 April 1992. [Recently, the subspecific name (*emoryi*) of Arkansas populations was changed to *meahllmorum* (Smith et al., 1994).] On the other hand, the black rat snake (*Elaphe obsoleta obsoleta*) is a very common species in Arkansas and becomes active in early April. Previtellogenic ova (< 10 mm in diameter) dominated ovaries throughout April (Fig. 2). Clutch size using **POF** averaged 24.0 ± 3.1 (16-33; n = 10) and was approximately twice the size of the mean (12.1; 7-17; n = 7) derived using **VOF**. A grand mean of 11.6 ± 2.7 (7-17; n = 9) was found using **VOF**, **OE**, and one egg clutch. This two-fold decrease in clutch size is possibly the result of an especially high rate of follicular atresia in *E. o. obsoleta*. Rat snakes produce relatively large

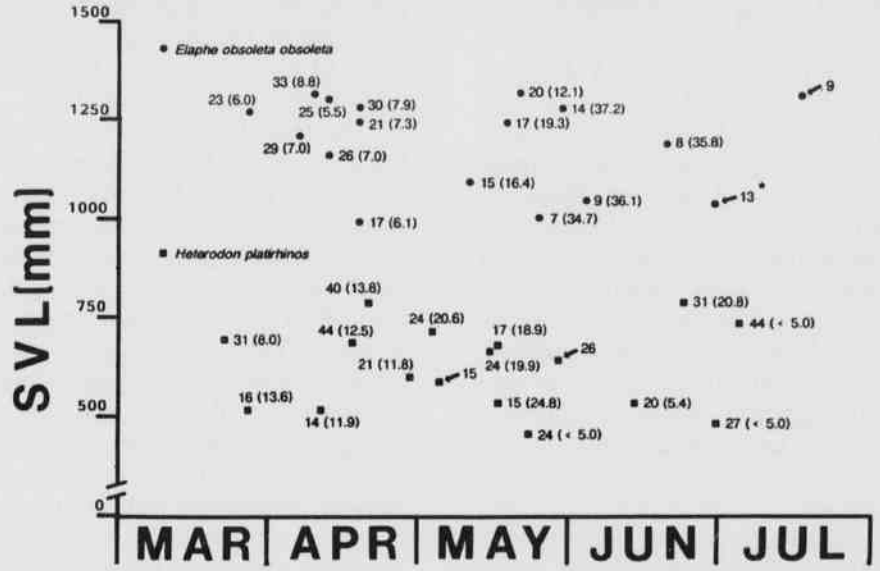

Fig. 2. Relationship between female body size (SVL) and reproduction condition in samples of two Arkansas snakes (*Elaphe obsoleta obsoleta* and *Heterodon platirhinos*). See Fig. 1 for explanation of numerals.

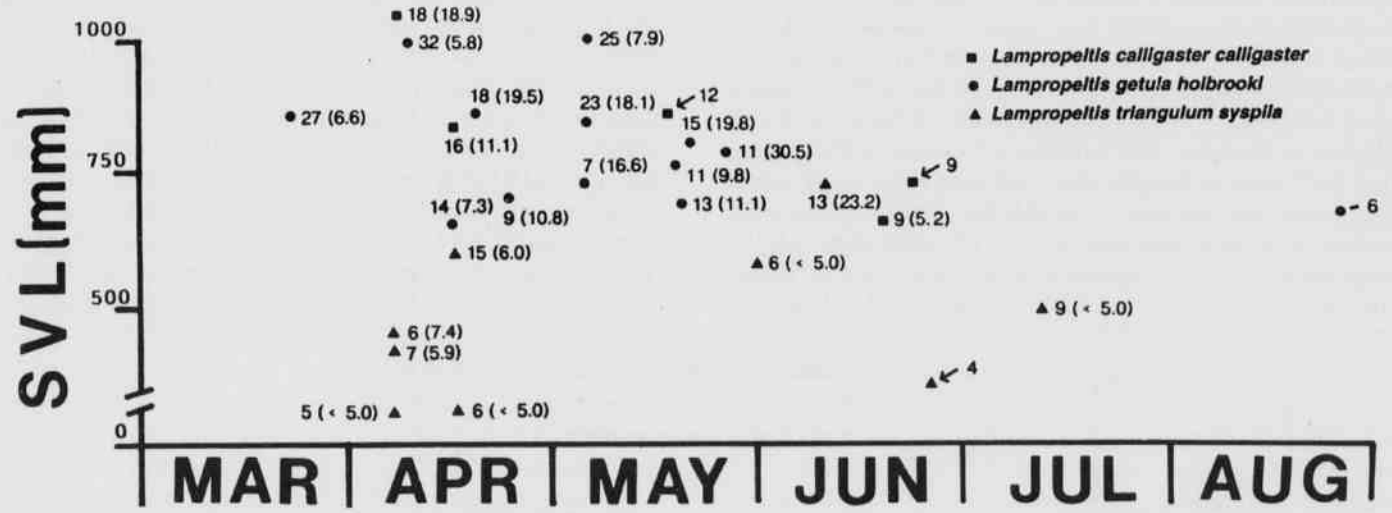

Fig. 3. Relationship between female body size (SVL) and reproduction condition in samples of three species of *Lampropeltis* from Arkansas. See Fig. 1 for explanation of numerals.

eggs (see below), and their coelomic cavity may be unable to expand in order to accomodate the potentially large numbers of eggs as evidenced by counts of **POF**. Fitch (1985) summarized the many records for clutch size in this species throughout its range in the United States; he reported mean clutch sizes (states grouped on a regional basis) to be the following: 13.9 (northeast), 11.2 (north-central), and 14.1 (southern). The mean for Arkansas specimens is closest to the northcentral states (Kansas and Missouri). In our study, only one female (a large specimen, 1308 mm SVL collected 16 July 1989), contained **OE** which numbered 9. (Early embryogenesis had begun within these eggs; the average crown-rump length of these embryos was around 5 mm.) Egg length and width of these eggs averaged 53.4 mm by 24.2 mm, whereas the average dimensions of two egg clutches of 8 and 9 eggs (collected in fallen trees on 30 July 1991 and 7 August 1986) were 47.0 mm by 26.6 mm and 41.4 mm by 25.4 mm, respectively. Corpora lutea (n = 13) were counted in one postreproductive female collected 30 June 1986.

Three subspecies of racers (*Coluber constrictor*) occur in Arkansas; two of these (*anthicus* and *priapus*) were examined during this study. A single specimen of the buttermilk racer (*C. c. anthicus*) yielded a clutch size of 16 (Fig.

4); otherwise, the rest of the reproductive data was derived from specimens of the southern black racer (*C. c. priapus*). Using counts obtained from **POF**, **VOF**, and **OE**, mean clutch sizes were 25.0 ± 4.2 (17-29; n = 7), 15.6 ± 2.2 (8-23; n = 13), and 16.3 ± 6.9 (14-26; n = 6), respectively. By combining the latter two methods, a grand mean was calculated to be 16.9 ± 2.0 eggs per clutch (8-26; n = 19). Racers begin vitellogenesis when follicles are approximately 6.0 mm in diameter; vitellogenic follicles reach a maximum of around 25.0 mm. Ovulation occurs in larger females by mid-May and in smaller females by late May. Oviposition occurs from mid-June until mid-July (Fitch, 1963). Fitch (1985) stated the *C. c. priapus* produced an average of 12.0 eggs per clutch in southern states (South Carolina, Florida, and Georgia) and that the maximum clutch size tended to occur in more northern populations of the species.

Two kingsnakes, the prairie kingsnake (*Lampropeltis calligaster calligaster*) and the speckled kingsnake (*L. getula holbrooki*), are common throughout Arkansas; clutch characteristics for both species are found in Fig. 3. Reproductive information on *L. c. calligaster* was limited; the largest female (1040 mm in SVL) contained large **VOF** ($\bar{x}$ = 18.9 mm in diameter) in early April. Clutch size based upon combined counts of **VOF** and **OE** averaged 14.0 ± 3.9 (9-20; n = 6). One specimen (908 mm in SVL) collected in October 1973 contained enlarged **POF** averaging 9.23 mm in length; this indicates that, as in some other snake species (e.g., *Carphophis vermis* and *Nerodia sipedon*--Aldridge and Metter, 1973; Aldridge, 1979, respectively), previtellogenic ova showed some enlargement prior to hibernation. Fitch (1985) noted that southern populations of prairie kingsnakes (specifically, southern parts of Illinois and Missouri) have clutch sizes averaging 11.0 (5-17; n = 9). Oviposition was observed in late June in Missouri (Johnson, 1987).

The transition from previtellogenic to vitellogenic follicles in female *L. g. holbrooki* occurred at approximately 8.0 mm in length. By early May, most large females have greatly enlarged **VOF**; yet, several specimens (both large and small) still possessed early-developing **VOF** in mid-May. Clutch size ranged from 14 to 32 ($\bar{x}$ = 23.5; n = 4) using **POF**, whereas the average was 13.1 ± 3.3 (7-23; n = 9) using **VOF**. Here again, the discrepancy between clutch size estimates using numbers of follicles may be similar to that observed in *Elaphe obsoleta* (i.e., a reduction in the reproductive potential due to follicular atresia). No females contained **OE**; however, one specimen (675 mm in SVL) in August exhibited six **CL**. Anderson (1965) reported egg laying in captive females in early July in Missouri. Average clutch size for southeastern states as reported by Fitch (1985) was 9.8 (5-17; n = 15).

The reproductive biology of the eastern coachwhip (*Masticophis flagellum flagellum*) is poorly known throughout its range in the United States; nothing has been published on its reproduction in Arkansas. Only two specimens of the eastern subspecies (*M. f. flagellum*) yielded data on clutch size (Fig. 4); one of these, an individual (1272 mm in SVL) collected 18 May 1986, had the largest average **VOF** (37.2 mm; n = 18) of all the large, oviparous colubrids examined during this study. The other specimen contained 14 **OE**; together, a mean clutch size of 16.0 was recorded. Postovipositional females (1265 mm in SVL, 19 June 1987; 1272 mm in SVL, 29 June 1986; 1148

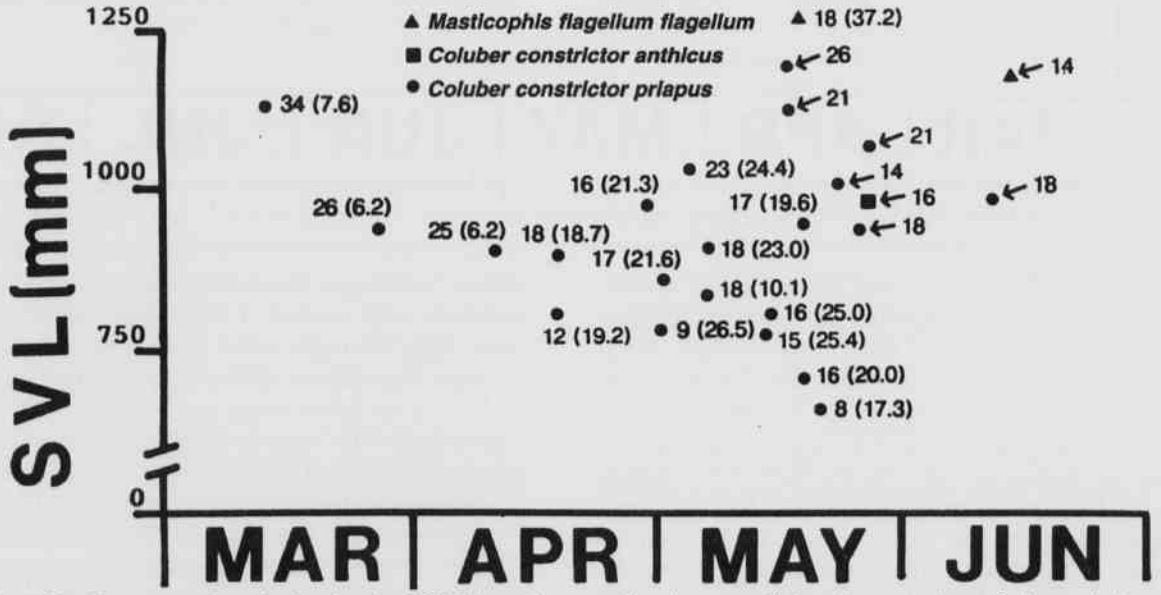

Fig. 4. Relationship between female body size (SVL) and reproduction condition in samples of three Arkansas snakes (*Masticophis flagellum flagellum, Coluber constrictor anthicus,* and *C. c. priapus*). See Fig. 1 for explanation of numerals.

mm in SVL, 6 July 1975) were also observed. From 8 to 24 eggs have been reported for this species in Missouri (Johnson, 1987), and Ford et al. (1990) recorded a clutch of 11 eggs in a female (1160 mm in SVL) in northeastern Texas. Ernst and Barbour (1989) determined that for 16 clutches ranging from 4 to 24 eggs, clutch size averaged 12.3 eggs.

Small Viviparous Colubrid Species.--Two genera comprising four species fall within this category of small woodland snakes; there exists a considerable amount of reproductive data on these species from the literature. Clutch and/or litter characteristics for the midland brown snake (*Storeria dekayi wrightorum*) and the northern redbelly snake (*S. occipitomaculata occipitomaculata*) are shown in Fig. 1. In *S. d. wrightorum*, vitellogeneis begins in ova around 3.0 mm in length sometime in late March or early April. Clutch size averages using **POV** and **VOF** were 16.5 (12-20; n = 4) and 13.8 (10-25; n = 6), respectively. Two litters averaged 9.5 neonates; a grand mean of 14.0 ± 2.8 (10-25; n = 12) was found when utilizing all methods. One female (205 mm in SVL) gave birth on 18 July 1989; the total lengths (in mm) of all young were as follows: 72, 74, 79, 83, 84, 85, 85, 87, 87, and 89. In addition, this female exhibited four large atretic follicles. Another female gave birth to a litter of 9 young on 4 August 1987 (no measurements available for these young). Fitch (1970) reported a mean of 14.0 (3-27) in 62 litters (a value identical to what we found as a grand mean). In Louisiana, Kofron (1979a) also reported a similar mean litter size of 14.9 (using several methods), whereas Ford et al. (1990) found a lower average litter size of 9.3 (4-15; n = 15) in northeastern Texas. Carpenter (1958) observed three litters (8, 12, and 9) in Oklahoma; dates of parturition were 26 July, 7 August, and 12 August, respectively.

There have been few studies that have adequately documented the reproductive biology of *S. o. occipitomaculata* in the southwestern portions of its range as compared to studies in other regions (Blanchard, 1937; Semlitsch and Moran, 1984; Brodie and Ducey, 1989). In Arkansas, redbelly snakes emerge from hibernation in March and have ovaries with developing follicles soon thereafter. Using counts of **POF**, **VOF**, and **OE**, a mean clutch size of 7.6 ± 1.2 (5-9; n = 7) was found. The largest female (235 mm in SVL) available for examination contained **OE** on 7 May 1994 (Fig. 1). Average litter size varies according to geographic region–8.2 (3-15) in the northeastern region, 7.2 (1-15) in the northcentral region, and 9.7 (3-18) in the northwestern region (Fitch, 1985). In Texas, Ford et al. (1990) reported on two litters (10 and 15) in *S. o. obscura* with females giving birth in July.

The rough earth snake (*Virginia striatula*) is one of the most common species of small snake encountered during the spring in Arkansas. Mean clutch size was calculated using **POF** (7.3 ± 0.8; 3-10; n = 18), **VOF** (7.0 ± 1.1; 5-9; n = 8), and **OE** (6.5; 4-9; n = 4). A grand mean using all methods was 7.1 ± 0.3 (3-10; n = 30). In our study, clutch size (using only greatly enlarged **VOF**) was positively correlated with SVL (r = 0.76; $P < 0.01$; n = 22). The regression equation (CS = - 5.5560 + 0.0620SVL) predicts that for every increase of 16 mm in SVL, and accompanying increase in one in clutch size will be observed. Atretic follicles were prevalent in most adult females examined; for example, the following data compares a series of clutches (using **VOF** and **OE**) and the number of atretic follicles encountered (clutch size/number of atretic follicles): 5/4, 6/4, 9/0, 7/4, 3/6, 10/3, 6/4, 7/1, 8/4, 10/5, 6/1, and 9/1. Clutch characteristics are shown in Fig. 5; no litters were examined during this study. The smallest reproductively-active female measured 147 mm in SVL; the mean SVL of adult females was 194.2 mm ± 3.8 (153-236; n = 32). Reproductive data are available from numerous published reports; litter size apparently varies little throughout this species' range (Fitch, 1985). For example, Fitch (1970) reported an average litter size of 4.9 (3-8; n = 16) from all regions, whereas in Texas, Clark and Fleet (1976) found 4.8 young per litter, and Ford et al. (1990) reported an average of 4.5 in two litters. In Oklahoma, Carpenter (1958) found litter size averaging 5.0 (3-6; n = 3); however, in a large sample, Stewart (1989) reported an average of 6.7 ± 0.4 (4-10; n = 33) from eastern Oklahoma. The similarity in fecundity between our sample and that of Stewart was not surprising considering his sample of snakes (from eastern Oklahoma) as well as most of ours was taken from the Interior Highlands Region.

Clutch characteristics (Fig. 5) of the smooth earth snake (*Virginia valeriae elegans*) in Arkansas are similar to those of the *V. striatula*. Mean clutch size using **POF** was 9.7 (7-14; n = 7), with **VOF**, 6.2 (6-7; n = 4), and with **OE**, 5.0 (5 and 5; n = 2). A grand mean using only **VOF** and **OE** was 5.8 (5-7; n = 7). As in *V. striatula* atretic follicles were numerous. Data on atretic follicles as above were as follows: 6/3, 6/3, 8/2, 9/2, 11/6, 6/3, and 8/2. Mean adult body size was 202.6 ± 9.4 mm in SVL (175-237; n = 13). For the southern states, Fitch (1985) compiled a mean litter size of 6.1 (4-14; n = 22), whereas Ford et al. (1990) indicated that two captive females in northeastern Texas had litters of 3 and 6.

Medium-sized Viviparous Colubrid Species.--Three natricine snakes were represented in this group. One was Graham's crayfish snake (*Regina grahamii*); a majority of these specimens was taken in a series collected in 1988 from Mallard Lake in Mississippi County (northeastern Arkansas). Females possessing **POF** were mostly collected in March and early April. The transitional size from **POF** to **VOF** was approximately 9.0 mm in length; this condition was evident in several females on 14 April 1988. By

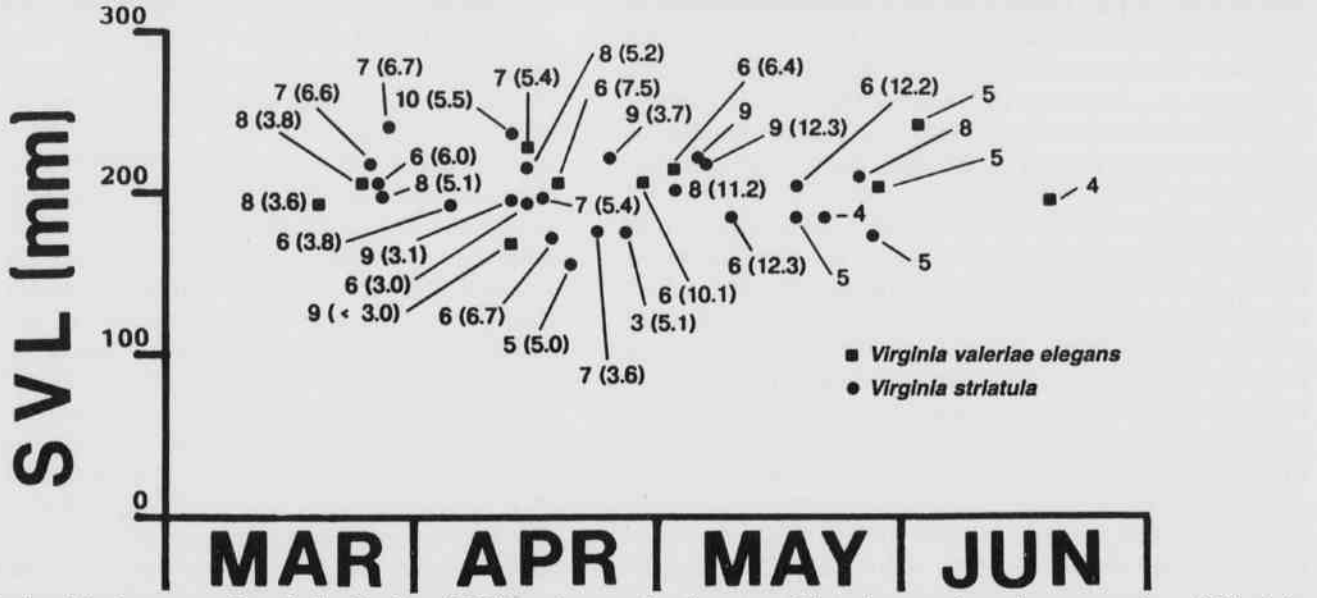

Fig. 5. Relationship between female body size (SVL) and reproduction condition in samples of two species of *Virginia* from Arkansas. See Fig. 1 for explanation of numerals.

early May most females contain **VOF** greater than 15 mm in diameter. A female containing the largest **VOF** ($\bar{x}$ = 23.5; n = 16) was collected on 8 June 1989; the only specimen with **OE** was collected on 29 May 1988. Using counts of **POF** and combined **VOF** and **OE**, mean clutch sizes were 32.9 ± 4.8 (18-44; n = 12) and 22.8 ± 3.7 (16-33; n = 10), respectively. Adult females (those with enlarged **VOF** or **OE**) averaged 703 ± 33.6 mm in SVL (625-775; n = 10). Data illustrated by Kofron (1979b) on reproduction in *R. grahamii* in Louisiana allowed for direct comparisons of the largest **VOF** between the Arkansas and Louisian females. Kofron found vitellogenesis beginning in ova 16 mm in length, whereas we found this to occur at around 9 mm. Kofron failed to mention an average clutch or litter size for *R. grahamii*; however, for northern states of Kansas, Missouri, Illinois, and Iowa, Fitch (1985) provided a combined average litter size of 16.4 (4-39; n = 24).

The other two species within this category are in the genus *Thamnophis*: for the most part, both have been well studied in most geographic areas in North America, except for the southcentral portions of their ranges (including Arkansas). In Arkansas the western ribbon snake (*T. proximus proximus*) becomes active on the first warm days in mid-March. Vitellogenesis generally begins in ova greater than 8.0 mm in length (Fig. 6). Mean clutch/litter size was generated using counts of **POV** (19.5 ± 4.3; 13-26; n = 6), **VOF** (20.3 ± 4.4; 8-34; n = 13), and **OE/OEM** (17.0; 12-26; n = 4). Using the latter two methods, a mean of 19.5 ± 3.7 (8-34; n = 17) was calculated; all methods are fairly consistent predictors of clutch/litter size. One female (642 mm in SVL collected 12 May 1988) contained large unovulated ova (n = 5) and one atretic follicle along with 26 **OE**. Another female (564 mm SVL collected 15 April 1968) contained a well-developed embryo (145 mm in SVL) in her right oviduct; this unusual occurrence would indicate a failure of this female to give birth to all offspring during the preceding late summer/early fall birthing period. The earliest data observed for **OE** was 19 May and the latest was 30 June. Clutch/litter size was generally much greater in Arkansas populations than what was found in other geographic areas. For example, Fitch (1985) gave a mean value of 11.6 (4-24; n = 41) for the central states (Oklahoma, Texas, and Louisiana) and only 12.4 (6-28; n = 14) for the northwestern states (Kansas, Nebraska, and Missouri). In another study, Clark (1974) reported an average of 8.4 (6-13; n = 8) in a Texas population.

The geographic variation in litter size of the eastern greater snake (*T. sirtalis sirtalis*) has been extensively documented (Fitch, 1970, 1985); however, nothing has been published on this subspecies in Arkansas. Clutch characteristics for 10 females are shown in Fig. 6; using counts of **VOF** and **OE/OEM**, mean clutch/litter sizes of 29.3 (26-33; n = 6) and 18.5 (16 and 21), respectively, were calculated. Combining these methods yielded a grand mean of 26.6 ± 4.0 (16-33; n = 8). Oviductal eggs were first noted in early May; only one female (517 mm in SVL collected 14 June 1993) contained **OEM** during the present study. Fitch (1985) summarized the literature on litter size in this species. The subspecies *sirtalis* in Canada exhibited average litter sizes of 25.0 (n = 14) and 29.0 (12-49; n = 7) in two separate studies. These estimates are similar to mean values of Arkansas specimens (using mostly ovarian counts), whereas Fitch (1970) found a mean of 14.5 in

132 gravid females (oviductal counts) of the subspecies *parietalis* in Kansas. Year-to-year intrapopulation variation in clutch size was documented in Kansas populations of *parietalis* (Seigel and Fitch, 1985). Several exceedingly large litters have been reported for this species (Fitch, 1985) and, especially, for the subspecies *sirtalis*; Dyrkacz (1975) reported a litter of 103 young of a captive female (1005 mm in SVL). Consequently, it was not surprising to find that the largest female (744 mm in SVL) observed during the present study contained a total of 79 **POF**.

Large Viviparous Colubrid Species.--Four of the five species of large aquatic natricine snakes of the genus *Nerodia* were examined during this study. The fifth species, the diamondback water snake (*N. r. rhombifer*), has been intensively studied in Arkansas (Plummer, 1992) as well as in the surrounding states of Louisiana (Kofron, 1979b), Missouri (Betz, 1963), and Texas (Ford et al., 1990). Plummer found an average litter size of 23.1 (12-48) in 21 litters, whereas Betz determined this to be 40.6 (28-56; n = 10). Ford et al. (1990) reported litters of 26, 37, and 30 in this species. Trends in geographic variation in litter size for this species are not fully understood (Fitch, 1985).

Reproduction in the Mississippi green water snake (*N. cyclopion*) is the least known of the water snakes in this group. In Arkansas, an average clutch size using combined counts of **POF**, **VOF**, and **OE/OEM** was 24.1 ± 7.3 (8-40; n = 11). If only **OE/OEM** are used, this count would be 18.3 (8-34; n = 3). Kofron (1979b) found a similar average count of 18.4 in 16 litters; he also stated that litter size generally increased in larger females. The smallest mature female (collected in April) measured 658 mm SVL; based upon size/age classes for this species as reported by Trauth (1990), she was in her third year of life. A similar size for the smallest mature female (measuring 637 mm SVL on 30 April 1976) was reported in Louisiana by Kofron (1979b). The largest female in the present study measured 961 mm in SVL and contained 34 well-developed embryos on 24 July 1988 (Fig. 7); this individual was estimated to be in her fifth year of life.

A large series of the yellowbelly water snake (*N. erythrogaster flavigaster*) yielded the following average clutch/litter sizes: **POF** = 34.6 ± 5.1 (22-57; n = 21), **VOF** = 21.6 ± 4.2 (9-33; n = 16), and **OE/OEM** = 21.8 (17-32; n = 4). By combining counts of **VOF** and **OE/OEM**, the average was 21.1 ± 9.4 (9-33; n = 20). Although female *N. e. flavigaster* become active in Arkansas starting in mid-March, vitellogenesis does not intensify until late April or early May (Fig. 8). This delay in ovarian development was also observed in Louisiana for this species (Kofron, 1979b) and was observed in other *Nerodia* species examined during the present study (Figs. 7 and 8). (Compare ovarian enlargement in *Nerodia* to *Agkistrodon* species–Fig. 9, or *Lampropeltis* species–Fig. 3). The smallest mature

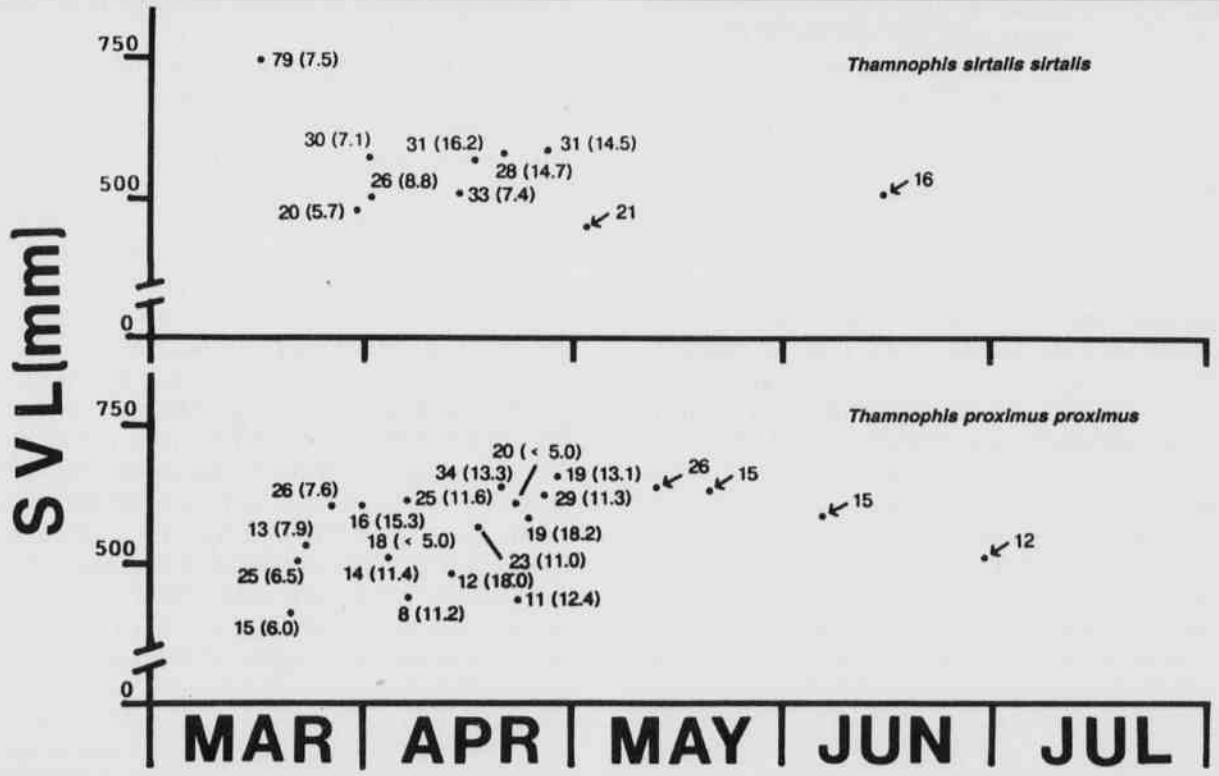

Fig. 6. Relationship between female body size (SVL) and reproduction condition in samples of two species of *Thamnophis* from Arkansas. See Fig. 1 for explanation of numerals.

female in the present study, measuring 638 mm in SVL on 15 May 1987, contained 13 **VOF** averaging 18.9 mm in length; on the other hand, the largest individual (a senescent female measuring 1167 mm in SVL on 29 May 1987), exhibited 57 **POF** averaging 6.4 mm in length. Kofron (1979) reported a female 734 mm SVL that showed the earliest onset of vitellogenesis. The transition between **POF** and **VOF** occurred in ova approximately 7.5 mm in length; the largest average of **VOF** was 27.7 mm. Failure of **POF** to develop accounted for about a 38% decrease in available ova for maturation. A significant positive correlation ($r = 0.67$; $n = 20$; $P < 0.01$) between CS and SVL was found. The regression equation (CS = -10.3546 + 0.0374SVL) indicates that as SVL increases by 27 mm, clutch size will be expected to increase by one. Fitch (1985) reported a much smaller average litter size (12.0; 4-22; n = 10) for southern population in this species and only a slightly larger average (15.7; 8-30; n = 20) for northern populations.

Anderson (1965) briefly mentioned litter sizes of 7, 13, and 19 (born in July and August) for Arkansas specimens of the broad-banded water snake (*N. fasciata confluens*). In our study average clutch size was determined (using **POF**, **VOF**, and **OE/OEM**, respectively) to be 33.6 ± 8.1 (19-56; n = 10), 20.2 ± 4.8 (12-31; n = 11), and 19.4 (17-25; n = 5). A combination of the latter two methods yielded an average of 20.6 ± 3.3 (12-31; n = 16). This estimate of litter size was similar to litter size in eastern states ($\bar{x} = 20.5$; n = 97), but larger than the average of 16.5 (n = 22; from Fitch, 1985) from Louisiana specimens. Regression analysis between CS and SVL in Arkansas specimens yielded the equation, CS = - 17.7703 + 0.0534SVL; as a result, for every increase of 19 mm in SVL, clutch size should increase by one. A significant positive correlation ($r = 0.71$; $P < 0.01$) was also observed between CS and SVL. The smallest mature females ranged between 523 and 558 mm in SVL; regardless of female body size, active vitellogenesis did not begin for most specimens until the month of May (Fig. 7). This general timing of vitellogenesis in Arkansas specimens contrasts sharply with the timing in Louisiana (Kofron, 1979b) populations which experience ova development as early as 27 March. Likewise, oviductal eggs were first observed during early June in Arkansas, whereas May was the rule in Louisiana populations. Interspecific comparisons revealed late June for the presence of **OE** in *N. e. flavigaster* and early July for *N. sipedon pleuralis* (Fig. 7).

Clutch characteristics in the midland water snake, *N. s. pleuralis*, were from samples taken mostly from the northeastern part of its range in Arkansas. We found average clutch sizes of 29.7 ± 7.2 (18-48; n = 10), 26.1 ± 5.7 (15-46; n = 9), and 19.0 (6-40; n = 3) using **POF**, **VOF**, and **OE/OEM**, respectively; a combined value of 24.3 ± 6.5 (6-46; n = 12) was calculated using the latter two methods. A significant positive correlation ($r = 0.76$; $P < 0.01$) existed between CS and SVL. The regression equation (CS = -32.4074 + 0.0793SVL) indicates that for every increase of 13 mm in SVL, clutch size will increase by one. Vitellogenesis occurred rapidly during the latter half of May; this feature was also observed in the northern water snake, *N. s. sipedon*, in Missouri (Bauman and Metter, 1977). The smallest mature female with **VOF** measured 593 mm in SVL was collected in mid-May (Fig. 7); this size was also similar to the value found by Aldridge (1982) in Missouri. The largest female (a specimen 940 mm in SVL collected in Crawford County on 8 August 1990) contained 40 well-developed embryos. We found two nonreproductive females of mature size in July and August; as pointed out by Collins (1993) for females in Kansas, all females may not breed annually. Fitch (1985) summarized the geographic variation in litter size in this species and found no clear trends; moreover, our estimate of litter size was slightly smaller than the average value (25.7) indicated for the subspecies *sipedon* for Missouri.

In general the reproductive traits in four of the five *Nerodia* species in Arkansas can be summarized as follows: 1) average litter size ranged from approximately 18 to 25, 2) minimal size at maturity ranged from 550 to 650 mm in SVL, 3) rapid development in ovarian follicles began in May, 4) the range in numbers of **POF** was from 15 to 60, and 5) the degree of follicular atresia appeared greatest in *N. erythrogaster* and *N. fasciata* and least in *N. cyclopion* and *N. sipedon*.

Small Viperid Species.--One species, the western pigmy rattlesnake (*Sistrurus miliarius streckeri*), falls into this category. An average clutch/litter size of 10.0 ± 2.2 (6-14; n = 8) was generated using combined counts of **POF**, **VOF**, and **OE/OEM**. Six **OE** averaging 17.1 mm in length were recorded from a female (338 mm in SVL) collected on 22 May 1994, and six well-developed embryos were observed in a female 420 mm in SVL collected on 29 June 1972. A litter of 13 neonates was born to a female of undetermined size on 9 September 1988 collected near Batesville (Independence County). Fitch (1985) and Ford et al. (1990) reported an average litter sizes of 8.6 (3-32; n = 9) and 7.4 (6-9; n = 5), respectively, for this subspecies from Texas; Anderson (1965) found litter size to range from 3 to 7 young in Missouri.

Medium-sized Viperid Species.--Two species of *Agkistrodon* are represented in this group. The southern copperhead, *A. contortrix contortrix*, is distributed throughout most of the eastern and southern parts of Arkansas; in the northwestern region of the state, this subspecies intergrades with *A. c. phaeogaster*. Most of the copperheads in our study were collected in northeastern Arkansas. The average clutch/ litter size using counts of **POF**, **VOF**, and **OE/OEM** (and neonates from litters) were 15.2 (12-18; n = 4), 12.4 ± 2.8 (7-25; n = 10), and 9.9

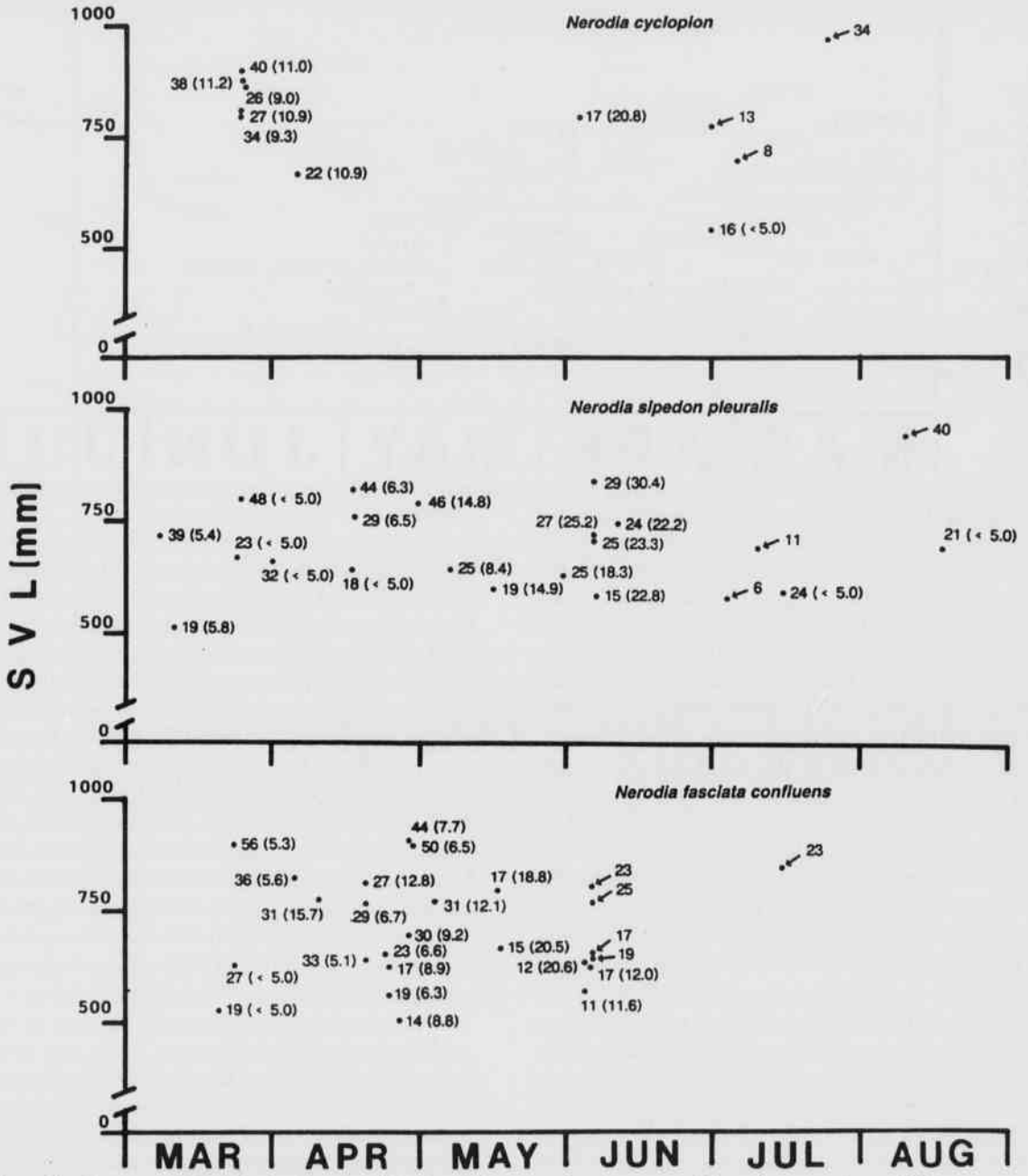

Fig. 7. Relationship between female body size (SVL) and reproduction condition in samples of three species of watersnakes (genus *Nerodia*) from Arkansas. See Fig. 1 for explanation of numerals.

± 3.7 (4-16; n = 7), respectively. [Litter sizes from Meshaka et al. (1989) were included in the latter estimate.] By combining the latter two counts, a mean of 11.4 ± 2.3 (4-25; n = 17) was determined. Clutch size was significantly correlated with SVL (r = 0.63; $P < 0.01$). The regression equation (CS = -11.8802 + 0.0353SVL) indicates that for every increase of 28 mm in SVL, an accompanying increase of one would occur in clutch size. Fitch (1985) reported litter size for the subspecies *contortrix* in the southeastern United States to average 6.6 (5-11; n = 17), whereas Ford et al. (1990) found an average of 6.9 (4-10; n = 8) in populations in northeastern Texas. The relatively high estimate of litter size as well as the actual high litter sizes observed in northeastern Arkansas (Fig. 9) may be a reflection of a locally-abundant food source (i.e., a possible increased availability of small mammals in this region related to intensive grain agriculture) or may be directly ralated to larger female body size attained in this region of the state.

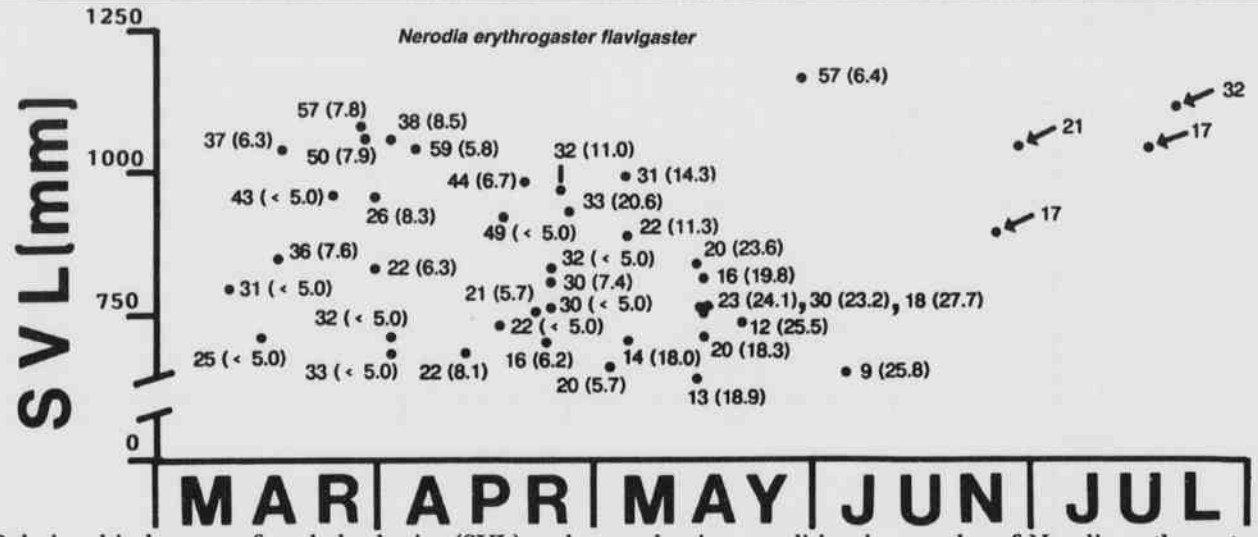

Fig. 8. Relationship between female body size (SVL) and reproduction condition in samples of *Nerodia erythrogaster flavigaster* from Arkansas. See Fig. 1 for explanation of numerals.

Mature females ranged in size from a little over 500 to around 750 mm in SVL. The largest female in a Texas sample as reported by Ford et al. (1990) was 600 mm in SVL, and Fitch (1960) reported no females greater than 690 mm in SVL. A biennial breeding pattern is common in this species (Fitch, 1960, 1970, 1985); Seigel and Ford (1987) reported that 60% of the mature females were gravid, whereas we found 86% of the adult females to be reproductively active.

Clutch characteristics of the western cottonmouth (*A. piscivorus leucostoma*) were compiled from samples taken from all parts of Arkansas. Using counts of **POF**, **VOF**, and **OE/OEM**, average clutch/litter sizes were 11.9 ± 2.5 (4-17; n = 10), 7.2 ± 1.3 (5-12; n = 12), and 4.8 (3-6; n = 4), respectively; a mean generated by combining the latter two methods yielded a value of 6.6 ± 1.2 (3-12; n = 16). Clutch size was not significantly correlated with SVL ($r = 0.49$; $P > 0.05$). In Louisiana Kofron (1979b) found 87% of female *A. p. leucostoma* gravid, whereas in eastern Texas, Burkett (1966) found only 42% (29 of 69). We determined that 67% of females we collected were reproductively active; this suggests a biennial reproductive cycle in this species in Arkansas. Our estimation of litter size was similar to a value of 6.8 (2-15; n = 21) reported by Fitch (1985) for specimens from the western and northwestern portions of its range. Vitellogenesis was underway in late March; the first **OE** were observed in late May. The smallest mature female was around 540 mm in SVL.

Large Viperid Species.--The timber rattlesnake (*Crotalus horridus*) is the lone representative in this category. [There are no records on reproduction in the western diamondback rattlesnake (*C. atrox*) from Arkansas, but see Fitch and Pisani (1993) for Oklahoma populations.] In Arkansas timber rattlesnakes usually emerge from hibernation dens sometime in April. Of the five female specimens collected in April, three exhibited **POF** averaging 12.3 in number and 6.1 mm in length (female SVL's = 1234, 977, and 948 mm); the other two females (1055 and 1008 mm in SVL) contained 16 greatly enlarged **VOF** averaging 37.6 mm in length and nine **OE** averaging 42.0 mm in length, respectively. (The latter female was collected on 19 April but was not killed until 4 June). Another female (908 mm in SVL collected 6 July 1985) exhibited **POF** < 5.0 mm in length. Vitellogenesis requires more than a single activity season (usually around 13-14 months–Martin, 1993). The reproductive pattern in this species is low-frequency birthing and delayed maturity (Brown, 1993). Geographic variation in litter size was summarized by Fitch (1985) with southern populations averaging 9.7 (7-11; n = 7) young per litter.

Conclusions

Our study focused on presenting female reproductive information, including such traits as clutch or litter size and the timing of ovarian development, on a large number of Arkansas snake species; this kind of data was inadequately known or unavailable for most snakes within the state. The results of our work provide pertinent life history data that will hopefully enable future researchers to include Arkansas populations when making geographic comparisons on intraspecific variation in snake ecology. Because our study included reproductive data from females collected from different populations over several years, data for each species included possible annual, seasonal, and geographic variation in parameters. Nearly one half (n = 13) of the 27 species and subspecies examined

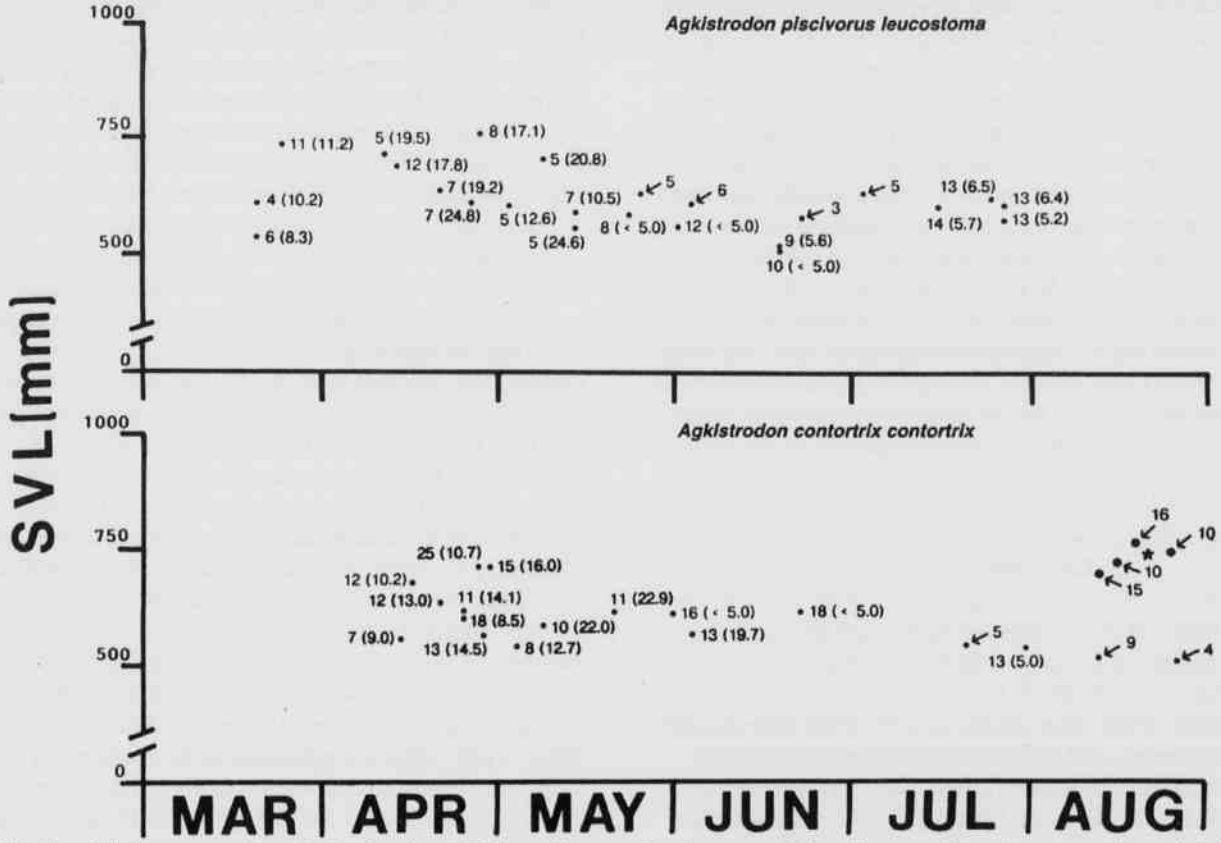

Fig. 9. Relationship between female body size (SVL) and reproduction condition in samples of two species of *Agkistrodon* from Arkansas. Asterisk denotes data (four litters) extracted from Meshaka et al. (1989). See Fig. 1 for explanation of numerals.

exhibited very similar clutch characteristics to populations in states bordering Arkansas. On the other hand, eight species had greater values with only one species exhibiting a smaller value.

Researchers in the field of snake reproductive ecology have focused their attention in recent years on identifying factors affecting the total reproductive investment by female snakes, and, especially, on those factors independent of phylogeny or less attributable to a female's genetic makeup (see reviews in Seigel and Fitch, 1985; Seigel et al., 1986; Seigel and Ford, 1987; Dunham et al., 1988). Any number of proximate environmental conditions (e.g., female nutritional state and food availability) can greatly influence critical reproductive parameters (clutch frequency and size). This is true in temperate zone snakes (and probably for tropical forms as well), a group whose overall reproductive biology is the best known of the ophidians. For many snakes species, increases in female body length are generally associated with greater clutch or litter size (e.g., Aldridge, 1982; Plummer, 1984; Seigel and Ford, 1987; Ford and Seigel, 1989); however, from year to year, female snakes sometimes increase offspring number and at the same time reduce offspring size, or vice versa. Some temperate zone viviparous species, especially viperids, exhibit a biennial reproductive cycle (Fitch, 1970; Aldridge, 1979). Blem (1982) noted, however, that female *Agkistrodon piscivorus* lacking sufficient amounts of stored lipids did not reproduce annually and that large cottonmouths were gravid more frequently than small ones. Short-term reproductive studies may fail to detect these types of variation in clutch data, whereas significant annual variation has been demonstrated in some species studied over periods of time up to 30 years (Seigel and Fitch, 1985). Consequently, long-term field investigations on snake reproductive biology are essential to our understanding of the multitude and complexity of factors related to reproductive success and must be undertaken to provide important data to support generalizations concerning reproductive characteristics of a given species.

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Literature Cited

Aldridge, R.D. 1979. Female reproductive cycles of the snakes *Arizona elegans* and *Crotalus viridis*. Herpetologica 35:256-261.

Aldridge, R.D. 1982. The ovarian cycle of the watersnake *Nerodia sipedon*, and effects of hypophysectomy and gonadotropin administration. Herpetologica 38:71-79.

Aldridge, R.D. and **D.E. Metter.** 1973. The reproductive cycle of the worm snake, *Carphophis vermis*, in Missouri. Copeia 1973:472-477.

Anderson, P. 1965. The reptiles of Missouri. Univ. Missouri Press, Columbia, xxiii + 330 pp.

Ballinger, R.E. 1978. Variation in and evolution of clutch and litter size. Pp. 789-825, *In* The vertebrate ovary (R.E. Jones, ed.) Plenum Press, New York, xxiii + 853.

Bauman, M.A. and **D.E. Metter.** 1977. Reproductive cycle of the northern watersnake, *Natrix s. sipedon* (Reptilia, Serpentes, Colubridae). J. Herpetol. 11:51-59.

Betz, T.W. 1963. The gross ovarian morphology of the diamond-backed water snake, *Natrix rhombifera*, during the reproductive cycle. Copeia 1963:692-697.

Blanchard, F.N. 1937. Data on the natural history of the red-bellied snake, *Storeria occipito-maculata* (Storer), in northern Michigan. Copeia 1937:151-162.

Blem, C.R. 1982. Biennial reproduction in snakes: an alternative hypothesis. Copeia 1982:961-963.

Brodie, E.D., III and **P.K. Ducey.** 1989. Allocation of reproductive investment in the redbelly snake *Storeria occipitomaculata*. Amer. Midl. Nat. 122:51-58.

Brown, W.S. 1993. Biology, status, and management of the timber rattlesnake (*Crotalus horridus*): a guide for conservation. Soc. Stud. Amph. Rept. Herpetol. Circ. No. 22, vi + 78 pp.

Burkett, R.D. 1966. Natural history of the cottonmouth moccasin, *Agkistrodon piscivorus* (Reptilia). Univ. Kansas Publ. Mus. Nat. Hist. 17:435-491.

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

Carpenter, C.C. and **J.J. Krupa.** 1989. Oklahoma herpetology: an annotated bibliography. Univeristy of Oklahoma Press, Norman, vii + 258.

Clark, D.R., Jr. 1970. Ecological study of the worm snake *Carphophis vermis* (Kennicott). Univ. Kansas Publ. Mus. Nat. Hist. 19:89-194.

Clark, D.R., Jr. 1974. The western ribbon snake (*Thamnophis proximus*): ecology of a Texas population. Herpetologica 30:372-379.

Clark, D.R., Jr. and **R.R. Fleet.** 1976. The rough earth snake (*Virginia striatula*): ecology of a Texas population. Southw. Nat. 20:467-478.

Cobb, V.A. 1990. Reproductive notes on the eggs and offspring of *Tantilla gracilis* (Serpentes: Colubridae), with evidence of communal nesting. Southw. Nat. 35:22-24.

Collins, J.T. 1993. Amphibians and reptiles in Kansas. 3rd ed. Univ. Kansas Mus. Nat. Hist. Publ. Edu. Ser. No. 13:1-397.

Conant, R. and **J.T. Collins.** 1991. A field guide to reptiles and amphibians of eastern and central North America. Houghton Mifflin Co., Boston, 450 pp.

Dixon, J.R. 1987. Amphibians and reptiles of Texas with keys, taxonomic synopses, bibliography, and distribution maps. Texas A&M University Press, College Station, 434 pp.

Dunham, A.E., D.B. Miles, and **D.N. Reznick.** 1988. Life history patterns in squamate reptiles. Pp. 441-522, *In* Biology of the reptilia, Vol. 16 and ecology B, defense and life history, (C. Gans and R.B. Huey, eds.). Alan R. Liss, Inc., New York, xi + 659 pp.

Dundee, H.A. and **D.A. Rossman.** 1989. The amphibians and reptiles of Louisiana. Louisiana State Univ. Press, Baton Rouge, xi + 300 pp.

Dyrkacz, S. 1975. Life history (litter size): *Thammophis s. sirtalis*. Herpetol. Rev. 6:20.

Ernst, C.H. and **R.W. Barbour.** 1989. Snakes of eastern North America. George Mason Univ. Press, Fairfax, VA, vii + 282 pp.

Fitch, H.S. 1960. Autecology of the copperhead. Univ. Kansas Mus. Nat. Hist. 13:85-288.

Fitch, H.S. 1963. Natural history of the racer *Coluber constrictor*. Univ. Kansas Publ. Mus. Nat. Hist. 15:351-468.

Fitch, H.S. 1970. Reproductive cycles in lizards and snakes. Univ. Kansas Mus. Nat. Hist. 52:1-247.

Fitch, H.S. 1975. A demographic study of the ringneck snake (*Diadophis punctatus*) in Kansas. Univ. Kansas Mus. Nat. Hist. Misc. Publ. 62:1-53.

Fitch, H.S. 1985. Variation in clutch and litter size in New World reptiles. Univ. Kansas Mus. Nat. Hist. 76:1-76.

Fitch, H.S. and **G.R. Pisani.** 1993. Life history traits of the western diamondback rattlesnake (*Crotalus atrox*)

studied from roundup samples in Oklahmoma. Univ. Kansas Mus. Nat. Hist. Occ. Pap. No. 156:1-24.

Force, E.R. 1935. A local study of the opisthoglyph snake *Tantilla gracilis* Baird and Girard. Papers Michigan Acad. Sci., Arts Letters 20:645-659.

Ford, N.B., V.A. Cobb and **W.W. Lamar.** 1990. Reproductive data on snakes from northeastern Texas. Texas J. Sci. 42:355-368.

Ford, N.B. and **R.A. Seigel.** 1989. Relationships among body size, clutch size, and egg size in three species of oviparous snakes. Herpetologica 45:75-83.

Johnson, T.R. 1987. The amphibians and reptiles of Missouri. Missouri Dept. Cons., Jefferson City, xi + 368 pp.

Kofron, C.P. 1979a. Female reproductive biology of the brown snake, *Storeria dekayi*, in Louisiana. Copeia 1979:463-466.

Kofron, C.P. 1979b. Reproduction of aquatic snakes in south-central Louisiana. Herpetologica 35:44-50.

Martin, W.H. 1993. Reproduction of the timber rattlesnake (*Crotalus horridus*) in the Appalachian Mountains. J. Herpetol. 27:133-143.

Meshaka, W.E., S.E. Trauth, B.P. Butterfield and **A.B. Bevill.** 1989. Litter size and aberrant pattern in the southern copperhead, *Agkistrodon contortrix contortrix*, from northeastern Arkansas. Bull. Chicago Herpetol. Soc. 24:91-92.

Platt, D.R. 1969. Natural history of the hognose snakes *Heterodon platyrhinos* and *Heterodon nasicus*. Univ. Kansas Publ. Mus. Nat. Hist. 18:253-420.

Plummer, M.V. 1983. Annual variation in stored lipids and reproduction in green snakes (*Opheodrys aestivus*). Copeia 1983:741-745.

Plummer, M.V. 1984. Fèmale reproduction in an Arkansas population of rough green snakes (*Opheodrys aestivus*). Pp. 105-113, *In* Vertebrate ecology and systematics: a tribute to Henry S. Fitch. (R.A. Seigel, L.E. Hunt, J.L. Knight, L. Malaret and N.L. Zuschleg, eds.). Univ. Kansas Mus. Nat. History, Lawrence, viii + 278 pp.

Plummer, M.V. 1992. Relationships among mothers, litters, and neonates in diamondback water snakes (*Nerodia rhombifer*). Copeia 1992:1096-1098.

Robinette, J.W. and **S.E. Trauth.** 1992. Reproduction in the western mud snake, *Farancia abacura reinwardtii* (Serpentes: Colubridae), in Arkansas. Proc. Arkansas Acad. Sci. 46:61-64.

Seigel, R.A. and **H.S. Fitch.** 1985. Annual variation in reproduction in snakes in a fluctuating environment. J. Anim. Ecol. 54:497-505.

Seigel, R.A. and **N.B. Ford.** 1987. Reproductive ecology. Pp. 210-252, *In* Snakes: Ecology and evolutionary biology (R.A. Seigel, J.T. Collins, and S.S. Novak, eds.). Macmillan Publ. Co., New York, xiv + 529 pp.

Seigel, R.A., H.S. Fitch and **N.B. Ford.** 1986. Variation in relative clutch mass in snakes among and within species. Herpetologica 42:179-185.

Semlitsch, R.D. and **G.B. Moran.** 1984. Ecology of the redbelly snake (*Storeria occipitomaculata*) using mesic habitats in South Carolina. Amer. Midl. Nat. 111:33-40.

Stewart, J.R. 1989. Facultative placentotrophy and evolution of squamate placentation: quality of eggs and neonates in *Virginia striatula*. Amer. Nat. 133:111-137.

Smith, H.M., D. Chiszar, J.R. Staley, II and **K. Tepedelen.** 1994. Populational relationships in the corn snake *Elaphe guttata* (Reptilia: Serpentes). Texas J. Sci. 46:259-292.

Sutton, K.B. and **V.R. McDaniel.** 1979. Unusual concentration of scarlet snakes (*Cemophora coccinea*) in Village Creek State Park, Arkansas. Proc. Arkansas Acad. Sci. 33:92.

Trauth, S.E. 1982. *Cemophora coccinea* (Scarlet Snake). Reproduction. Herpetol. Rev. 13:126.

Trauth, S.E. 1990. Flooding as a factor in the decimation of a population of green water snakes (*Nerodia cyclopion cyclopion*) from Arkansas. Bull. Chicago Herpetol. Soc. 25:1-3.

Trauth, S.E. 1991. Distribution, scutellation, and reproduction in the queen snake, *Regina septemvittata* (Serpentes: Colubridae), from Arkansas. Proc. Arkansas Acad. Sci. 45:103-106.

Williams, K.L. 1988. Systematics and natural history of the American milk snake, *Lampropeltis triangulum*. Milwaukee Publ. Mus., Milwaukee, WI x + 176 pp.

Wright, A.H. and **A.A. Wright.** 1957. Handbook of snakes of the United States and Canada. Comstock Publ. Associates, Cornell Univ. Press, Vol. 1, xviii + 564 pp; Vol. 2, ix + 565-1105 pp.