

The Relationship between Location and Displays in a Territorial Lizard

STEPHEN MCMANN^{1,2} AND ANN V. PATERSON³

¹*Math and Science Division, Arkansas State University at Beebe, Beebe, Arkansas 72012, USA;*
E-mail: scmcmann@asub.edu

³*Department of Natural Sciences, Williams Baptist College, Walnut Ridge, Arkansas 72476, USA;*
E-mail: apaterson@wbcoll.edu

ABSTRACT.—We examined whether display behavior of territorial male lizards (*Anolis sagrei*) differed between locations within heavily used portions of their activity areas (cores), and locations outside of these heavily used regions. In a southern Florida hardwood hammock, we observed six males in each of four 20 × 20 m plots, recording each male's location and display behavior for three, 1-h sessions. When males were outside of their core activity areas, they produced more bobbing displays relative to nodding displays than when they were within their core areas. Similar relationships have been reported in other taxa, such as birds, but they have been little studied in reptiles. The causes and consequences of this display variation remain to be determined.

For territorial animals, important social variables such as territory boundaries can be associated with specific locations. Therefore, we might expect territorial animals to produce different signals in different locations. Many territorial lizards produce several different visual displays, which are presumably signals. However, we know little about how the location of an individual lizard in its activity area/home-range affects its behavior.

Here we report a study on *Anolis sagrei* investigating whether the relative frequencies of two types of head-bob displays (bobbing displays and nodding displays; McMann, 2000) differ between the core and the rest of an adult male's activity area. Previous work indicates that social context affects the relative frequencies of these two displays (e.g., Paterson, 1999; McMann, 2000); thus we might expect their relative frequency to vary depending on an individual's location in its activity area.

MATERIALS AND METHODS

Data were collected during 1997 at Castellow Hammock Park in Miami-Dade County, Florida, during the breeding season of *A. sagrei* (Lee et al., 1989). The study site consisted of a subtropical hardwood hammock forest (Snyder et al., 1990) that had been recently disturbed by a hurricane and subsequent management (Horvitz et al., 1998) and provided a spatially complex habitat with high densities of *A. sagrei*. Adult males of this species attempt to exclude other adult males from territories on the ground and lower portions of tree trunks (see Schoener and Schoener, 1980, 1982; Tokarz, 1998).

We studied four groups of male *A. sagrei*, each residing in a 20 × 20 m plot. We marked each plot with a grid of surveyor's flags at 2-m intervals on the ground. We created the first plot in March, the second plot in April, and the other two plots in May. We spent several days capturing the males that we saw in an area extending from the center of the plot to several meters beyond its borders. We measured the snout-vent length and tail length of each lizard to the nearest

millimeter and marked each lizard with bead tags at the base of its tail (Fisher and Muth, 1989). In each plot we chose six males near the center of the plot for behavioral observations.

Plots were observed from 22 March to 14 April for plot 1; 24 April to 8 May for plot 2; 14–23 May for plot 3; and 31 May to 14 June for plot 4. Lizards were observed during conditions conducive to high display rates (i.e., not during rain, heavily overcast conditions, or when sustained winds were forecast above 7 m/s). Each lizard was observed during part of its first activity period of the day. We defined this activity period as starting when the first focal lizard of the day began to display, and we finished each day's observations well before a dramatic decline in activity signaled the end of the activity period. Early in the season, there was one daily activity period during midday. Later in the season, activity began and ended earlier in the day, then sometimes resumed late in the day.

After the observer became familiar with the general location of each focal lizard's home range during several days of ad hoc observations, each focal lizard was observed for three 1-h observation sessions within a one-week period. The observer sat generally > 2 m outside the focal lizard's suspected home range and initially > 5 m from the lizard, relocating when necessary to keep the lizard in view. Sugerma (1990) found that *A. sagrei* are unaffected by a stationary observer, and the lizards appeared to ignore the observer in this study. Two focal lizards disappeared before three observation sessions could be completed, so replacement males in the same plots as the missing lizards were subsequently observed for three sessions. Normally, several lizards were observed during a day's activity period. To minimize possible time of day effects, we changed the order in which lizards were observed so that each was observed during the early, middle, and late portion of a day's activity period.

During each observation session, the observer recorded the focal lizard's location (to the nearest meter) for all times that it was stationary for more than 10 sec, the times during which it changed locations, and behavior (numbers of bobbing displays and nodding

² Corresponding Author.

displays) at each location. A nodding display is a volley of continuous rapid dorso-ventral oscillations of the front part of the lizard's body, and a bobbing display is a specific stereotyped pattern of discontinuous dorso-ventral movements of the front part of the body (McMann, 2000).

We defined the minimum convex polygon including all of a lizard's locations as its activity area. We divided each activity area into two regions based on observations of the lizard's location at the start of each minute. The core was the minimum convex polygon that included the locations of 90% of observations. The area outside of this polygon was outside the core. There are many ways to define the core of an activity area (Kenward et al., 2001), and our choice to specifically include locations of 90% of observations was arbitrary.

We tested whether the proportion of headbob displays that were bobbing displays differed between cores and areas outside the cores. We used plot means of the proportion as sampling units to avoid pseudoreplication, and we analyzed the data with a paired *t*-test after confirming that the data met the appropriate assumptions.

We also tested whether the frequency of headbob displays differed between cores and areas outside cores despite the fact that we did not originally hypothesize a difference between the locations. However, our data suggested that this analysis could be of interest (see Results). We analyzed the data with a paired *t*-test after confirming that the data met the appropriate assumptions.

We conducted analyses using Calhome (J. G., Kie, J. A. Baldwin, and C. J. Evans, CALHOME: Home-range analysis program. Electronic user's manual. U.S. Forest Service, Fresno, CA, 1994) and PC-SAS (rele. 8.2, SAS Institute, Inc., Cary, NC, 2001). An alpha value of ≤ 0.05 was used for all hypothesis tests. Means are given \pm SE along with ranges using plot means as sampling units.

RESULTS

The four plots each contained six focal males that averaged 52.5 ± 1.43 mm. in SVL ($N = 4$, range = 49.0–55.0) and 93.2 ± 4.9 mm. in mean tail length ($N = 4$; range = 78.7–99.3). These lizards occupied individual activity areas of 14.0 ± 2.1 m² (range = 8.8–17.7) where they spent $95 \pm 1\%$ of their time within locations classified as within cores (range = 93–96%). The cores occupied on average 9.1 ± 1.3 m² (range = 5.8–12.0). All lizards displayed within the cores of their activity areas, whereas 23 of 24 lizards displayed when they were outside of the cores. Overall the lizards produced 1.06 ± 0.08 headbob displays per minute, of which $28 \pm 6\%$ were bobbing displays (range = 18–43%).

The mean proportion of headbob displays that were bobbing displays was significantly higher outside the cores (overall mean: 0.58 ± 0.08) than it was inside the cores (overall mean: 0.27 ± 0.06 ; two-tailed paired *t*-test, $t_3 = 7.27$, $P = 0.0054$; mean difference within plots = 0.31 ± 0.04). The total frequency of headbob displays was somewhat lower outside cores (overall mean: 0.75 ± 0.34) than inside cores (overall mean: 1.26 ± 0.11), but the difference was not significant

(two-tailed paired *t*-test, $t_3 = 1.35$, $P = 0.27$; mean difference within plots = 0.51 ± 0.38).

DISCUSSION

There have been few studies of whether signals differ with the signaler's location in reptiles, although there may be evidence for a home-range, center-edge effect in the lizard *A. carolinensis* (T. A. Jenssen, pers. comm.). Our study indicates that breeding male *A. sagrei* produce larger proportions of headbob displays that are bobbing displays when they are outside of the cores of their activity areas. The overall number of headbob displays does not differ among these locations.

Several factors may differ between times that focal males are inside versus outside of their cores, and experimental manipulations may later allow an identification of specific factors causing the display differences. We describe some possibilities below.

First, display differences may have been caused by variation in the signaler's proximity to persistent features such as physical structures, or territory borders. Such features may be intrinsically important, or they may be cues for other factors (Stamps, 1994), such as the possibility that unseen neighbors are nearby. There is evidence that the perceived proximity of a potential rival can affect the display behavior of *A. sagrei* (McMann, 2000).

Second, the signaler's observation of other individuals could cause it to move to a particular location and display in a particular way. For example, a particular display may have more utility nearer a threatening rival or receptive female. Our study does not indicate a role for the intense close-range interactions common in laboratory investigations of *Anolis* behavior (e.g., Tokarz, 1985; McMann, 1993); in our study other males were almost always at least several meters away when visible to the observer, and the focal lizards were not observed copulating. However, more subtle longer-distance interactions may have been occurring in our study.

Last, display patterns may reflect internal factors such as sympathetic or aggressive arousal. Male *A. sagrei* produce a higher proportion of bobbing displays in several contexts that may increase aggressive arousal, such as when first establishing territories, when intruders are nearby, and when meeting unfamiliar rivals (Paterson, 1999; McMann, 2000). Aggressive arousal may be related to a male's position in his activity area.

Acknowledgments.—R. R. Tokarz, T. A. Jenssen, J. C. Lee, W. A. Searcy, and K. D. Waddington provided advice throughout the study. Data analysis and manuscript preparation benefited from comments by Y. Brandt, E. D. Brodie III, G. R. Smith, and three anonymous reviewers. This study was carried out under permit 340 from Dade County Natural Areas Management as well as the Animal Care and Use Review Committee Protocol 95-103 at the University of Miami.

LITERATURE CITED

- FISHER, M., AND A. MUTH. 1989. A technique for permanently marking lizards. *Herpetological Review* 20:45–46.
- HORVITZ, C. C., J. B. PASCARELLA, S. MCMANN, A.

- FREEDMAN, AND R. H. HOFSTETTER. 1998. Functional roles of invasive non-indigenous plants in hurricane-affected subtropical hardwood forests. *Ecological Applications* 8:947–974.
- KENWARD, R. E., R. T. CLARKE, K. H. HODDER, AND S. S. WALLS. 2001. Density and linkage estimators of home range: nearest-neighbor clustering defines multinuclear cores. *Ecology* 82:1905–1920.
- LEE, J. C., CLAYTON, D., EISENSTEIN, S., AND I. PEREZ. 1989. The reproductive cycle of *Anolis sagrei* in southern Florida. *Copeia* 1989:930–937.
- MCMANN, S. 1993. Contextual signaling and the structure of dyadic encounters in *Anolis carolinensis*. *Animal Behaviour* 46:657–668.
- . 2000. Effects of residence time on displays during territory establishment in a lizard. *Animal Behaviour* 59:513–522.
- PATERSON, A. V. 1999. Relationships in Territorial Neighborhoods: Factors Influencing Interactions in a Lizard, *Anolis sagrei*. Unpubl. Ph.D. diss. Univ. of Miami, Miami, FL.
- SCHOENER, T. W., AND A. SCHOENER. 1980. Density, sex ratio and population structure in some Bahamian *Anolis* lizards. *Journal of Animal Ecology* 49:19–53.
- . 1982. Interspecific variation in home-range size in some *Anolis* lizards. *Ecology* 63:809–823.
- SNYDER, J. R., A. HERNDON, AND W. B. ROBERTSON JR. 1990. South Florida Rockland. In R. L. Myers and J. J. Ewel (eds.), *Ecosystems of Florida*, pp. 230–277. Univ. of Central Florida Press, Orlando.
- STAMPS, J. A. 1994. Territorial behavior: testing the assumptions. *Advances in the Study of Behavior* 23:173–322.
- SUGERMAN, R. A. 1990. Observer effects in *Anolis sagrei*. *Journal of Herpetology* 24:316–317.
- TOKARZ, R. R. 1985. Body size as a factor determining dominance in staged agonistic encounters between male brown anoles (*Anolis sagrei*). *Animal Behaviour* 33:746–753.
- . 1998. Mating pattern in the lizard *Anolis sagrei*: implications for mate choice and sperm competition. *Herpetologica* 54:388–394.

Accepted: 6 December 2002.

Journal of Herpetology, Vol. 37, No. 2, pp. 416–419, 2003
Copyright 2003 Society for the Study of Amphibians and Reptiles

Reproductive Female Common Watersnakes (*Nerodia sipedon sipedon*) Are Not Anorexic in the Wild

ROBERT D. ALDRIDGE¹ AND ANGELO P. BUFALINO²

Department of Biology, Saint Louis University, St. Louis, Missouri 63103-2010, USA

ABSTRACT.—The active season of the Common Watersnake (*Nerodia sipedon sipedon*) in Missouri lasts about 170 days, from mid-April to early October. Females begin vitellogenesis in April, ovulate in June, and give birth in August to September. Reproduction occupies about 130 days (76%) of the active season. Food was present in 71% of vitellogenic snakes, 64% of pregnant snakes, and 43% of postpartum snakes. Coelomic fat mass decreased during vitellogenesis but increased during pregnancy. At parturition, 40% of females had sufficient fat reserves to reproduce the following year. Dry mass of ovulated ova/developing young did not change through pregnancy; however, wet mass increased from 45% in freshly ovulated ova to 78% at parturition. We conclude that reproductive females are not anorexic and that the increase in water content of the embryos adds considerable mass to the mother during pregnancy.

Reproduction in snakes is energetically expensive in both males and females. In males, energy is used to produce sperm, develop the sexual segment of the kidney, and search for mates. Aldridge et al. (2003) showed that size of both the testis and the sexual segment of the kidney is correlated with coelomic fat mass in Diamond-Backed Watersnakes (*Nerodia rhombifer*). In females, much of the coelomic fat mass is converted to vitellogenins by the liver and deposited as yolk into developing follicles (Stewart et al., 1990). Watersnakes appear to be predominantly lecithotrophic, because the yolk is the primary source of organic and inorganic nutrients for the embryo (Stewart and Castillo, 1984; Stewart et al., 1990). Therefore, successful embryonic development only requires an exchange of oxygen, carbon dioxide, and water between

mother and embryo (Packard et al., 1982; Weatherhead et al., 1999). Bonnet et al. (1998) have discussed temporal aspects of energy income and reproduction and concluded that most ectothermic vertebrates are capital breeders, that is, they accumulate much of the energy and nutrients needed for reproduction prior to initiating vitellogenesis.

Barron and Andraso (2001) studied effect of food intake on reproduction in female *Nerodia sipedon*. In their study, pregnant females were collected in July and maintained, apparently without food, until parturition. Following parturition, females were randomly assigned into two treatment groups, one group received 30%, and the other group received 15% of their body mass in pureed carp (*Cyprinus carpio*) per week. The postparturient snakes were fed until early November, when they were placed in an artificial hibernaculum. Barron and Andraso (2001) showed that postparturient females fed the high food ration had a

¹ Corresponding Author. E-mail: aldridge@slu.edu

² E-mail: bufalino@slu.edu

significantly higher body mass and more previtellogenic follicles at hibernation than the low ration group. They added that females with more previtellogenic follicles could potentially have larger clutch sizes in the spring.

Because pregnant females were not fed, Barron and Andraso (2001) apparently assumed that females do not feed during pregnancy (i.e., they are anorexic). Barron and Andraso (2001) cited a review by Derickson (1976), who stated that the available literature suggests that, in reptiles, lipid storage only occurs after the reproductive season. However, the assumption that pregnant females are anorexic may not be true for many species of snakes. Weatherhead et al. (1999) reported that captive female *N. sipedon* fed throughout vitellogenesis and pregnancy (P. J. Weatherhead, pers. comm.). The purpose of the present paper is to describe the frequency of feeding, the seasonal pattern of coelomic fat storage, and the changes in the water content of the developing embryo, during the reproductive cycle of the Common Watersnake (*Nerodia sipedon sipedon*) in the wild.

Nerodia sipedon is a medium-sized natricine snake found in riparian habitats throughout much of the eastern United States and southern Canada. In Missouri, females reproduce annually (Bauman and Metter, 1977), and the mating season is restricted to the spring (RDA, unpubl. data). In our study population, *N. s. sipedon* are active from April through September with smaller numbers of individuals encountered in March and October and rarely in other months (RDA, pers. obs.). The active season lasts about 170 days (mid-April to early October). In females, reproduction occupies much of the active season. Females begin vitellogenesis in April, ovulate in early June, and give birth in late August (occasionally early September). Thus, reproduction occupies about 130 days or 76% of the active season. A similar (although delayed by about two weeks) seasonal pattern was reported by Weatherhead et al. (1999) for this species in Ontario, Canada.

MATERIALS AND METHODS

The snakes examined in this study were collected between 1976 and 1979 on streams in east-central Missouri. The reproductive cycle of these specimens was reported by Aldridge (1982). Over 80% of the watersnakes were quiescent at the time of capture, basking on branches over the water. Presence of food in the gut was determined by examination of preserved specimens and was scored as positive if fleshy remnants were present in the stomach or post digestive matter was present anywhere in the intestine. Coelomic fat mass in the abdominal cavity was weighed to the nearest gram. Coelomic fat mass was analyzed by linear regression across Julian day and by ovarian mass during vitellogenesis, and also across Julian day during pregnancy. Ovaries were examined for the number of atretic follicles. The number of atretic follicles was regressed against coelomic fat mass and female snout-vent length (SVL). Six embryos were removed from 21 preserved females, separated into yolk and somatic mass, and weighed. Yolk and embryos were then dehydrated in an oven at 70°C for two days, and reweighed to compute water content (%). All statistics were computed with StatView 4.5 (SAS Institute

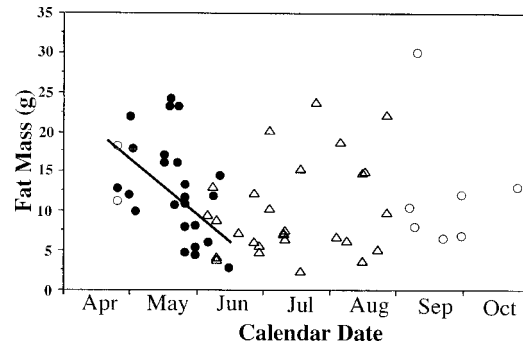


FIG. 1. Coelomic fat mass during the reproductive cycle of the female Common Watersnake (*Nerodia sipedon sipedon*). Closed circles represent coelomic fat mass of vitellogenic snakes, triangles represent pregnant snakes, and open circles represent postpartum and previtellogenic (April) snakes. Line is regression of coelomic fat mass across Julian day for snakes with vitellogenic follicles.

Inc., Cary, NC). For all statistical tests, $\alpha = 0.05$, and we report means ± 1 SD.

RESULTS

Food was present in 71% (17 of the 24) of vitellogenic snakes, 64% (18 of 28) of pregnant snakes, and 43% (three of seven) of postpartum snakes. Coelomic fat mass decreased significantly during vitellogenesis across Julian day ($F = 6.4$, $P = 0.02$, $N = 24$, $r^2 = 0.2$, $Y = 42.1 - 0.021x$, Fig. 1). Coelomic fat mass was also inversely correlated with ovarian mass over the same period ($F = 4.5$, $P = 0.047$, $N = 24$, $r^2 = 0.18$, $Y = 16.8 - 0.14x$). Based on regression of coelomic fat mass and Julian day, coelomic fat mass at the beginning of vitellogenesis was 18.0 g. Coelomic fat mass in snakes with large vitellogenic follicles or recently ovulated ova (May 24 to June 13) was 7.8 ± 3.9 g ($N = 14$, range 2.9–14.6 g). Mean SVL of vitellogenic females was 712 mm and the mean number of vitellogenic follicles was 22. Based on these data, coelomic fat mass decreased by 0.46 g per vitellogenic follicle produced.

Coelomic fat mass increased during pregnancy but the change was not significant ($F = 2.4$, $P = 0.15$, $N = 28$, $r^2 = 0.08$). Number of atretic follicles (3.57 , ± 2.7 , range 0–8) was not significantly correlated with coelomic fat mass ($F = 0.58$, $P = 0.45$, $N = 24$) or SVL ($F < 0.01$, $P = 0.99$, $N = 24$).

Dry mass of ovulated ova/developing young (yolk included) did not change through pregnancy (Fig. 2). Total wet mass increased during pregnancy because of water uptake. Water content of developing embryos increased during pregnancy from 45% (SD = 0.096) in freshly ovulated ova (first half of June), to 50% (SD = 0.083) in mid-June through July, to a maximum of 78% (SD = 0.042) in August. Mean wet mass of recently ovulated ova (early June, $N = 5$) was 2.64 ± 0.32 g and the mean mass of late term embryos (late August, $N = 2$) was 8.3 ± 0.64 g. Based on an average litter of 22 young for a 712 mm SVL female, maternal mass would increase by 124.5 g during pregnancy only because of water uptake of the embryos.

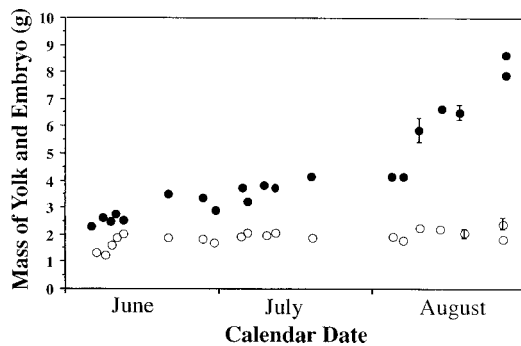


FIG. 2. Mean mass of combined yolk and embryo of the Common Watersnake (*Nerodia sipedon sipedon*) during pregnancy. Open circles represent the dry mass and solid circles wet mass. Error bars represent the standard error of the mean. Standard error bars missing are within the diameter of the circle.

DISCUSSION

Our data indicate that female watersnakes feed throughout the active season. Because the vast majority of our sample consisted of basking snakes, we feel we did not sample snakes that were searching for food. Bauman and Metter (1975) reported a feeding frequency of 35% (based on food in the stomach only) in a population of *N. sipedon* inhabiting a fish hatchery in central Missouri. They attributed the low frequency to two factors: one, they captured only moving snakes and two, they captured the snakes at the beginning of the activity period, that is, the snakes had just begun searching for food. We feel that using food presence in the stomach and/or the intestine is an accurate method of determining the feeding frequency because of the fast passage of food in the gut. Brown (1958) reported that gastric digestion in *N. sipedon* was temperature, meal size, and snake size dependent. Brown (1958) estimated that gastric digestion took about two days at 24°C, and postgastric digestion took roughly 36 h, with extensive variation either way expected.

In the females undergoing vitellogenesis, 71% had eaten. During vitellogenesis the coelomic fat mass decreased and ovarian mass increased. Ovarian mass at the beginning of vitellogenesis was less than 4 g and increased to a preovulatory mass of over 60 g in six to seven weeks. Coelomic fat mass decreased from a mean of 18.0 g at the beginning of vitellogenesis to 7.8 g during late vitellogenesis and early pregnancy. Based on the predicted number of vitellogenic follicles produced by females in this population, coelomic fat mass decreased 0.46 g per vitellogenic follicle produced. Because dry mass of the ova (1.8 g) exceeds the average coelomic fat mass loss per ovum, it is likely that other stored energy, or energy from food eaten during vitellogenesis, contributed to the total egg mass. The extent that current food intake contributed to reproductive tissue could not be determined with the methods employed in this study. Weatherhead et al. (1999) reported that captive female *N. sipedon* fed ad libitum during vitellogenesis did not produce larger litters nor larger offspring than control females.

In our study, 66% of the pregnant snakes had eaten, and seven of the 18 pregnant snakes in July and Au-

gust had coelomic fat masses greater than 15.0 g. The coelomic fat masses in July and August snakes were substantially higher than the coelomic fat masses of snakes that had recently ovulated. It is generally assumed that all of the energy for the development of the young is provided prior to ovulation of the ova (Stewart et al., 1990; Weatherhead et al., 1999). This assumption, however, is not universal. Stewart and Castillo (1984) stated that in the development of embryos, in which the dry mass of the embryos does not decrease during embryogenesis (as in the current study), the final dry mass "undoubtedly result(s) from maternal replacement of metabolized organic molecules." Although the role of energy gained during pregnancy could not be addressed by this study, two major uses seem possible. The energy obtained during pregnancy could be stored as fat (or protein) and used for reproduction the following spring, or energy could be used to increase SVL/mass of the female. Both uses are possible since (1) coelomic fat mass increased in some of our females and (2) Brown and Weatherhead (1997) reported that free-living *N. sipedon* grow in length and mass during pregnancy. Brown and Weatherhead (1997) found that reproductive females grew over 0.4 mm/day, whereas nonreproductive females grew almost 0.7 mm/day (measured from May to September). Our methods do not allow us to determine whether the variation in the coelomic fat mass of pregnant snakes reflects a difference in feeding frequency among the pregnant females or a difference in the energy allocated to growth in SVL or in body mass.

The interpretation of the increase in total body mass during pregnancy is more problematic. Brown and Weatherhead (1997) reported that free-living nonreproductive females grew significantly more in SVL compared to reproductive females from May to September. They added that reproductive females increased in mass more than nonreproductive females (from May to August), but the differences were not significant. Brown and Weatherhead (1997) also reported on the change in body mass corrected for SVL in these same individuals. They found that the body mass increased significantly in reproductive females compared to nonreproductive females between May and August (period of vitellogenesis and pregnancy). However, following parturition, nonreproductive females were significantly heavier than reproductive females. Brown and Weatherhead (1997) attributed some of the gain in pregnant females to uptake of water by developing embryos. They also concluded that reproductive females had done little feeding during pregnancy. Our data indicate that Brown and Weatherhead's (1997) interpretation is partially correct. Female body mass not only increases because of water uptake by developing embryos, but also by feeding (in some females) during pregnancy. In our study, about 40% of the females accumulate coelomic fat reserves equivalent to those of reproductive females in the spring.

The water content of developing embryos in our study is similar to that reported by Stewart and Castillo (1984) in *N. rhombifer*. They found that recently ovulated eggs were composed of 48% water, eggs with early embryos were 51% water, and near term embryos were composed of 74% water. Stewart and

Castillo's (1984) results differed from ours in that the total dry mass decreased in their sample by about 25%. Dry mass of developing embryos in our study remained constant during development, similar to the results obtained by Clark and Siskin (1956) and Shine (1977).

If the primary purpose of stored energy is to maximize reproductive output, snakes should maximize the number (or size) of the offspring and reduce coelomic fat reserves to near starvation levels. Such a scenario apparently occurs in the viper *Vipera aspis*. Bonnet et al. (1994) and Naulleau and Bonnet (1996) have found that *V. aspis* uses virtually all of their fat reserves during reproduction and are emaciated after giving birth. This is clearly not the case in *N. sipedon*. We found that peri-ovulatory females have from 2.9–14.6 g of coelomic fat at ovulation. With an average loss of 0.46 g of coelomic fat per ovum, it appears several more offspring could be produced with the remaining coelomic fat mass. Such a pattern might be especially true in a species that feeds during pregnancy. The data on the mass of coelomic fat used per ovum support the contention of Brown and Weatherhead (1997) that watersnakes with low coelomic fat mass may be able to breed if foraging in the spring was possible.

Large energy stores may exert a cost to females by decreasing mobility, increasing vulnerability to predation while searching for food, increasing costs of locomotion, and reducing locomotor ability to catch food (Bonnet et al., 1998). Other factors, such as too little room in the trunk for both developing embryos and additional coelomic fat, may also account for reduced food intake during pregnancy (Gregory et al., 1999). These demographic costs do not seem to apply to *N. sipedon*. We have found that watersnakes feed routinely during the reproductive cycle and some females gain significant coelomic fat reserves during pregnancy. In addition, Brown and Weatherhead (1997) found no strong evidence that reproduction reduced swimming speed or winter survival in the watersnake. Thus, the fitness costs associated with reproduction in *N. sipedon* do not appear to be uniformly high.

In summary, *N. sipedon* appear to feed throughout the active season including during vitellogenesis and pregnancy. Some pregnant snakes gained sufficient energy (coelomic fat reserves) during pregnancy to reproduce the following year with little additional feeding. We see no evidence that female watersnakes are anorexic at any time during the reproductive cycle. The gain in mass of females during pregnancy as reported by Brown and Weatherhead (1997) and Gregory et al. (1999) is at least partially caused by the increase in water mass of the developing embryo.

Acknowledgments.—We thank G. Maha, D. Coombs, C. Aldridge and J. Uzzle for assistance in the laboratory analyses and P. Weatherhead and P. Andreadis for comments on an earlier version of this manuscript. All specimens used in this study were collected and preserved in accordance with Animal Care Guidelines of Saint Louis University and with permits from Department of Conservation, Missouri, USA.

LITERATURE CITED

- ALDRIDGE, R. D. 1982. The ovarian cycle of the water snake, *Nerodia sipedon* and effects of hypophysectomy and gonadotropin administration. *Herpetologica* 38:71–79.
- ALDRIDGE, R. D., K. A. WILLIAMS, AND R. RIVERA TIELLERY. 2003. Seasonal feeding and coelomic fat mass in the watersnake *Nerodia rhombifer* in Veracruz, Mexico. *Herpetologica* 59:43–51.
- BARRON, J. N., AND G. M. ANDRASO. 2001. The influence of fall foraging success on follicle number in the northern water snake, *Nerodia sipedon*. *Journal of Herpetology* 35:504–507.
- BAUMAN, M. A., AND D. E. METTER. 1975. Economics, feeding, and population structure of *Natrix s. sipedon* in a goldfish hatchery. *Progressive Fish-Culturist* 37:197–201.
- . 1977. Reproductive cycle of the northern watersnake, *Natrix s. sipedon* (Reptilia, Serpentes, Colubridae). *Journal of Herpetology* 11:51–59.
- BONNET, X., G. NAULLEAU, AND R. MAUGET. 1994. The influence of body condition on 17- β estradiol levels in relation to vitellogenesis in female *Vipera aspis* (Reptilia, Viperidae). *General and Comparative Endocrinology* 93:424–437.
- BONNET, X., D. BRADSHAW, AND R. SHINE. 1998. Capital versus income breeding: an ectothermic perspective. *Oikos* 83:333–342.
- BROWN, E. E. 1958. Feeding habits of the northern water snake, *Natrix sipedon sipedon* Linnaeus. *Zoologica* 43:55–71.
- BROWN, G. P., AND P. J. WEATHERHEAD. 1997. Effects of reproduction on survival and growth of female northern water snakes, *Nerodia sipedon*. *Canadian Journal of Zoology* 75:424–432.
- CLARK, H., AND B. F. SISKIN. 1956. Nitrogenous excretion by embryos of the viviparous snake *Thamnophis s. sirtalis* (L). *Journal of Experimental Biology* 33:384–393.
- DERICKSON, W. K. 1976. Lipid storage and utilization in reptiles. *American Zoologist* 16:711–723.
- GREGORY, P. G., L. H. CRAMPTON, AND K. M. SKEBO. 1999. Conflicts and interactions among reproduction, thermoregulation and feeding in viviparous reptiles: are gravid females anorexic? *Journal of the Zoological Society of London* 248:231–241.
- NAULLEAU, G., AND X. BONNET. 1996. Body condition threshold for breeding in a viviparous snake. *Oecologica* 107:301–306.
- PACKARD M. J., G. C. PACKARD, AND T. J. BOARDMAN. 1982. Structure of eggshells and water relations of reptilian eggs. *Herpetologica* 38:136–155.
- SHINE, R. 1977. Reproduction in Australian elapid snakes. *Australian Journal of Zoology* 25:655–666.
- STEWART, J. R., AND R. E. CASTILLO. 1984. Nutritional provision of the yolk of two species of viviparous reptiles. *Physiological Zoology* 57:377–383.
- STEWART, J. R., D. G. BLACKBURN, D. C. BAXTER AND L. H. HOFFMAN. 1990. Nutritional provision to embryos in a predominantly lecithotrophic placental reptile, *Thamnophis ordinoides* (Squamata: Serpentes). *Physiological Zoology* 63:722–734.
- WEATHERHEAD, P. J., G. P. BROWN, M. R. PROSSER, AND K. J. KISSNER. 1999. Factors affecting neonate size variation in northern water snakes, *Nerodia sipedon*. *Journal of Herpetology* 33:577–589.

Accepted: 12 December 2002.