The Relationship between Reproduction and Lipid Cycling in the Skink Eumeces laticeps with Comments on Brooding Ecology

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THE RELATIONSHIP BETWEEN REPRODUCTION AND LIPID CYCLING IN THE SKINK *EUMECES LATICEPS* WITH COMMENTS ON BROODING ECOLOGY

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ABSTRACT: Reproduction and lipid cycling of the broad-headed skink (*Eumeces laticeps*) were studied from 1982 through 1984. Both sexes become active in early spring and mate from late April to early June. Females deposit eggs in nests constructed in rotted areas of hardwood logs during June. The male reproductive cycle is similar to that of most temperate zone lizards, in which testes are enlarged in spring but are subsequently reduced in size as breeding activities are terminated. Vitellogenesis in females commences in April, with ovulation and egg laying occurring from mid-May through Mid-June. Clutch size varies from 9–18. Females remain with the nest until eggs hatch. Clutches of eggs may be moved by females in the field, an apparent response to nesting conditions becoming unfavorable. Eggs gain over 60% of their original mass prior to hatching, but the hatchlings weigh considerably less than recently laid eggs. The brooding period lasts approximately 48 days. Hatchlings appear during late July to mid-August. Sexual maturity is reached at an age of 21 mo in both sexes, and virtually all sexually mature females in the population breed each year.

The pattern of lipid cycling for males and females is inversely associated with reproduction. Lipid reserves are reduced during reproduction and are increased at other times. In both sexes, lipids in carcasses, tails, and fat bodies cycle with reproduction, and the tail alone comprises nearly half of the standing lipids in an individual.

Key words: Brooding; Lizard; Lipids; Parental care; Reproduction; Reptilia; Lacertilia; Scincidae; *Eumeces laticeps*

DURING the past two decades, the study of the reproductive biology of reptiles has flourished. As a consequence of the high interest in this topic, it has been possible to synthesize data on many species (particularly lizards) in an attempt to hypothesize how natural selection might operate to adjust reproductive characteristics under various biotic and abiotic circumstances. Seminal synthetic studies by Tinkle (1969) and Tinkle et al. (1970) set the stage for much of the work that was to follow. Initially, it was believed that the local environment (physical and demographic) was the major determinant of the "reproductive strategy" one might observe in a natural population (Tinkle et al., 1970; Williams, 1966). Although there is no doubt that the local environment plays an important role in adjusting life history characteristics among populations within a species (Dunham, 1982), differences among species and higher taxa occurring at the same locality are often greater than differences among geographically separated populations of a single species. More recent studies have implicated foraging mode and phylogenetic inertia as additional factors potentially influencing the directions that natural selection might take in molding life history and reproductive characteristics (Ballinger, 1983; Huey and Pianka, 1981; Vitt and Congdon, 1978; Vitt and Price, 1982). Morphological "constraints" may also play a role in canalizing selection on certain life history variables (Vitt, 1981).

Because investment in egg production by female lizards is energetically expensive (Nagy, 1983; Tinkle and Hadley, 1975) data on fat storage patterns can greatly aid the interpretation of reproductive cycles of lizards (Derickson, 1976). Knowledge of lipid cycles, for example, has played a key role in estimation of the proportion of the energy budget partitioned to reproduction (Congdon et al., 1982; Nagy, 1983).

In this paper, we describe the reproductive cycle and its relationship to the

lipid cycle in the broad-headed skink (*Eumeces laticeps*) studied in the southeastern United States. This skink is of particular interest because females brood clutches of eggs from the time of deposition until the time of hatching (Fitch, 1970; Noble and Mason, 1933). Among lacertilian reptiles, only a few species of lizards in the families Scincidae and Anguidae are known to brood eggs (Shine and Bull, 1979; Tinkle and Gibbons, 1977). Among species in the genus *Eumeces*, there appear to be no "typical" (i.e., non-brooding) oviparous forms. All species for which there are reasonable data are either oviparous and brood eggs or are viviparous (Fitch, 1970; Hasegawa, 1984; Hikida, 1981). The viviparous species appear to occur at high elevations (Fitch, 1970; Guillette, 1983). Egg brooding is often considered an alternative to viviparity (Fitch, 1970; Tinkle and Gibbons, 1977).

Available information on reproduction in *E. laticeps* is anecdotal in nature, consisting primarily of observational data on time of hatchling appearance (Goin and Goin, 1951), egg laying sites (Martof, 1956; Mount, 1975), or copulation (Carr, 1940). There may be considerably more information available, but problems in distinguishing this species from *E. fasciatus* and *E. inexpectatus* (Murphy et al., 1983) render many published observations on North American species in the *fasciatus* group of *Eumeces* questionable.

We focus our study on several rather broad questions. (1) What is the seasonal reproductive cycle of males, and is it associated with the lipid cycle? (2) What is the seasonal cycle in female reproductive activity, and is the female cycle associated with patterns of lipid storage and utilization? (3) What are clutch size, egg size, and clutch frequency and how does *E. laticeps* compare with closely related species for these variables? (4) Does clutch size vary with female size and/or age? (5) Does parental care (egg brooding) impose any constraints on other aspects of the reproductive biology of species possessing it?

METHODS

Description of the Species and Study Area

Eumeces laticeps is a large-bodied skink [maximum snout–vent length (SVL) = 144 mm] which is widespread throughout much of the southeastern and central United States (Conant, 1975). It is most often associated with remnant hardwood forests, and in the southeastern part of its range, it is often found in stands of live oak (*Quercus virginianus*). Individuals are diurnally active, and most of their daily activity period is spent foraging in leaf litter on the forest floor or on large logs and tree trunks. They eat a variety of prey items, most of which are themselves not surface active (Vitt and Cooper, unpublished data). These skinks become active in early spring and, depending on the severity of the winter, may be seen basking as early as March.

Most of our reproductive data were collected from specimens sampled either on the Savannah River Plant in Aiken and Barnwell counties, or Kiawah Island in Charleston County, South Carolina, although we include some data on body sizes and clutch sizes from museum specimens (University of Georgia Museum of Natural History collections) collected in Georgia, South Carolina and Alabama. Despite some habitat differences between these localities, the oak woodlands in which the populations were studied are quite similar structurally. Both habitats contain large hardwood trees and there are many rotting logs and stumps suitable for nesting. In both habitats, pine trees are interspersed with the hardwoods, but *E. laticeps* rarely use them. Although we observed no apparent differences in the body and clutch size data from different localities, the possibility exists that differences might be detected with larger samples.

Field Methods

Lizards were collected by hand, noose, and BB rifle primarily during the spring,

summer and fall of 1982, 1983 and 1984. All lizard samples for necropsy were collected during 1983 on Kiawah Island and were placed on ice in the field. Upon return from the field, the necropsy samples were thawed and the following pertinent morphological measurements were taken: snout–vent length (SVL), tail length, and length of regenerated portion of the tail (if any) to 1 mm, total body mass to 0.001 g, stomach mass to 0.0001 g, and fat body mass to 0.0001 g. In males, both testes were weighed, and in females, oviductal eggs or vitellogenic follicles were weighed to 0.0001 g. In addition, because it is apparent that the tails of these lizards may serve as important fat storage organs, tails were cut at the base (approximately 2.0 mm posterior to the cloaca) and were weighed to 0.0001 g. Testes of males were preserved in 10% buffered formalin for later histological examination.

For lipid analysis, fat bodies, tails, eggs, and carcasses were freeze-dried (−60 C) to constant mass and reweighed (0.0001 g). This allowed determination of water content of each sample. Samples of dried fat bodies and eggs were ground with a mortar and pestle, and dried bodies and tails were ground with a Wiley Mill. Lipids were extracted by soaking samples in petroleum ether (minimum of 20 to 1 solvent to solute ratio) at room temperature for a minimum of 24 h (see Congdon and Tinkle, 1982).

Size at sexual maturity for females was estimated in part as the SVL of the smallest female with enlarged vitellogenic follicles or oviductal eggs. Among males, size at sexual maturity was based in part on the size of the smallest male containing mature sperm-producing testes. Correlated with this in males were enlarged and highly convoluted epididymides and a color change of the head region (from light brown to orange or red) characteristic of mature males during the breeding season (Vitt and Cooper, 1985). It was possible to estimate age at maturity by plotting the size of all animals captured in the field against the month of capture. The size of the smallest male and female at the time most individuals would be entering their first breeding year also was utilized in estimating minimum size at sexual maturity. Values from this analysis were very close to those based on condition of reproductive organs described above.

Data on clutch size were acquired from preserved specimens, fresh animals at autopsy, females captured while brooding their clutches in the field, and live lizards that oviposited in captivity. Our clutch size estimates are based on counts of enlarged vitellogenic follicles, oviductal eggs, and clutches that females were brooding. We include the latter in the "oviductal" group for data analyses.

During summers of 1983 and 1984, we reared clutches of eggs in the laboratory. Clutches of eggs were obtained in two ways. Some females were collected in the field just prior to oviposition. These females were placed in plastic terraria (30 × 16 × 9 cm) with slightly dampened litter taken from rotted oak logs, the material in which clutches are laid in the field. A 10 × 10 × 2 cm wood block was placed in each plastic box to provide cover for the skink. Food (crickets and mealworms) and water were provided ad libitum. Females constructed nests under the wood blocks, deposited, and brooded their eggs (see results). Females collected in the field while they were brooding clutches were brought into the laboratory and were set up in the same way as the gravid females. Each of these constructed a nest within 24 h and brooded its clutch. Based on our laboratory stock of females, we were able to estimate approximate times to hatching. We consider these estimates to be reliable, because our in-laboratory oviposition and hatching dates corresponded closely with dates on which we first collected nesting females and observed hatchling lizards, respectively, in the field.

For a number of clutches studied during 1984, each individual egg was given a number with carbon ink, and individual
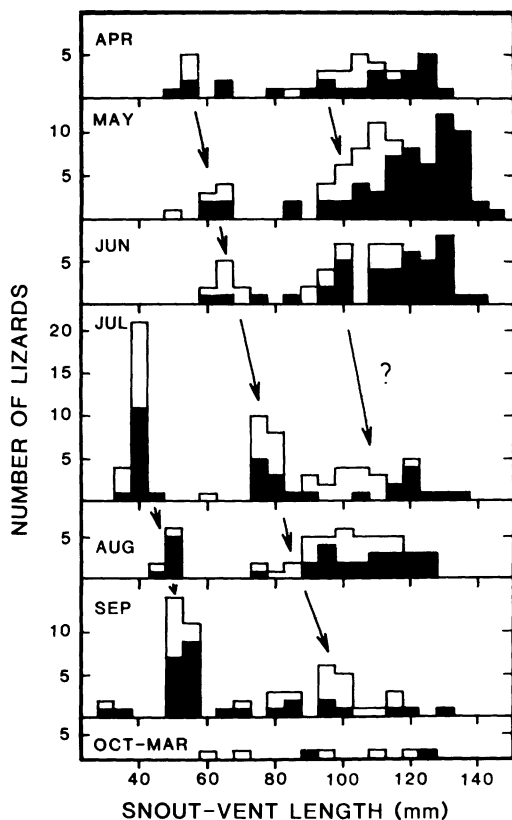
FIG. 1.—Seasonal size (SVL) distributions of male (closed bars) and female (open bars) *E. laticeps*. Because of small winter samples, data are pooled for October–March. Arrows indicate presumed growth patterns of a given age class from month to month.

egg masses were recorded nearly each week from shortly after the eggs were laid until hatching. This allowed a determination of the gain in mass of eggs due to water uptake during development. When the eggs hatched, after being brooded by the female parent, each neonate was measured and weighed. This allowed a comparison of offspring size within and among clutches (females).

Standard parametric statistical tests were used when the assumptions of the tests could be reasonably met. Otherwise, nonparametric counterparts were substituted. Differences were considered statistically significant at $\alpha = 0.05$. Means are presented ± 1 SE.

RESULTS

Size and Age at Sexual Maturity

The minimum size at sexual maturity for males and females was estimated to be 85 mm SVL based on condition of reproductive organs. Even though sexual maturity is reached at the same body size in both sexes, males attain much larger body size than females (Fig. 1). A more thorough analysis of sexual differences in morphology appears elsewhere (Vitt and Cooper, 1985). Based on seasonal size distributions of these skinks (Fig. 1), sexual maturity is reached by the beginning of an individual's second full summer at an age of 21 mo. Individuals have the potential to enter the breeding population during May at a SVL of approximately 82 mm, although most are slightly larger than this. Estimating the age of most individuals after the second full summer based on SVL is virtually impossible, as is apparent in Fig. 1.

Female Reproduction, Nesting and Brooding

Females emerge from overwintering during late March or early April. At that time, the ovarian follicles are small and translucent. Vitellogenic follicles averaged 2.84 ± 0.37 mm ($n = 10$) in April samples and 3.88 ± 0.30 mm ($n = 4$) in early May samples. By mid- to late May, at least some of the females are near ovulation. Females deposit clutches from mid-May to mid-June. Our impression is that virtually all sexually mature females in the population deposit clutches each year. All females collected prior to oviposition were gravid, and we were unable to find non-brooding females of adult size in the field populations during the brooding period. Once the clutches are deposited, females are rarely seen on the surface, because they remain with or near the clutch until hatching.

The female constructs a nest in rotted areas of hardwood trees or logs (usually *Quercus virginianus*) under bark or under relatively thin surface strips of wood.
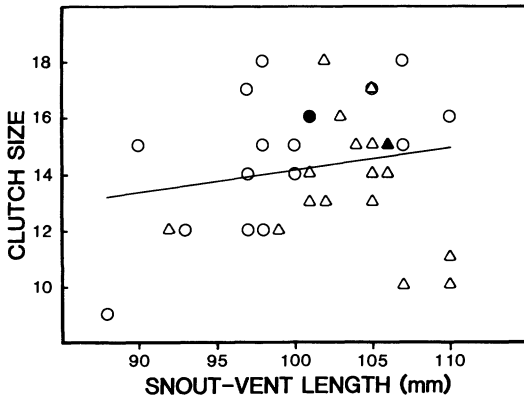
FIG. 2.—Relationship of clutch size and female body size (SVL) in *E. laticeps*. Circles represent counts based on oviductal eggs or eggs laid by females, triangles represent counts of vitellogenic follicles, and solid figures indicate more than one data point at a given set of coordinates.
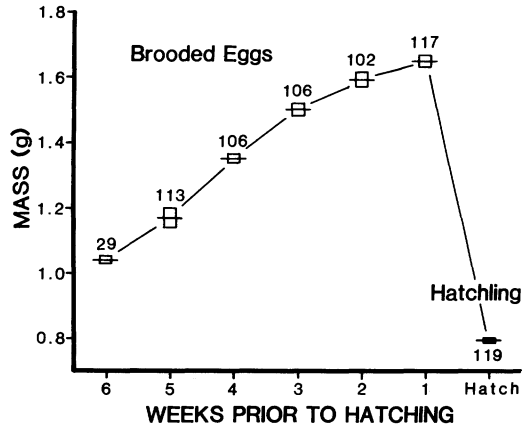

FIG. 3.—Mass of eggs brooded by female *E. laticeps*. Data are sorted according to the number of weeks prior to hatching. Hatchling mass is also shown. Means are presented ± 1 SE.

All of the field nests that we have found were located in areas within rotted wood that had been cleared, with the debris packed against the sides. The nest chambers appear to be nearly completely sealed from the outside. In the laboratory, we observed these skinks to reconstruct their nests by circling the egg clutch and thereby pressing the debris against the sides of the terraria. The resultant nest chamber is scarcely large enough for the skink and its clutch. When the skinks exit the nest to feed, they simply push an opening into the debris, using it as an exit and entrance. Upon re-entering the nest, they again circle the clutch, packing the sides of the nest and closing the exit.

Clutch size varies from 9–18 (all data) and exhibits a weak and statistically insignificant ($F_{1,33} = 1.09$, $P > 0.05$) correlation with SVL (Fig. 2), with SVL explaining only 3.2% of the variance. Among females containing oviductal eggs or brooding clutches ($n = 18$; $\bar{x}$ SVL = 103.8 ± 0.98 mm), clutch size averaged 13.7 ± 0.52 eggs and SVL explained only 1.45% of the variance. In females containing vitellogenic follicles ($\bar{x}$ SVL = 99.2 ± 1.42 mm) clutch size averaged 14.8 ± 0.58

eggs but 37.9% of the variance in clutch size could be attributed to SVL ($F_{1,15} = 9.16$, $P < 0.01$). The apparent discrepancy in R^2 values can be attributed partially to the three data points showing low clutch size at relatively high SVL (Fig. 2). In addition to those low values, several females in the laboratory produced exceptionally small clutches (as low as two). These were females that we had kept in captivity during the winter prior to egg deposition, and thus those animals were not included in the clutch size estimates. Some follicles may also become atretic, reducing actual clutch size compared to the follicle count. Finally, these are minimal estimates, because some of our data (included as oviductal eggs) are counts of eggs being brooded by females in the field. There is the possibility that some eggs (see below) had been eaten by females or predators.

Shelled eggs at oviposition averaged 1.079 ± 0.022 g (51 eggs, four clutches). During the brooding period, eggs increase in size and mass due to water uptake. The gain in mass of eggs from ovulation to hatching is shown in Fig. 3. Because these data include eggs for which we do not have exact deposition date, we have grouped the data as "time prior to hatch-

TABLE 1.—Descriptive statistics for 12 female *Eumeces laticeps* that successfully brooded their egg clutches in the laboratory (see Methods) during summer 1984. Even though there was an increase in body mass during the brooding period for most of the females, the final body mass of females was not significantly different from the original mass based on a one way analysis of variance ($F_{1,22} = 2.26$, $P > 0.05$).

Variable	$\bar{x}$	SE	Min.	Max.
Initial SVL (mm)	104.5	1.11	99	110
Initial body mass (g)	25.52	1.11	19.51	32.40
Final body mass (g)	27.87	1.09	21.39	34.12
Gain in mass (g)	2.344	0.675	−0.81	5.38
Body mass gain/day	0.048	0.015	−0.021	0.137
Clutch size	12.1	0.9	5	16

ing," because we know the hatching dates of all clutches. The sample sizes vary among time periods due to some mortality in the nest and the addition of females and their clutches at various time intervals. Hatchling mass was considerably less than that of eggs at oviposition (Fig. 3). With all data pooled, hatchlings averaged 31.4 ± 0.1 mm SVL and 0.797 ± 0.005 g ($n = 119$). Because it is nearly impossible to determine sex of hatchlings without killing them, sexes were pooled. An analysis of variance, however, revealed significant differences ($F_{9,106} = 19.02$, $P < 0.01$) in hatchling mass among clutches produced by different females (only broods with >3 hatchlings were included in the analysis). Clutch mass/body mass (just after oviposition) averaged 0.541 ± 0.112 g, and clutch mass/total mass (body + clutch) averaged 0.341 ± 0.046 g in four females ranging from 10.36–16.34 g body mass.

Ten of 12 laboratory females were captured either just prior to or just after ovipositing in 1984. Four of these deposited clutches just after capture. Because we recorded exact oviposition dates for these four females, we obtained data on the number of days of brooding in the laboratory. In these females, eggs were brooded for 45.0 ± 4.5 days. We estimated that the other six females averaged a minimum of 51.2 ± 3.3 days brooding, using the date of capture as an approximation of oviposition date. A one way analysis of variance revealed no significant difference between known brooding periods and

the estimated period ($F_{1,8} = 1.28$, $P > 0.05$). Pooling the data yielded a mean of 48.7 ± 2.7 (37–59) days for the brooding period. Although most of these females gained small amounts of body mass during the brooding period, the gain was not statistically significant (Table 1). More importantly, females did not lose body mass during the brooding period.

Hatchlings appeared from mid-July through early August. The earliest date that we observed hatchlings in the field was 12 July. This coincides closely with hatching dates in the laboratory. During the summer of 1984, laboratory clutches hatched from 31 July through 12 August, slightly later than hatching dates we have observed in the field and laboratory in the past (early to mid-July). This presumably is a consequence of relatively cool weather during spring and summer of 1984 compared to past years.

In the laboratory, all eggs within a given clutch hatched on the same day. The parchment-like shell is slit open with the egg tooth of the hatchling and the neonate exits shortly thereafter. At hatching, neonates have a substantial supply of yolk, which is visible through the ventral body surface. Similar yolk deposits were observed in newly hatched skinks in the field as well. An umbilical scar is present, which fades within several days. We have seen no indication in the laboratory that the female plays any part in helping the neonates free themselves from the eggs. Once all of the eggs have hatched, the neonates remain aggregated with the female under

the surface item in the cage. Because we provide only one surface item, this apparent aggregative behavior may simply reflect a shortage of cover items. We have no field evidence suggesting post-hatching parental care in *E. laticeps*. Within one day post-hatching in the laboratory, the neonates explore the cage and if offered termites, they feed.

Male Reproductive Cycle

Males are first seen active in the field during late March. By April, the change in head coloration takes place (from light brown to orange or red), and males become aggressive toward other mature males. The color change of the male's head, as well as the aggressive behavior towards other males and the courtship behavior towards females, can be induced by androgen treatment of non-reproductive males that have been gonadectomized (Cooper and Vitt, unpublished data). Thus it appears that these characteristics are under androgenic control. Testes of males are largest during April and May and begin to decline in size during June, reaching minimum size by September (Fig. 4). The period during which testes are enlarged coincides with the period during which red head coloration, aggression towards other males, and courtship behavior were observed in the field.

Males were observed courting or "guarding" (see Vitt and Cooper, 1985) females in the field as early as 13 May, and on this occasion, copulation was observed. Copulation generally takes place primarily during May and early June, but it potentially could occur as early as late April. The female from the above pair oviposited in the laboratory on 13 June. In the field, females that have mated and presumably ovulated disappear into nesting sites by mid-June, coincident with oviposition dates of females in the laboratory.

Males often remain with an individual female in the field for several days. We have not yet determined whether this represents an extended courtship period or
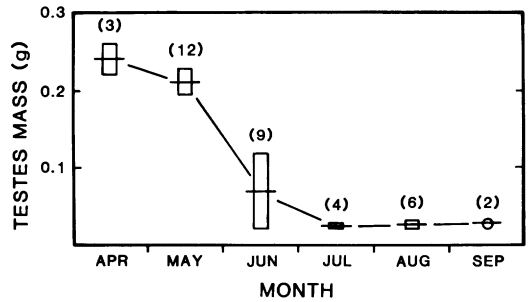

FIG. 4.—Cycle of testes mass for male *E. laticeps*. Sample sizes are indicated in parentheses.

post-copulatory mate guarding. Based upon our laboratory observations, it appears as though the courtship may be brief and thus the latter is more likely. Once a female has retreated into a nesting area within a tree or log, it becomes unavailable to males. The short period of receptivity for individual females compared to males suggests that males may have the opportunity to mate with more than one female (see Vitt and Cooper, 1985).

Lipid Cycling

Fat is stored in abdominal fat bodies, the tail, and the carcass in males and females. In almost all variables related to lipid cycling, there were significant differences between sexes (Table 2). Most striking is the low contribution by fat bodies to the total lipid content of the lizards and the high proportional contribution of the tail to total lipids. Seasonal variation was apparent not only in the proportions of total lipids comprised by each storage compartment (Fig. 5), but also in the percent of the compartments comprised of lipids (Fig. 6). Fat storage in females was minimal during egg production and increased following the brooding period, reaching a maximum in fall prior to overwintering. Presumably much of the energy used in producing the clutch stems from fat storage based on resource acquisition during the preceding summer. In a general sense, seasonal lipid cycling in males was similar to that in females (Figs.

TABLE 2.—Comparisons of variables calculated in lipid analyses for male and female *Eumeces laticeps*. Lizards were divided into three compartments (body, fat bodies, and tail) and variables are calculated for each compartment. Because body masses of male and female samples were significantly different ($F_{1.66} = 36.6$, $P < 0.0001$), with males averaging 39.59 ± 2.02 g and females averaging 23.77 ± 1.48 g wet mass, a portion of the differences in variables between sexes may be attributed to body size differences between samples. Probability values listed below are based on the Mann-Whitney U test.

Variable	Males (n = 37)	Females (n = 30)	P
Percent lipids of dry samples			
Body	3.78 ± 0.30	7.51 ± 5.59	<0.0001*
Fat bodies	76.06 ± 4.66	82.88 ± 5.76	0.0347*
Tail	20.92 ± 2.82	37.69 ± 2.63	<0.0001*
Actual lipids (% lipids × dry mass)			
Body (g)	0.3600 ± 0.0301	0.4636 ± 0.0550	0.2690 NS
Fat bodies (g)	0.0867 ± 0.0177	0.2244 ± 0.0438	0.0253*
Tail (g)	0.4832 ± 0.0719	0.7631 ± 0.1096	0.0621 NS
Lipid ratios (as % of total lipids)			
FB lipids	6.86 ± 0.77	11.51 ± 1.68	0.0277*
Tail lipids	46.80 ± 1.81	51.57 ± 2.15	0.0130*
Wet mass ratios (as % of total)			
[1]FBWM/total × 100	0.36 ± 0.06	1.07 ± 0.16	0.0006*
[1]FBDM/total × 100	0.75 ± 0.13	2.35 ± 0.37	0.0011*
[1]Tail WM/total × 100	15.30 ± 0.38	16.30 ± 0.61	0.0557 NS
[1]Tail DM/total × 100	18.34 ± 0.53	22.08 ± 9.90	0.0003*
Water content of fresh compartment			
Body	69.97 ± 0.24	70.74 ± 0.44	0.1399 NS
Fat bodies	44.68 ± 3.45	34.96 ± 3.98	0.0130*
Tail	62.49 ± 0.78	56.52 ± 1.35	0.0009*

[1] "Total" refers to mass of body, fat bodies, and tail combined. FB = fat bodies. WM = wet mass (fresh). DM = dry mass.
* Significant differences at $P < 0.05$.

5 and 6), with peak lipid levels late in the summer after the breeding season.

DISCUSSION

Determinants of the Reproductive Cycle

Eumeces laticeps clearly falls into the long-lived, late-maturing reproductive strategy recognized by Tinkle et al. (1970), reaching sexual maturity after the second year of life and producing one clutch per year. Species that are viviparous or exhibit parental care (brooding) generally fall into this category. Although we do not yet have an estimate of longevity, individual *E. laticeps* are certainly capable of living at least 5 yr. We have held a number of individuals collected as adults (>2 yr of age) for more than 3 yr in captivity. One individual captured as a large adult (>3 yr of age) was held in captivity 5 yr by WEC. Pertinent aspects of the life history of *E. laticeps* have been summarized elsewhere (Vitt and Cooper, 1985). The proximate cause of the restricted reproductive season is associated with hormonal cycles. This is suggested by data on pheromonal communication and on morphological and behavioral changes associated with the testicular cycle in males. Both sexual recognition and identification of sexual receptivity of females by males is accomplished by the use of chemical cues emanating from the cloacal region. This chemical communication system is influenced by gonadal steroid hormones (Cooper and Vitt, 1984a,b). The exact timing of reproduction (spring) is most likely a consequence of temperate zone climatic seasonality and its effect on reptilian ac-
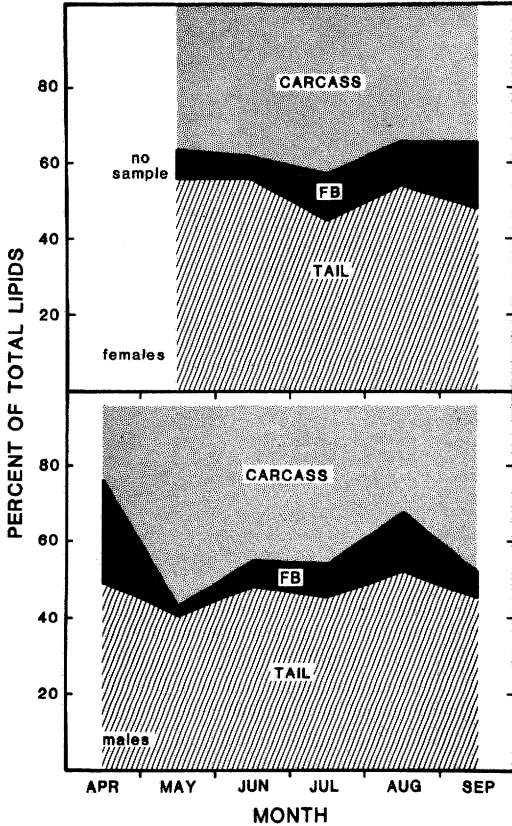
FIG. 5.—Seasonal distribution of lipids in various storage compartments expressed as percent of total lipids for male and female *E. laticeps*.
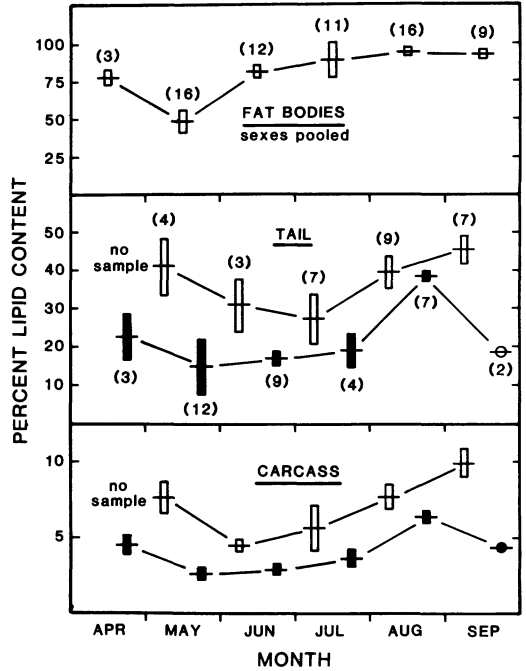
FIG. 6.—Seasonal variation in percent lipid content of various storage compartments in *E. laticeps*. Because there were no significant differences between males and females in percent lipids of fat bodies, data are pooled by month. Males are represented by closed bars, females by open bars. Means ± 1 SE are presented. Sample sizes are indicated in parentheses.

tivity (Duvall et al., 1982). Nearly all temperate zone reptiles are spring breeders (Fitch, 1970).

It appears that *E. fasciatus* and *E. inexpectatus* in the southeastern United States are similar to sympatric *E. laticeps* in being long-lived, late-maturing, and producing one clutch per year (Vitt and Cooper, unpublished data). Indeed, all species of *Eumeces* for which there are data appear to reach sexual maturity at an age of 2–3 yr, produce but one clutch or brood per year (fewer in *E. obsoletus*), and are relatively long-lived (Breckenridge, 1943; Fitch, 1954, 1955, 1970; Hasegawa, 1984; Hikida, 1981; Mount, 1963; Tanner, 1957). The prevalence of similar life history traits among species of *Eumeces* suggests that

this set of traits represents an example of the constraining effect of "phylogenetic inertia" on life history variables (Ballinger, 1983).

Likewise, oviparous species of *Eumeces* that do not brood clutches are unknown, and the viviparous species all occur at higher elevations (Fitch, 1970; Guillette, 1983). These data suggest that viviparity in *Eumeces* may have arisen within brooding species as an adaptation to high elevations (cold climates) (Shine, 1983a). In order for this to be a reasonable hypothesis, it is necessary to consider the intermediate condition between oviparity (with brooding) and viviparity. For viviparity to arise from oviparity, it is necessary that natural selection favor egg retention (Blackburn, 1982; Shine, 1983a;

Shine and Bull, 1979; Tinkle and Gibbons, 1977). Egg retention should be selectively advantageous in habitats where the probability of a clutch hatching decreases with the time period that the clutch is in the nest. This would be particularly likely at higher elevations. In such environments, decreased length of a thermally suitable season could favor reduction in the length of the brooding period in spite of the advantages of established brooding. Decreased brooding duration could be accomplished by (1) females frequently basking and returning to the clutch and thereby increasing the developmental temperature and reducing developmental time or (2) retention of eggs in the oviduct and basking to achieve higher body and consequently clutch temperatures resulting in oviposition of a clutch requiring a shorter brood period. The first option seems highly unlikely, at least for *Eumeces*. In his extensive study of *E. fasciatus* in Kansas, Fitch (1954) found no indication of skinks basking, increasing their body temperatures, and returning to the nest to transfer heat to eggs. Moreover, as skinks moved into higher elevations (colder climates), this would become less and less efficient. The second option is much more tenable, because , it simply requires that females retain eggs, bask, and lay clutches that require less time for development and consequently a reduced brooding period. A large number of lizards retain eggs for various lengths of time (Tinkle and Gibbons, 1977; see Shine, 1983*b*, for a much more extensive discussion). Most lizards bask, including nearly all viviparous species, and there are numerous examples of lizard species at high elevations that lay eggs with embryos in advanced stages of development (Fitch, 1970; Guillette, 1982; Tinkle and Gibbons, 1977).

It is possible that the extended brooding period of female *Eumeces* is a major determinant of low clutch frequency. Females do not emerge from brooding until mid- to late July. Even though there would be enough time to produce and brood another clutch, the potential costs of doing so would be higher than the gains unless the probability of a female surviving to breed again were extremely low. Costs include: (1) reduced energy stores necessary to invest in another clutch due to presumed reduced feeding during brooding, and (2) reduced time to forage and store fat necessary for overwintering and/or production of the first clutch during the next season. Also, hatchlings born late in the season in geographical areas experiencing unfavorable climatic conditions for prolonged reptilian activity might not be able to acquire adequate energy reserves for overwintering. It is well established that lipid stores may be partially used during overwintering in lizards (Avery, 1970, 1974; Ballinger and Tinkle, 1979).

Brooding of eggs for an extended time period by the females affords the female some control over development and presumably increases the probability of eggs hatching (Fitch, 1970; Noble and Mason, 1933; Shine and Bull, 1979; Tinkle and Gibbons, 1977). Typical oviparous species have no control over the environment or potential predators that the eggs might encounter during development once the eggs have been deposited. In all of the field nests that we have found, every egg appeared viable. Each egg was turgid, and in instances when we brought the female and its clutch into the laboratory, nearly all eggs hatched. There is the possibility that eggs occasionally die in nests. Our failure to observe such eggs may be a consequence of females ingesting dead eggs. We have taken reptile eggs from the stomachs of field-fresh *E. laticeps* (Vitt and Cooper, unpublished data), and there are reports of closely related skinks (*E. fasciatus*) eating dead eggs from nests in the laboratory (Groves, 1982; McCauley, 1945). We have little field evidence, however, that females eat their own eggs (dead or alive). A female whose nest we disturbed in the field on 17 July 1984 was brooding a clutch of 12 eggs, all of which

looked viable and in good condition. We carefully replaced the cover material over the nest. On 26 July, the nest was again uncovered. It had been moved approximately 20 cm by the female, which was brooding the clutch. However, only 10 eggs were present. Whether or not the female ate her own eggs remains unknown. Some females in our laboratory have eaten eggs while brooding. For example, among 15 females with broods that we reared in the laboratory during summer, 1984, seven ate one or more (not exceeding three), and three ate all of their eggs.

Offspring size is generally believed to be relatively constant among females within animal populations. From a theoretical point of view, selection should favor females that produce offspring of a size most appropriate for given environmental and competitive conditions (Smith and Fretwell, 1974). Some lizards that produce clutches at different times within a reproductive season are known to produce relatively more small offspring when resources are abundant and relatively fewer large offspring when resources are scarce (Ferguson et al., 1980; Nussbaum, 1981). The variation in offspring size among female *E. laticeps* in this study and *E. fasciatus* in another study (Vitt and Cooper, unpublished data) is perplexing, partially because females synchronously produce one clutch per season. In the laboratory, all females and their clutches were exposed to similar environmental conditions, but we did not monitor thermal and moisture conditions within individual terraria. Thus the possibility exists that interclutch variation in offspring size could be a consequence of differing environmental conditions for the eggs. Water relations of eggs have been shown to affect offspring size in some reptiles (Packard et al., 1981). If environmental conditions in skink nests can cause changes in relative offspring size, brooding behavior and the ability of females to move the clutch provide a proximate behavioral mechanism for adjustment of offspring size. If overall environmental conditions (presumably predicting resource availability) are reflected in the nest, selection should favor females capable of predicting resource availability to offspring on the basis of environmental cues and moving the clutch to nest sites providing conditions appropriate for optimal adjustment of offspring size. Although variation in offspring size might partially reflect the nutritional state of the female during vitellogenesis, clutch size adjustment would provide an alternative to females under resource stress in environments where offspring survival is size dependent. There is also the possibility that differences in offspring size among females are genetically determined and reflect a history of selection favoring given offspring sizes associated with microhabitat differences among family lineages (Ferguson et al., 1980). Regardless of the cause for the differences in offspring size, our observations indicate that *Eumeces* that brood clutches provide an ideal system for examining environmental, behavioral, and evolutionary determinants of offspring size.

Lipid Cycling and Reproduction

It is well known that lipid storage cycles are correlated with reproductive cycles in reptiles (see Derickson, 1976, for review). In most instances, lipid storage is high prior to the reproductive season and declines in males during the time period when territorial or courtship behavior occurs, and in females during the time period when lipids are deposited in vitellogenic follicles. This correlation seems to hold in temperate and tropical lizards, including *E. laticeps*, regardless of the exact season when reproduction occurs. The lipid analysis presented here raises several interesting points relevant to lipid cycles in reptiles in general. First, we have shown that the percentages of lipids in various compartments cycle seasonally with reproduction as well as the actual amounts of lipids. Many studies only report actual amounts of lipids and many other studies

present only data on mass of abdominal fat storage organs (Vitt, 1983). Our observation that the percent lipid composition of fat bodies and other compartments (Fig. 6) cycle seasonally suggests that cyclical variation in fat body mass alone may not accurately reflect cyclical patterns of fat body lipid content. Although our data do show that the mass of abdominal fat bodies cycles with reproduction, the percentage of the total standing lipid reserves represented in fat bodies is quite small. The lipids contained in the tail of *E. laticeps* cycle with reproduction similarly to those in fat bodies, but the proportion of the total standing lipid content of the lizard represented by the tail is nearly 50%. It has been suggested that tail lipids correlate negatively with egg production in the gecko *Hemidactylus* (Greene, 1969) based on a reduction in tail size of females producing eggs. Recently, Dial and Fitzpatrick (1981) demonstrated that loss of a high energy content tail in the gecko *Coleonyx brevis* resulted in a reduction in egg size.

Even though mass of fat bodies generally seems to cycle with reproduction and may represent the overall state of the lizard population with respect to lipid storage, extreme caution must be taken in interpreting lipid cycle data based solely on fat bodies. During periods when fat reserves in fat bodies are low, almost nothing about the physical state of the lizard can be predicted. An individual lizard with small fat bodies could have high amounts of lipids stored elsewhere (tail, carcass) or it could have no lipids stored elsewhere. The consequences of these two alternatives for reproduction are drastically different.

In view of the potential problems associated with the use of wet mass data on abdominal fat bodies of lizards as operational estimates of overall fat storage, they may serve well to gauge fat storage patterns of lizard populations across time. We performed regression analyses with mean monthly total lipids as the dependent variable against monthly mean fat body wet mass, fat body dry mass, and percent lipid content of fat bodies for males and females separately. In females, all regressions were significant ($P < 0.05$), and the highest R^2 value (0.983) resulted from the fat body wet mass versus total lipids comparison ($F_{1,4} = 225.7$, $P < 0.001$). Thus fat body wet mass was the best predictor of total lipids. These population patterns, however, reveal little about the significance of differences in lipid content among individuals.

CONCLUSIONS

Among the species of *Eumeces* studied to date, *E. laticeps* differs from most only in the production of a relatively large clutch of eggs. This may, however, simply be a consequence of its large body size relative to other species of *Eumeces*. Whether or not *E. laticeps* is unusual in terms of the large proportion of lipids stored in the tail and carcass cannot be determined at this time due to a lack of comparative data.

Viviparity appears to have arisen a number of times in *Eumeces*. The lack of any typical non-brooding oviparous forms suggests that viviparity arose from oviparity with brooding. The relatively low variation in life history traits among species of *Eumeces*, regardless of locality studied, suggests that the suite of adaptations associated with egg brooding acts as a "design constraint" (Ballinger, 1983; Stearns, 1976, 1977) rendering unlikely the operation of selection simultaneously favoring all associated adaptations necessary to regain typical oviparity. This may partially explain the similarity among species of *Eumeces* in life history characteristics.

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