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Locomotor impairment and defense in gravid lizards (*Eumeces laticeps*): behavioral shift in activity may offset costs of reproduction in an active forager

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Summary. Female *Eumeces laticeps* experience a substantial decrease in running speed (ca. 25%) and an even greater loss of endurance (slightly over 50%) while gravid. Because some widely foraging lizards, including *E. laticeps*, rely primarily on running to escape predators, the decreases in speed and stamina may contribute to an increased risk of predation. However, observations suggest that gravid females become less active or conspicuous on the surface. Ambush foraging lizards rely relatively more on crypsis associated with immobility to avoid predation and thus can have greater average relative clutch mass (RCM) than active foragers. Behavioral compensation for locomotor impairment by becoming less active or conspicuous may allow some species the advantages inherent in both high relative clutch mass when gravid and the increased energetic profitability of active foraging when not gravid. As females gain weight during the breeding season, they may forage actively until the risk due to increasing locomotor impairment becomes too great and then change defensive strategy to greater reliance on crypsis. Without such a shift, widely foraging squamate reptiles may be less able than ambush foragers to exploit life-historical strategies demanding high current investment in reproduction.

Introduction

Recent interest in measuring cost of reproduction in squamate reptiles has centered on differences in locomotory performance between gravid and nongravid females (Shine 1980; Bauwens and Thoen 1981; Reznick 1985; Seigel et al. 1987; Brodie 1989). Central to this interest is the hypothesis that in species depending on mobility for escaping predators, gravid females suffer greater risk of mortality than nongravid females because the clutch mass lessens mobility. Being slowed, gravid females might reduce their risk of predation by altering defensive behavior to decrease the likelihood of being detected during the interval of locomotor impairment. Obvious possibilities include reducing activity and remaining close to refuges.

The prediction that squamates having increased mass have reduced locomotor performance has been verified. Gravid squamate reptiles and those that have recently eaten large meals have reduced locomotor abilities (e.g., Shine 1980; Bauwens and Thoen 1981; Garland and Arnold 1983; Huey et al. 1984; Garland 1985; Seigel et al. 1987; Brodie 1989; Sinervo et al., in review). In some taxa, gravidity per se may impair locomotion in addition to the effect of increased mass (Brodie 1989). That squamates are more vulnerable to predation when gravid has been confirmed in the laboratory for the scincid lizard *Leiolopisma coventryi* (Shine 1980) and in the field for the snakes *Vipera berus* (Andren 1985) and *Natrix natrix* (Madsen 1987) as a cost of reproduction.

The cost imposed by decreased mobility undoubtedly varies among reptilian taxa, presumably being greatest in species heavily dependent on speed and endurance for escape. Many species of widely or actively foraging lizards move almost continuously while searching for prey. This movement places them at risk of being detected by visually oriented predators (Gerritson and Strickler 1977; Huey and Pianka 1981). Thus, Vitt and Price (1982) argued that crypsis may have greatly reduced effectiveness during active foraging. In ambush foragers, crypticity combined with immobility is an important defense (Vitt and Congdon 1978; Huey and Pianka 1981; Vitt and Price 1982).

Among actively foraging lizard species, those suffering the greatest decrements in speed and stamina should suffer a greater increase in risk of predation. For species of similar body proportions within a lineage, those having large clutch mass relative to body mass (relative clutch mass = RCM = clutch mass/body mass) should be most affected (see Dunham et al. 1988b and Brodie 1989, for other ways of measuring relative clutch and body sizes). As predicted, the degree of slowing in several

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Offprint requests to: Reprint Department, Savannah River Ecology Laboratory, Drawer E, Aiken, SC 29801, USA scincid species increases with RCM (Shine 1980), suggesting that increased predation may result from increases in RCM. This relationship is not found in the snake *Thamnophis ordinoides* (Brodie 1989).

Our study combines field observations of behavior related to activity with laboratory studies of locomotor performance in gravid (having oviductal eggs) and nongravid females of the widely foraging scincid lizard *Eumeces laticeps* (Vitt and Cooper 1986). RCM in this species (0.541; Vitt and Cooper 1985) is considerably higher than reported for other skinks (0.380; Shine 1980; Vitt and Price 1982). This suggests that mortality of gravid females would be high unless females compensate by becoming less conspicuous. (Although most RCM values in Vitt and Price were for clutch mass/[clutch mass + body mass], the mean would be well below that for *E. laticeps* if the values were converted to clutch mass/body mass, the units reported by Shine.)

Methods

Animals, housing, and maintenance. Eleven gravid *Eumeces laticeps* were collected on Kiawah Island and Johns Island, Charleston County, South Carolina on 12, 13, and 27 May 1987. they were transported initially to the Savannah River Ecology Laboratory (SREL) in Aiken, South Carolina. At SREL the skinks were housed in a laboratory building having translucent walls. They were thus exposed to the natural photoperiod of the surrounding area. The temperature cycle also approximated that of the surrounding area, with elevations of a few degrees Celsius in late afternoons. Lizards were kept individually in 49 × 49 × 32 cm glass terraria, each of which contained a sand substrate, a water bowl, and a shelter site. Lizards were fed 8–10 crickets dusted with a commercial vitamin and mineral preparation three times per week. Water was continously available.

The skinks were mailed to the University of Washington (UW), where they arrived on 5 June 1987. Upon arrival the lizards were placed in individual plastic cages in an environmental chamber (14:8 LD, 33°:25° C) and were given crickets and water ad libitum. Gravid skinks were tested for maximal speed on 5 June and for endurance on 7 June. They were then returned to SREL for collection of eggs to be incubated in the labortory. All deposited their eggs by mid-June. The females were returned to UW in early July and were tested again for speed and endurance on 9 July.

Females were weighed to the nearest 0.1 g before measurement of maximal speed in June and July. We had planned additionally to determine clutch masses and to weigh the females immediately after oviposition. However, because several females laid their eggs either at UW or during the return trip to SREL, clutch masses could not be determined accurately.

Speed. Maximal speed was measured using a 2-m horizontal racetrack with photocells at 0.25 m intervals (Hertz et al. 1983). The photocells were connected to a microprocessor that calculated average speeds in meters per second over each 0.25 m interval. Each lizard was chased down the racetrack five times over a 4-h period. Most runs were separated by 1 h, but the fourth trial immediately followed the third. The trial with no rest period was included because some lizards attain higher speeds in such trials (R. Huey, unpublished observations). Maximal sprint speed for an individual was its single fastest speed over 0.5 m. The temperature was 33° C in all trials.

Endurance. Endurance was measured on a treadmill with a belt speed of 0.75 km/h. An attempt was made to keep lizards moving smoothly and continually by gently tapping them on the tail when they slowed or stopped. The measure of endurance was the elapsed time from beginning of the test until exhaustion, which was verified by loss of the righting response (Huey et al. 1984). If a lizard was still moving after 90 min, its endurance was recorded as 90 min. The temperature was 32°–33° C in all tests.

Change in female surface activity. If females minimize the effects of decreased mobility by becoming less conspicuous or less active, an increase in the observed sex ratio (male/female) should occur during the gravid period, assuming that male activity patterns do not change at this time. Females in the first half of May are not gravid; by late May nearly all females are gravid. Because female *E. laticeps* develop a visibly distended trunk while gravid in late May, we predicted that the sex ratio of lizards observed in the field would increase between the first and second halves of May. The sexes of lizards were easily identified visually without any necessity for capture due to sex differences in size, head shape, and head coloration (Vitt and Cooper 1985). Years of experience in collecting these lizards allows relatively efficient detection of both moving and motionless individuals; however, moving lizards were much easier to detect. During the breeding season, field data were collected on Kiawah Island and Seabrook Island. In 1984 and 1987, numbers of adult males and females observed were recorded on a total of 4 days in the first half of May (7–8 May 1984 and 12–13 May 1987) and on 4 days in the second half of May (23–27 May). Because data were collected in years that may have differed slightly in timing of reproductive events, separate analyses were conducted for each year and for the pooled data. To ascertain whether changes in sex ratios of lizards sighted were due to decreased conspicuousness or activity of females or to corresponding increases by males, numbers of males and females sighted per hour were calculated.

Statistical tests. We predicted that nongravid females would run faster and have greater endurance. Possible differences between gravid and nongravid lizards in maximum speed and endurance were examined by t tests for correlated samples (paired). Homogeneity of variance was ascertained by Hartley's F_{max} tests and was achieved by natural logarithmic transformation when necessary. Relationships between body mass and maximum speed were examined for gravid and nongravid females by parametric correlation. Differences in apparent abundance of females relative to males were examined by chi-square (and in one case Fisher) tests of pooled data and of separate data for each year. We predicted that gravid females would be relatively less abundant in late May than in early May. Because all predictions were directional, we used one-tailed tests. Alpha was 0.05 in all cases. Data are presented as means (±SE).

Results

Speed

All 11 females had reduced sprint speeds when gravid (Table 1). The maximum speed decreased by 26.9 ± 2.9%. Variances in maximum speed were homogeneous ($F_{max} = 1.24$; $df = 2, 10$; $P > 0.10$). Females had significantly greater running speeds when nongravid than when gravid ($t = 8.411$); $df = 10$; $P < 0.001$). The lower speed in the initial runs is attributable to the gravid condition of the lizards rather than to effects of captivity, which did not alter maximum speed in the agamid lizard *Amphibolurus nuchalis* in the longer 8-week period of captivity (Garland 1985). Maximum sprint speed was not significantly correlated with body mass for gravid females ($r = 0.33$, $df = 10$, $P > 0.05$) or nongravid females ($r = 0.09$, $df = 10$, $P > 0.05$).

Table 1. Maximum speeds attained on a racetrack and endurances on treadmill at 0.75 km/h by gravid and nongravid female *Eumeces laticeps*

	Sprint speed (m/s)			Endurance[a] (min)		
	Mean	S.E.	Range	Mean	S.E.	Range
Nongravid	2.77	0.08	1.96–3.29	35.46	8.71	8.58–90.00
Gravid	2.01	0.07	1.70–2.38	15.21	2.56	6.28–26.35

[a] The maximum endurance allowed was 90 min

Endurance

Although all females completed the sprint trials, several (three) had to be eliminated from the analysis of endurance data due to escape from the apparatus, injury (an additional female injured a foot during escape), and atypical treadmill performance (one female ran rapidly until exhaustion; the experimenter described its behavior as frantic). These losses reduced the sample size to six. All six females had less endurance when gravid than when not gravid (Table 1), the reduction being 55.7± 11.1%. For the raw data, the variance of time until exhaustion was greater for nongravid than gravid females ($F_{max}=11.75$; $df=2,5$; $P=<0.05$): all gravid females ran btween 6.28 and 26.35 min whereas nongravid females ran 8.58–90.00 min, with all but one over 30 min. Data produced by logarithmic transformation had homogeneous variances ($F_{max}=1.81$; $df=2,5$; $P>0.05$). For these data the endurance of nongravid females was significantly greater than that of gravid females ($t=2.11$; $df=5$; $P=<0.05$). The lower endurance in the initial runs is attributable to the gravidity rather than a training effect because repeated exposure of lizards to endurance trials does not affect stamina (Garland et al. 1987).

Female surface activity

The proportion of females observed was greater in the first half of May than in the second half of May in both years (Fig. 1). In 1984, 24 males and 26 females were observed in early May, whereas 38 males and only 12 females were observed in late May. The proportion of females was significantly lower in late than in early May ($X^2=7.71$, $df=1$, $P=<0.001$). In 1987, 34 males and 24 females were observed in early May and 12 males and 2 females in late May. Although the proportion of females was lower in the late May sample, it did not differ significantly from that for the early May sample bey a chi-square test ($X^2=2.72$, $df=1$, $0.05<P<0.10$). Due to the small sample size in late May, the assumption of expected values greater than 5 was barely satisfied (expected number of females in late May= 5.18). A Fisher exact test conducted for comparative purposes showed a marginally significant difference ($P=0.045$). Because the early sample for 1987 was taken on 12–13 May, a reduction in female activity or conspicuousness may have already begun. This would account for the high proportion of males in the early sample. Due to this high proportion of males in the early sample in 1987, a relatively large sample size is required to show a significant decrease in female proportion. The proportion of females was significantly lower in late than in early May for the pooled sample for both years ($X^2=9.64$, $df=1$, $P<0.005$). An alternative test, statistically preferable because it combines probabilities from the separate tests of significance in 1984 and 1987 without pooling data, agrees in showing a significantly reduced proportion of females in late May ($18.42<X^2<19.81$, $df=4$, corresponding to a maximum $P<0.002$, Sokal and Rohlf 1981).

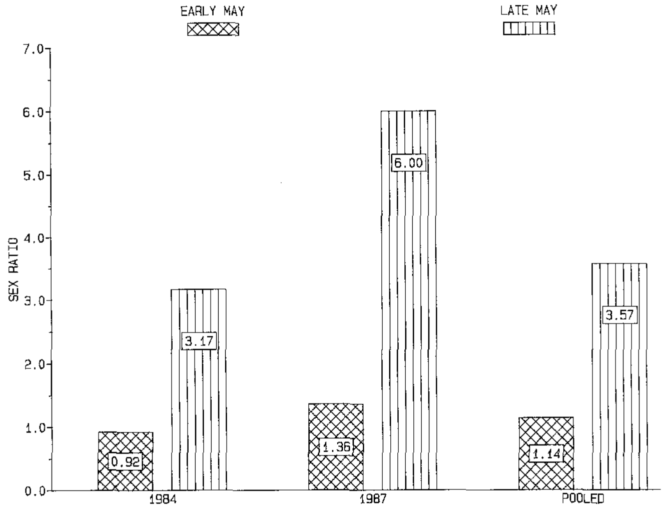

Fig. 1. Sex ratios (male/female) of skinks observed increased from the first to the second half of May in both years

The lower proportion of females in late May in both years is largely attributable to a decrease in female conspicuousness or activity rather than to increased male detectability. In 1984, 2.82 and 2.79 males/h were observed in early and late May; the comparable figures in 1987 were 2.11 and 2.64. Male activity appears to change little, if at all, in this interval. In contrast, females observed per hour declined in both years between early and late May, from 3.06 to 0.88 in 1984 and from 1.49 to 0.44 in 1987. The relatively low rate of females observed in early May 1987 hints further that female activity or detectability may have begun to decrease by 12–13 May.

Discussion

Locomotor deficits, reproduction, and predation

Females were markedly slower and had greatly reduced endurance when gravid. The 27% decrease in speed is potentially very important because running to a refuge is a primary means of escape by *E. laticeps* (WEC and LJV, personal observations). In four other scincid species, gravid females having high RCM were slowed by 20% to 30% (Shine 1980), comparable to the reduction in female *E. laticeps*. That gravid females of one skink, *Leiolopisma coventryi*, suffered greater predation than males in laboratory tests (Shine 1980) strengthens the presumption that gravid *E. laticeps* may be especially vulnerable once detected.

There is no evidence for increased predation on gravid *E. laticeps*, but because *E. laticeps* often escapes from predators by fleeing, the assumption is reasonable. W.E.C. has observed *E. laticeps* attempt to escape by running away from larger conspecifics, human observers, black racers (*Coluber constrictor*), and grackles (*Quiscalus major*) in the field and from scarlet kingsnakes (*Lampropeltis triangulum elapsoides*) and shrews (*Blarina carolinensis*) in the laboratory (Cooper and Vitt 1985). These skinks often climb trees to escape. Although the climbing speed of gravid females has not been studied, it very likely would be impaired to a greater degree than running speed (Huey and Hertz 1982).

The proportional loss of endurance in gravid females of over 0.50 is substantial, but its biological impact is difficult to gauge. Some data suggest lizards usually move at well below maximum aerobically sustained speeds (Hertz et al. 1988). While on the ground, *E. laticeps* usually remain close to trees, holes, or other refuges. Because these habits usually allow the skinks to escape without having to run far, the initial acceleration and maximum speed attained may be more important for avoiding predation than endurance. Nevertheless, drastically reduced stamina might manifest itself quickly during escape attempts, especially if foraging or other activity further reduces endurance.

If energy used in reproduction is stored over winter, as it appears to be in *E. laticeps* (Vitt and Cooper 1985), females might become vulnerable not from weight gain, but primarily due to redistribution of fat from the body, fat bodies, and tail to the eggs, resulting in distention of the trunk. A similar suggestion has been made for snakes (Shine 1988a).

Gravid females appear to compensate for the increased probability of being captured following detection by decreasing the probability of being detected, whether through reduced activity, increased crypticity, or both. The increase in the sex ratio of active lizards coupled with the decrease in females observed per hour during late May is consistent with this interpretation. An alternative hypothesis is that the sex ratio of active lizards increases because some females are brooding in late May. Except for brief absences, female *E. laticeps* remain with the eggs from oviposition until hatching (Vitt and Cooper 1989). Some females may oviposit in late May (Vitt and Cooper 1985), but none did so before June in extensive laboratory and field observations made by LJV and WEC between 1978 and 1987. Another possibility is that gravid females forage less because they cannot eat as much. However, gravid females eat normally in the laboratory (Cooper, unpublished data).

Avoidance of increased predation due to slowing and loss of stamina remains the best explanation for reduced female activity. By simply being less detectable, female *E. laticeps* may lessen a major cost of being gravid. In the viviparous lizard, *Lacerta vivipara*, slowed gravid females allow closer approach by observers than do nongravid females. A similar result has been reported in a garter snake (Brodie 1989). This has been interpreted as a change in escape tactics to increase crypticity (Bauwens and Thoen 1981), which is consistent with the findings for *E. laticeps*. Our results suggest that gravid lizards of some species achieve decreased conspicuousness by decreasing activity.

If detectability decreases at the expense of foraging time, there could be an important energetic cost of decreased foraging. However, several factors could reduce this cost: (1) nesting sites often contain an abundance of insects and other invertebrates; (2) brooding females readily eat in the laboratory; and (3) cryptic prey likely to be found in nest sites form a substantial part of the diet (Vitt and Cooper 1986, unpublished data). Decreased detectability as a defense might also be related to maternal behavior in *Eumeces* (Shine 1988b; Vitt and Cooper 1989). In the field, females defend sites suitable for nests against conspecific females before becoming gravid and gravid females have been collected in potential nest sites in late May when males were active on the surface (WEC and LJV, unpublished observations). If enough food is available in nest sites or if locomotor impairment is sufficiently brief to avoid inanition, early withdrawal into nest cavities might have been naturally selected as an antipredatory mechanism.

Foraging mode, RCM, and antipredatory behavior

Foraging mode and escape strategy strongly affect RCM in lizards, active foragers having lower RCM than ambush foragers (Vitt and Congdon 1978; Dunham et al. 1988a). Vitt and Price (1982) argued that ambush foragers, which are thought to rely primarily on crypticity rather than escape after detection, can evolve higher RCM than wide foragers, which more frequently require speed to escape after detection. However, some widely foraging species have unexpectedly high RCM (Vitt and Price 1982; Bauwens and Thoen 1981). If females of species that are normally active foragers could reduce the cost of locomotor impairment by modifying their behavior when gravid, they might be able to evolve high RCM. Much of the decrease in survival due to increased locomotor deficits could be avoided by shifting antipredatory tactics from reliance on speed and endurance (Vitt and Price 1982) for escape after detection to defenses rendering gravid females inconspicuous. Females could then obtain the greater energetic profits of active foraging before becoming gravid (Anderson and Karasov 1981; Nagy et al. 1984) without reducing RCM to the levels typical of active foragers. Active foraging would allow greater efficiency in provisioning a large clutch with high RCM, perhaps leaving enough energy for substantial growth.

Inconspicuousness is attained in *E. laticeps* by decreased detectability, perhaps due a shift in the location of activity to sites with greater cover, increased reliance on immobility to avoid detection, decreased activity, and/or withdrawal into nest cavities. Females can continue to forage to some degree, but the rate of gain in weight presumably would decrease due to adoption of a less profitable foraging mode. In other widely foraging lizards species, a direct shift to ambush foraging might occur. Further data are needed to determine how widespread such behavioral shifts in escape strategies may be. Ambush foragers, because they presumably rely more heavily on crypticity, should be able to sustain greater reduction in speed when gravid. In the only ambush forager studied, *Sceloporus occidentalis*, sprint speed in gravid females decreases by over 45% in one population, the greatest decrement yet reported. This result is consistent with the prediction. However, in three other populations, the decreases were similar to those measured for skinks (Sinervo et al. in review). Therefore, female ambush foragers do not necessarily experience greater loss of speed when gravid than active foragers; nonpredatory selective factors affecting clutch size may be important.

Relationships among energetic investment in reproduction, foraging mode, and escape tactics may have strongly influenced squamate life histories (Vitt and Congdon 1978; Dunham et al. 1988a). Lizards that are ambush foragers depend less on rapid escape than on avoidance of detection (Vitt and Price 1982) and have high RCM; wide foragers rely more on rapid escape after being detected and have lower RCM (Vitt and Congdon 1978; Vitt and Price 1982). This suggests that, *ceteris paribus*, wide foragers may be less able than ambush foragers to exploit life-historical stategies demanding high current energetic investment.

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