

## Body Temperatures of Female *Sceloporus grammicus*: Thermal Stress or Impaired Mobility?

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Females of some lizard species exhibit lower body temperatures ( $T_b$ s) when reproductive (gravid or pregnant) than when not reproductive. Two hypotheses have been invoked to explain this phenomenon. One, the thermal stress hypothesis, is that the thermal optimum for embryos is lower than that of the female, and females thus actively select relatively low  $T_b$ s. The other, the encumbrance hypothesis, is that females are encumbered by their clutch/litter and thus passively accept relatively low  $T_b$ s. We collected field data on the thermal biology of *Sceloporus grammicus* at a high elevation site in Mexico during two seasons. In March, when thermoregulation was facilitated by high ambient temperature, lizards had high  $T_b$ s overall, and reproductive females had significantly lower  $T_b$ s than males; these observations were in accord with the thermal stress hypothesis. In June/July, when thermoregulation was difficult as a result of low ambient temperatures, lizards had low  $T_b$ s overall, and reproductive females had considerably lower  $T_b$ s than nonreproductive females. Thus, when thermal opportunities were limited, reproductive females had more difficulty thermoregulating than did nonreproductive females. These observations were in accord with the encumbrance hypothesis. The encumbrance hypothesis was also supported by the observation that females grew more slowly when reproductive than when nonreproductive. Thus, we suggest that the thermal stress and the encumbrance hypotheses are not alternatives but are complementary explanations for the thermal behavior of female *Sceloporus*.

REPTILES are capable of precise regulation of their body temperatures while they are active, largely by behavioral changes in their location relative to sources and sinks of thermal energy in the environment (Cowles and Bogert, 1944; Huey, 1982). Regulation includes fine-grained adjustments that match body temperature ( $T_b$ ) to physiological status. For example, many reptiles exhibit relatively high  $T_b$ s after eating, and relatively high  $T_b$ s are associated with enhanced digestion efficiency (Huey, 1982). At this time, the hypothesis that different physiological processes have different thermal optima is well supported by experimental data (Stevenson et al., 1985). However, the association between particular  $T_b$ s and particular physiological processes may have other explanations than the existence of multiple thermal optima (Huey, 1982). The association between  $T_b$  and reproductive status provides a good example of this problem.

Females of many lizard species exhibit higher or lower  $T_b$ s when reproductive (gravid or pregnant) than when not reproductive (Daut and Andrews, 1993). For example, female *Sceloporus cyanogenys* (Garrick, 1974), *Sceloporus jarrovi* (Beuchat, 1986), and *Sceloporus virgatus* (Andrews and Rose, 1994) have lower  $T_b$ s when reproductive than when not reproductive, and fe-

male *Chalcides ocellatus* (Daut and Andrews, 1993), *Gerrhonotus coeruleus* (Stewart, 1984), and *Hoplodactylus maculatus* (Werner and Whitaker, 1978) have higher  $T_b$ s when reproductive than when not reproductive.

Temperature shifts as a function of reproductive status are well documented and distributed widely among lizard taxa. The fact that the direction of the shift differs among taxa suggests that more than one set of causal factors may be operating. In this paper, we focus on the genus *Sceloporus*, a taxon in which females have relatively low  $T_b$ s during gestation. Two major hypotheses have been invoked for this phenomenon. One, the thermal stress hypothesis, posits that the thermal optimum for embryos is lower than that for the female and that females alter their thermal behavior during gestation to enhance their reproductive success or the quality of their offspring. Thus, Beuchat (1986, 1988) suggested that *S. jarrovi* females reduce their  $T_b$  when pregnant to avoid thermal stress on embryos, and Beuchat provided experimental data suggesting that high temperatures caused death or deformity of embryos.

Alternatively, the encumbrance hypothesis, posits that the reduction in body temperature of females during gestation is related to a cost of reproduction: the direct physical impairment

of the female by the mass or bulk of the clutch or litter per se. Reproductive females generally cannot run as fast as nonreproductive females (Shine, 1980; Sinervo et al., 1991). Thus, all other things being equal, reproductive females should have a higher risk of predation than would nonreproductive females. Females of some species, at least, minimize this cost of reproduction by becoming less mobile or more secretive during gestation than when nonreproductive (Bauwens and Thoen, 1981; Cooper et al., 1990; Braña, 1993). As a consequence, reproductive females may not be able to raise their body temperatures as readily as males or nonreproductive females because they are less likely to seek out basking opportunities in the environment.

Observations of selected body temperatures in thermal gradients under controlled laboratory conditions provide one avenue to evaluate the two hypotheses. In this situation, when all individuals can thermoregulate effectively, the thermal stress and the encumbrance hypotheses make different predictions about the thermal behavior of reproductive females and of males and nonreproductive females. The thermal stress hypothesis predicts that selected  $T_{b,s}$  of reproductive females will be lower than those of males or nonreproductive females because reproductive females actively select relatively low  $T_{b,s}$ . In contrast, the encumbrance hypothesis predicts that  $T_{b,s}$  of reproductive females and of males or nonreproductive females will be identical because reproductive females can thermoregulate without enhanced risk of predation.

Evaluating the two hypotheses with field data alone is more difficult because of the heterogeneity of the thermal environment. The availability of thermal opportunities affects the ability of individuals to attain preferred  $T_{b,s}$  (Huey, 1974), and thermal opportunities vary as a function of microhabitat, season, etc. However, the two hypotheses do make different relative predictions about  $T_{b,s}$  as thermoregulation becomes more difficult (assuming that thermoregulation largely involves the elevation of  $T_{b,s}$  in relatively cool environments). The thermal stress hypothesis predicts that  $T_{b,s}$  of reproductive females will be lower than those of males or nonreproductive females under thermal conditions where all individuals can readily reach and maintain their selected  $T_{b,s}$ . Moreover, when thermoregulation becomes difficult, the  $T_{b,s}$  of these two classes should become more similar, that is, their  $T_{b,s}$  will converge once attainable  $T_{b,s}$  are below the selected  $T_{b,s}$  of reproductive females. On the other hand, the encumbrance hypothesis predicts that the  $T_{b,s}$  of reproductive

females and males or nonreproductive females will be identical under thermal conditions where all individuals can readily reach and maintain their selected  $T_{b,s}$ . Moreover, as thermoregulation becomes more difficult, that is, as individuals have to move farther or become more active to thermoregulate, thermoregulation by reproductive females will become increasingly limited, and body temperatures of the two classes will diverge. Thus, a contrast of  $T_{b,s}$  exhibited under ideal thermal conditions with those exhibited when thermoregulation becomes difficult provides a means to assess the two hypotheses.

Such a contrast can be made at high elevations at tropical latitudes. Lizards are active year-round even at relatively low  $T_{b,s}$  (Vial, 1984; Marquet et al., 1989), and ambient temperatures ( $T_a,s$ ) vary seasonally. Typically, "winter" or dry-season months are relatively warm because of infrequent cloud cover, and "summer" or wet-season months are relatively cool because the sun is often obscured by clouds (Janzen, 1967). We used this situation to evaluate the predictions of the thermal stress and encumbrance hypotheses. To do so, we examined the thermal biology of *Sceloporus grammicus* during the two seasons at a high elevation site in México. We made observations in March, when thermoregulation was relatively easy because of high ambient temperatures and infrequent cloud cover. We also made observations in June/July, when thermoregulation was relatively difficult because of low ambient temperatures and frequent cloud cover.

Our objective was to determine whether the temperature shifts during gestation previously observed for temperate zone *Sceloporus* species could be extended to this species and, if so, to assess the thermal stress and encumbrance hypotheses. We also tested a corollary of the encumbrance hypothesis. If reproductive females must search for prey within a smaller area or are less efficient at catching prey than males or nonreproductive females, then they should grow relatively slowly. The null hypothesis was that both classes of females and males should grow at the same rate; growth rates of females and males are the same for species such as *S. grammicus* in which adult females and males are similar in size (Andrews, 1982).

The results of our studies suggested that the thermal stress and encumbrance hypotheses were not exclusive explanations for the relatively low  $T_{b,s}$  of female *S. grammicus* when they were reproductive. Rather, the appropriate hypothesis was contingent on the environmental context. When thermoregulation was easy, our ob-

servations supported the thermal stress hypothesis, and when thermoregulation was difficult, they supported the encumbrance hypothesis.

#### MATERIALS AND METHODS

*Subject and study site.*—Our subject was the viviparous lizard *S. grammicus*, a member of the *grammicus* species group (Sites et al., 1992). We observed *S. grammicus* at Parque Nacional Zoquiapán (Estado de México), at an elevation of approximately 3400 m. The study site had an open understory and an overstory of large, widely spaced, pine trees. *Sceloporus grammicus* was arboreal and was largely associated with trees and woody debris. Observations on *S. grammicus* have been made at this site by Méndez and Villagrán since June 1991 (unpubl. data).

To document seasonal changes in temperature and rainfall, we obtained climatic data from the Servicio Meteorológico Mexicano, Ciudad de México, for the town of Rio Frio, the nearest weather station to the study site. Rio Frio was located approximately 15 km from the study site and about 500 m lower in elevation. In March 1994, we also measured ambient temperatures in the shade 20 cm above the ground every 30 min for 5 d with an Omega OM-50 data logger.

We made observations on the thermal biology of adult *S. grammicus* during two periods: on nine days from 17 March through 2 April 1994 (March) and on nine days from 29 May through 22 July 1992 (June/July). These periods corresponded to different stages in the reproductive cycle. In March, all adult females were pregnant. The modal Dufaure and Hubert (1961) stage of embryonic development at this time is 37 (Villagrán-Santa Cruz, 1989). Parturition occurs during May through July (Villagrán-Santa Cruz, 1989). Our June/July observations included females with well-developed embryos and females that had recently given birth. Testicular growth occurs in March, and males have enlarged testes through July (Guillette and Casas-Andreu, 1980); eggs are fertilized with stored sperm in September (Villagrán-Santa Cruz et al., 1992).

*Field observations.*—We report body temperatures that were measured from 0900–1600 h, the period of highest lizard activity. We captured lizards with a noose or by hand, and measured their body (cloacal) temperatures ( $T_b$ ) either with a Shultheis quick-reading thermometer ( $\pm 0.2^\circ\text{C}$ ) or with a thermocouple thermometer ( $\pm 0.5^\circ\text{C}$ ). Because lizards were easy to capture, little time elapsed between sighting and measure-

ment of body temperature. We did not measure the  $T_b$  of individuals that were not captured quickly. In March, we measured shaded air temperatures 1 m ( $T_{a,1m}$ ) and 1 cm ( $T_{a,1cm}$ ) above the perch of each lizard. In June/July, we measured shaded air temperatures 20 cm ( $T_{a,20cm}$ ) above the perch of each lizard.

We measured snout-vent length (SVL) to the nearest mm and weighed each individual with a Pesola spring balance to the nearest 0.2 g. We determined reproductive condition of females by palpation. Overall, reproductive females ( $n = 49$ ) had mean SVLs of 50 (44–56) mm and mean masses of 4.0 (2.5–5.8) g, nonreproductive females ( $n = 11$ ) had mean SVLs of 47 (44–53) mm and mean masses of 3.1 (2.4–4.6) g, and males ( $n = 48$ ) had mean SVLs of 50 (44–58) mm and mean masses of 4.1 (2.8–6.2) g.

We used mark-and-recapture data to determine the growth rates of adult females and males. Observations made from November 1991 to March 1994 were divided into periods when females were reproductive (capture-recapture intervals of November 1991 to May and June 1992, November 1992 to June 1993, and December 1993 to March 1994) and when they were nonreproductive (capture-recapture intervals of May and June 1992 to November 1992 and June 1993 to December 1993). We excluded females that had recently given birth (May and June observations) from growth analyses for the period when females were reproductive. The nonreproductive period included the 2–4 months when females are not pregnant: some females would have been pregnant at the beginning of this period, and all females would have been in early stages of pregnancy for 2–3 months at its end.

*Statistics.*—We conducted parametric statistical analyses with Statistical Analysis Systems software (vers. 5, Cary, NC, unpubl., 1985). We reported results of ANCOVAs only when interaction terms were not significant ( $P > 0.05$ ). Means were presented plus and minus their standard errors. Nonparametric analyses were from Siegel (1956). Because the distribution of  $T_b$ s was not normal, we used medians as descriptive statistics and compared distributions of  $T_b$ s with nonparametric tests.

Time of capture was not considered in any of the analyses. Visual inspection of the data did not reveal any obvious relationship between  $T_b$  and time of capture, probably because we did not make observations early in the morning or late in the afternoon when body temperatures would have been relatively low. Moreover, the time of capture explained very little variation in

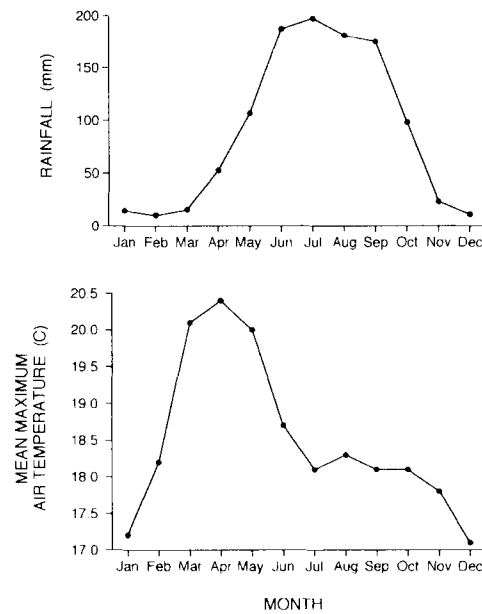


Fig. 1. Means of monthly rainfall (top) and maximum air temperature (bottom) at Rio Frio, Estado de México, México. Means are for 29 yr (1951–1980).

$T_b$ . In March,  $T_b$  was negatively related to time of capture ( $F_{1,62} = 4.6$ ,  $P < 0.05$ ,  $R^2 = 0.07$ ), although only 7% of the variation in  $T_b$  was explained by this variable. In June/July,  $T_b$ s were not related to time of capture ( $F_{1,40} = 2.4$ ,  $P > 0.05$ ,  $R^2 = 0.06$ , regression analyses, sexes combined in both seasons).

## RESULTS

**Climate.**—Air temperature at Rio Frio varied seasonally. Long-term means of maximum daily air temperature were 20.0–20.4°C for March to May and 17.1–18.7°C during the rest of the year (Fig. 1). The mean maximum air temperature that we observed at our study site in March 1994 ( $n = 5$  d) was similar to the long-term March mean for Rio Frio (22.5°C vs 20.1°C, respectively). Air temperatures measured when lizards were captured also illustrated seasonal differences in climate (Fig. 2). For example, mean air temperatures observed in March were higher ( $T_{a,1m}$  and  $T_{a,1cm} = 17.3$  and 21.6°C, respectively) than those observed in June/July ( $T_{a,20cm} = 14.8$ °C). Low ambient temperatures in midsummer (June/July) reflected high rainfall (Fig. 1) because cloud cover reduced solar radiation.

**Field body temperatures.**—Overall, field body temperatures paralleled ambient temperatures (Fig. 3). In March, the median  $T_b$  was 32.3°C, whereas

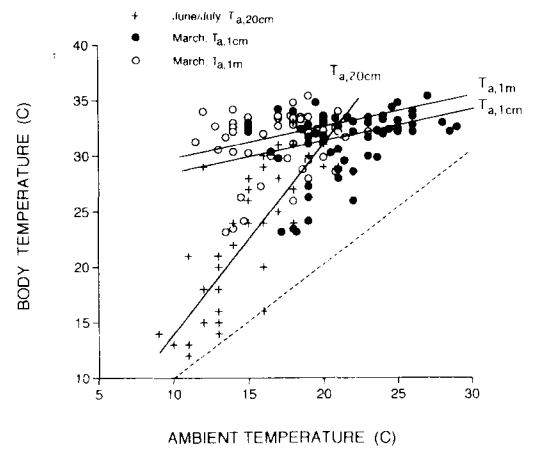


Fig. 2. Body temperatures of *Sceloporus grammicus* expressed as a function of ambient temperature. March: solid circles =  $T_{a,1cm}$  (shaded air temperature 1 cm above each lizard) and open circles =  $T_{a,1m}$  (shaded air temperature 1 m above each lizard); June/July: crosses =  $T_{a,20cm}$  (shaded air temperature 20 cm above each lizard). The dashed line represents isothermy; solid lines represent the regressions between body temperature and ambient temperature as indicated.

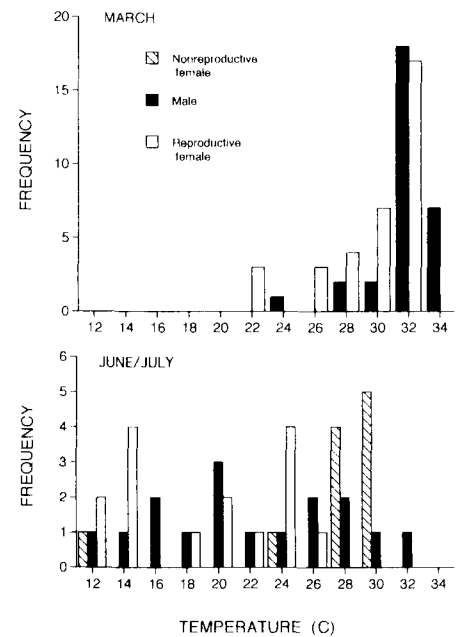


Fig. 3. Frequency distributions of body temperatures of *Sceloporus grammicus* in March and in June/July. Adult males = solid bars, reproductive females = open bars, and nonreproductive females = hatched bars.

in June/July the median  $T_b$  was 24.0 C.  $T_b$ s were also less variable in March than in June/July with respective interquartile ranges of 2.9 and 13.0 C.

Within each season,  $T_b$ s varied as a function of sex or reproductive status or both. In March, reproductive females ( $n = 34$ ) had significantly lower  $T_b$ s than males ( $n = 30$ ) with median  $T_b$ s of 31.9 and 33.0 C, respectively ( $\chi^2 = 9.0$ ,  $P < 0.002$ ,  $2 \times 2$  chi-squared test). In June/July,  $T_b$ s of reproductive females ( $n = 15$ ) and males ( $n = 16$ ) were similar with median  $T_b$ s of 20.0 and 21.5 C, respectively ( $\chi^2 = 1.3$ ,  $P > 0.05$ ,  $2 \times 2$  chi-squared test), whereas the median  $T_b$  of 29.0 C for nonreproductive females ( $n = 11$ ) was higher than that for reproductive females and males ( $\chi^2 = 5.8$ ,  $P < 0.05$ ,  $2 \times 2$  chi-squared test, and  $P < 0.005$ , Fisher Exact test, respectively).

**Body temperature and ambient temperature.**—To determine how seasonal differences in ambient temperature affected  $T_b$ , we compared  $T_b$ s with  $T_a$ s measured when lizards were captured. We pooled the data for all adults within seasons because the slope of the relationship between  $T_b$  and  $T_a$  did not differ among lizard classes (March:  $T_{a,1,m}$ ,  $F_{1,63} = 0.6$ ,  $P > 0.05$ ;  $T_{a,1,m}$ ,  $F_{1,59} = 0.3$ ,  $P > 0.05$ ; June/July:  $T_{a,20,m}$ ,  $F_{2,36} = 3.0$ ,  $P > 0.05$ , homogeneity of slopes tests). Thus, some of the variance within seasons was the result of differences in intercepts among lizard classes, although the overall pattern was independent of sex or reproductive class.

The relationship between  $T_b$  and  $T_a$  differed seasonally (Fig. 2). In March,  $T_b$  was related to  $T_a$  as  $T_b = 25.3 + 0.29 T_{a,1,m}$  ( $F_{1,62} = 8.1$ ,  $P < 0.01$ ,  $R^2 = 0.11$ ), and  $T_b = 26.5 + 0.29 T_{a,1,m}$  ( $F_{1,61} = 5.3$ ,  $P < 0.05$ ,  $R^2 = 0.08$ ). For both sets of data, the slopes are low, and  $T_a$  explains only about 10% of the variation in  $T_b$ . Thus, in March,  $T_b$ s were largely independent of  $T_a$ s, indicating that thermoregulation was relatively easy.

In June/July,  $T_b$  was related to  $T_a$  as  $T_b = -2.9 + 1.73 T_{a,20,m}$  ( $F_{1,40} = 70.0$ ,  $P < 0.001$ ,  $R^2 = 0.63$ ). The steep slope and the dependence of  $T_b$ s on  $T_a$ s ( $T_a$  explains more than half of the variation in  $T_b$ ) indicated that thermoregulation was difficult. Moreover, lizards had considerably lower  $T_b$ s in June/July than in March, a further indication that lizards had difficulty raising their  $T_b$ s to "preferred" levels in June/July.

**Growth.**—During the period when females were reproductive, females grew more slowly in both SVL and in mass than males, at least up to asymptotic sizes when detectable growth ceases

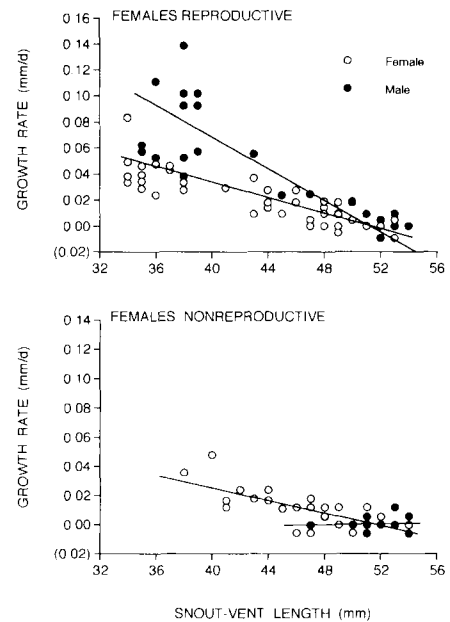


Fig. 4. Growth rates of female (open circles) and male (solid circles) *Sceloporus grammurus* during periods when females were reproductive (November to June) and when they were nonreproductive (May to December). Data for growth in mass are not illustrated.

(Fig. 4). For the statistical comparison, growth rate was the dependent variable, sex was the class variable, and initial snout-vent length the covariate in an ANCOVA. The interaction between body size at initial capture and sex was significant for both SVL and mass (SVL:  $F_{1,69} = 12.2$ ,  $P < 0.001$ ; mass:  $F_{1,57} = 9.6$ ,  $P < 0.01$ , homogeneity of slopes tests), indicating that the relationship between growth rate and initial size differed between males and females. The significantly lower slopes corresponded to lower growth rates for females than males.

In contrast, when females were not reproductive, females and males grew at the same rate (SVL:  $F_{1,34} = 0.1$ ,  $P > 0.05$ ; mass:  $F_{1,34} = 0.6$ ,  $P > 0.05$ , ANCOVAs with initial SVL or initial mass used as the covariate and sex as the class variable).

For females, growth in SVL did not differ between the periods when they were reproductive and when they were nonreproductive ( $F_{1,70} = 0.02$ ,  $P > 0.05$ , ANCOVA), although they grew more slowly in mass when they were reproductive than when they were nonreproductive ( $F_{1,58} = 5.9$ ,  $P < 0.05$ , ANCOVA). Adjusted mean growth rates in mass for the two periods were 3.4 and 5.1 mg/d, respectively. For males, growth in SVL and in mass did not differ be-

tween the periods when females were reproductive and when they were not (SVL:  $F_{1,34} = 1.1$ ,  $P > 0.05$ ; mass:  $F_{1,34} = 3.3$ ,  $P > 0.05$ , ANCOVAs). A caveat for this comparison was that no relatively small males were represented in the samples for the period when females were nonreproductive (Fig. 4).

#### DISCUSSION

Our observations, taken in conjunction with observations on the thermal biology of other species of *Sceloporus*, suggested that the  $T_{b,s}$  exhibited by female *S. grammicus* were contingent on the interaction between the thermal environment and their reproductive status. More specifically, when thermoregulation was easy,  $T_{b,s}$  of reproductive females were in accord with the predictions of the thermal stress hypothesis. In contrast, when thermoregulation was difficult,  $T_{b,s}$  of reproductive females were in accord with the predictions of the encumbrance hypothesis.

Ambient temperatures were the highest in March, and adults had relatively high body temperatures overall. Median  $T_{b,s}$  of reproductive females and of males were 32 and 33 C, respectively, and  $T_{b,s}$  were relatively independent of  $T_{a,s}$ , judging by the low regression slopes of the relationships between  $T_b$  and  $T_a$ . Adults also exhibited low variance in  $T_b$  overall; the interquartile range was only 3 C. These observations indicated that thermoregulation was easy and  $T_{b,s}$  were at "preferred" levels.

The  $T_{b,s}$  of reproductive females were similar to those of another viviparous *Sceloporus*; pregnant *S. jarrovi* also have mean  $T_{b,s}$  of 32 C (Becchat, 1986). Moreover, pregnant *S. jarrovi* select  $T_{b,s}$  that average 32 C when tested on a laboratory thermal gradient (T. Mathies, unpubl. data). Assuming that the thermal biology of *S. grammicus* was similar to that of *S. jarrovi*, these observations suggested that pregnant *S. grammicus* actively selected lower  $T_{b,s}$  than males in March, as predicted by the thermal stress hypothesis. This assumption was supported by the thermal conservatism of the genus. Typical field (Bogert, 1949; Brattstrom, 1965; Adolph, 1990) and selected (McGinnis, 1966; Greenberg, 1976)  $T_{b,s}$  of males and nonreproductive females fall within a narrow range (34–36 C), and selected  $T_{b,s}$  do not vary seasonally (McGinnis, 1966).

Ambient temperatures were low in June/July, and lizards had low  $T_{b,s}$  overall. Median  $T_{b,s}$  were 29.0, 20.0, and 21.5 C for nonreproductive females, reproductive females, and males, respectively. The  $T_{b,s}$  were highly dependent on  $T_{a,s}$ ;

the regression slope was greater than 1, and  $T_a$  explained more than 60% of the variance in  $T_b$ . Adults also exhibited a high variance in  $T_b$ ; the interquartile range was 13 C. These observations indicated that lizards not only had difficulty raising their  $T_{b,s}$  above ambient temperature but that the thermal environment was more heterogeneous than it was in March.

Observations in June/July were in accord with the prediction of the encumbrance hypothesis that reproductive females should become more impaired in their ability to raise their  $T_{b,s}$  as thermoregulation becomes more difficult. The  $T_{b,s}$  of reproductive females were 9 C lower than those of nonreproductive females and 12 C lower than those of reproductive females in March. Thus, in June/July, reproductive females acted as if they were encumbered relative to nonreproductive females but not relative to males.

If nonreproductive females could raise their  $T_{b,s}$  considerably above those of reproductive females in June/July, why did males, which were equally unencumbered, have  $T_{b,s}$  similar to those of reproductive females? We cannot answer this question, although the observation itself suggested that males may have constraints on their thermobiology that are independent of those acting on females. In any case, the most appropriate comparison for  $T_{b,s}$  of reproductive females was nonreproductive females. In March, we compared reproductive females with males because nonreproductive females were not available. However, even without data on males, the high  $T_{b,s}$  of reproductive females, and their similarity to those of reproductive female *S. jarrovi*, provided support for the thermal stress hypothesis.

Our data also supported another prediction of the encumbrance hypothesis, that is, that reproductive females should grow slowly relative to males and nonreproductive females because reduced mobility or activity should limit female's access to food. During the period when females were reproductive, females grew more slowly in both length and mass than males. The slow growth in mass as well as in SVL was surprising because growth in mass of females included the growth of embryos. The period when females were reproductive included March to May, the warmest time of the year. Females were thus apparently less able than males to take advantage of the favorable thermal conditions for growth.

During the period when females were not reproductive, their growth rates did not differ from those of males, although nonreproductive females grew faster in mass than when they were

reproductive. The ability of females to increase their rate of growth in mass during the coolest time of the year, and when  $T_b$ s were relatively low (our June/July observations), suggested that females could forage more effectively when they were nonreproductive than when they were reproductive. The ability of females to forage effectively prior to ovulation was important because *S. grammicus* is largely lecithotrophic (Vilagrán-Santa Cruz and Méndez-de la Cruz, 1993); embryos are nourished primarily by energy stored in ova during vitellogenesis.

Our observations on *Sceloporus* indicated that the thermal stress and the encumbrance hypotheses were not alternatives but complementary explanations for the thermal behavior of reproductive females. Two sets of data supported the encumbrance hypothesis: reproductive females had particularly low  $T_b$ s when thermoregulation was difficult; and they had low growth rates relative to males and to nonreproductive females. However, when thermoregulation was easy, reproductive females did not appear to be encumbered; they had high  $T_b$ s overall, but their  $T_b$ s were lower than those of males and similar to those of a species in which females are known to reduce their  $T_b$ s when pregnant. For *S. grammicus*, at least, environmental conditions determined whether reproductive females actively selected comparatively low  $T_b$ s to avoid thermal stress on embryos or whether they passively accepted even lower  $T_b$ s as a result of encumbrance.

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