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Influence of pregnancy on locomotor and feeding performances of the skink, *Mabuya multifasciata*: Why do females shift thermal preferences when pregnant?

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Abstract

It has been documented in the many-lined sun skink (*Mabuya multifasciata*) that pregnant females select lower body temperatures (27.6–30.8 °C) than do nonpregnant females and adult males (29.7–35.7 °C). We therefore used the skink to test the hypothesis that the maximization of reproductive benefits should be achieved in pregnant females by shifting thermal preferences towards the levels optimal for embryonic development but entailing relatively small costs of reproduction. Data on adult males showed that temperatures maximizing swimming stamina (indicative of locomotor endurance) fell within the range of body temperatures selected by nonpregnant females and adult males. Data on swimming stamina and feeding performance of pregnant females, nonpregnant females and adult males measured at 26 and 30 °C showed that: (1) pregnancy impaired locomotor and feeding performances, but such impairments did not persist after parturition; (2) the degree of locomotor impairment during pregnancy was greater at 26 °C than at 30 °C, but the degree of feeding impairment during pregnancy was greater at 30 °C than at 26 °C. Pregnant females of *M. multifasciata* selecting body temperatures at about 29 °C could not only produce good-quality offspring in a relatively short gestation length but also reduce reproductive costs associated with locomotor and feeding impairments to some extent. Thus, data from *M. multifasciata* validate the above hypothesis.

Keywords: Costs of reproduction; Swimming stamina; Feeding performance; Thermal preference; Scincidae

Introduction

Costs of reproduction have received considerable scientific interest over the past decades because such costs are believed to be the major determinants of life-history evolution (Williams, 1966; Roff, 1992; Stearns, 1992; Reznick et al., 2000). Reproductive costs result from the trade-off between current and future

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reproduction, and are usually categorized as fecundity or survival costs (Bell, 1980; Shine, 1980; Schwarzkopf, 1994; Miles et al., 2000). Fecundity costs occur because current reproductive investment can ultimately reduce future fecundity by diverting energy away from somatic tissue growth and storage (Congdon et al., 1982), whereas survival costs occur because current reproduction can decrease survival probability which, in turn, decreases the probability of future reproduction (Reznick, 1985; Magnhagen, 1991; Shine et al., 1998; Plaut, 2002). Among the potential survival costs of reproduction, reduced locomotor performance in pregnant females has been well studied. The influence of pregnancy on locomotor performance has been emphasized because locomotion is a measure of whole-animal performance that can set physiological constraints on ecologically relevant tasks, such as foraging and predator avoidance (e.g. Bell, 1980; Bennett and Huey, 1990; Magnhagen, 1991; Irschick and Garland, 2001; Husak, 2006).

Feeding performance, which can be evaluated by measuring food intake or food assimilation, is another ecologically relevant trait that has a pronounced impact on an organism's energy balance (Nagy, 1983). There is some evidence, from viviparous snakes such as *Elaphe rufodorsata* (red-backed ratsnake; Ji et al., 1997), *Sinonatrix annularis* (Asiatic banded water snake; Ji et al., 2001) and *Vipera aspis* (asp viper; Lourdais et al., 2002), that increase in mass or packed body volume associated with pregnancy reduces feeding performance. However, the possible consequences of variation in feeding performance of pregnant females have not yet been well evaluated within the context of reproductive costs (but see Lourdais et al., 2002). Increased body mass during pregnancy raises the energetic costs of locomotion (Schwarzkopf, 1994; Miles et al., 2000). Therefore, pregnant females are more likely to face a negative energy balance resulting from the conflicts between increased energy demands and increased physiological (reduced locomotor performance) and physical (highly packed body volume) constraints on feeding performance.

Locomotor and feeding performances have been studied in a wide variety of lizards, but few studies have simultaneously measured both locomotor and feeding costs of reproduction. Previous studies generally show that these two traits are very sensitive to variation in body temperature but often differ in thermal sensitivity and thermal optimum (Xu and Ji, 2006 and included references). Lizards typically maintain body temperatures within a species-specific range when thermoregulation is not constrained by any biotic or abiotic factors, such that they express locomotor and feeding performances at relatively high levels (Xu and Ji, 2006 and included references). However, females usually exhibit either higher or lower body temperatures when pregnant due to behavioral preferences or due to constraints on thermoregulating activities (e.g. Braña, 1993; Daut and Andrews, 1993; Mathies and Andrews, 1997; Le Galliard et al., 2003; Ji et al., 2006b). Because such shifts could reduce or increase costs of reproduction associated with locomotor and feeding performances depending on whether body temperature increases or decreases during gestation, we hypothesize that the maximization of reproductive benefits should be achieved in pregnant females shifting thermal preferences towards the levels optimal for embryonic development, but entailing relatively small costs of reproduction.

In the present study, we used the many-lined sun skink, *Mabuya multifasciata*, as a model animal to test our hypothesis. This medium-sized (up to 117 mm snout–vent length (SVL); Ji et al., 2006a), viviparous scincid lizard has an exclusively tropical distribution that ranges from southern China and Indochina to India, and south to Malaysia, Singapore, Indonesia, the Philippines, the Indo-Australian Archipelago and New Guinea (Huang, 1999). Females usually give birth to 2–7 offspring between May and June, with larger females producing more and larger offspring than do smaller ones (Ji et al., 2006a). Gestation temperatures within the range of 26–32 °C exert little differential effects on morphological and locomotor phenotypes of offspring, whereas gestation temperatures outside this range are harmful to embryonic development (Ji et al., 2007). The skink has no difficulty in attaining high-enough body temperatures in the field, but pregnant females select lower body temperatures (mean = 29.0 °C) than do nonpregnant females (mean = 32.9 °C) and adult males (mean = 32.5 °C; Ji et al., 2007). Clearly, *M. multifasciata* is a lizard species where females shift thermal preferences when pregnant, and is therefore ideally suited for testing our hypothesis.

Materials and methods

Collection and animal care

A total of 122 adults (40 males and 82 females) with intact tails were collected between mid-April and mid-May 2005 from a previously studied population in Ledong (18°45′N, 109°10′E), Hainan, southern China. Skinks were brought to our laboratory in Hangzhou, where they were weighed (to the nearest 0.1 g) and measured for SVL and tail length (to the nearest 1 mm). During the trial intervals, between six and eight skinks were housed together in a 1 m × 0.6 m × 0.5 m (length × width × height) glass cage with a substrate consisting of a 10 cm layer of moist soil, debris and grasses. All cages were placed in a room where ambient temperatures never exceeded 20 °C. A 275 W light bulb (14 h light:10 h dark) suspended above one end of each cage created a thermal gradient ranging from room temperature to 60 °C (2 cm above the cage floor), and skinks could regulate body temperature within their voluntary range during the light phase. Skinks were provided with mealworms (larvae of *Tenebrio molitor*) and water enriched with vitamins and minerals (Nekton-Rep, Nekton-product) *ad libitum*.

Measurement of locomotor performance

Racetracks did not work well with *M. multifasciata* that relies heavily on swimming to escape predators (Huang, 1999). Therefore, we evaluated locomotor performance by measuring swimming stamina (indicative of locomotor endurance) rather than sprint speed of experimental skinks inside a bath (0.6 m × 0.5 m × 0.4 m) filled with water to a height of 20 cm. The water temperature was maintained at the test level via a water bath heater fixed to a metal stand. A WMZ-3 electronic thermometer (Shanghai Medical Instrument, China) confirmed that the water temperature did not vary more than 0.3 °C during trials. We placed skinks into the bath individually, and then gently tapped on the mid-body with a paintbrush to encourage them to swim. The time it took for each skink to swim until exhaustion, as estimated from the loss of a righting response after strong stimulation on the head with the same paintbrush, was considered as the swimming stamina for the skink. To minimize the possible influence of diel variation in swimming stamina, we began measurements on any given day at 09:00 h (Beijing time) and ended within 3 h.

We used a repeated-measures experimental design to determine the effect of body temperature on swimming stamina; 20 adult males ($\mathrm{SVL}_{\mathrm{range}} = 99$–115 mm) collected in mid-April were used at all test temperatures ranging from 18 to 40 °C. The trial sequence was randomized across temperatures (38, 24, 18, 20, 30, 34, 40, 28, 26, 22, 32 and 36 °C). Skinks were placed into an incubator (Sheldon MFG Inc., USA) for approximately 3 h to achieve body temperatures at the test level, and were then measured for swimming stamina following the procedures described above. Trials at the 12 test temperatures were conducted on 12 consecutive days.

We used a repeated-measures experimental design to determine the effect of reproductive conditions on swimming stamina at two body temperatures (26 and 30 °C). This design also allowed examination of whether such an effect, if evident, could be repeated at different temperatures. In all 20 pregnant females ($\mathrm{SVL}_{\mathrm{range}} = 91$–111 mm) and 22 nonpregnant females ($\mathrm{SVL}_{\mathrm{range}} = 94$–111 mm) collected in mid-May were used in this experiment, and males measured in mid-April were used as control. The procedures for determination of swimming stamina exactly followed those described above, and trials at the two test temperatures were conducted on two consecutive days.

Measurement of feeding performance

This experiment was conducted in two temperature-controlled rooms, where skinks could maintain body temperatures at 26 and 30 (±0.3) °C, respectively. The fluorescent tubes in the two rooms were on a 14 h light:10 h dark cycle, and the photophase started at 07:00 h. Twenty pregnant females (body $\mathrm{mass}_{\mathrm{range}} =$ 23.3–37.5 g), 20 nonpregnant females (body $\mathrm{mass}_{\mathrm{range}} =$ 20.5–34.6 g) and 20 adult males (body $\mathrm{mass}_{\mathrm{range}}$ = 24.5–40.9 g) collected in mid-May were used in this experiment, and skinks of the same category (reproductive condition) were equally assigned to one of the two temperature treatments. Skinks individually housed in 30 cm × 25 cm × 30 cm glass cages were fasted at the test temperature for 4 days prior to feeding to ensure post-absorptive conditions, and were then provided with mealworms and water *ad libitum*. Feces and urates were collected at least six times daily. Trials lasted for 10 days so that sufficient feces and urates could be collected for accurate calorimetry.

Feces, urates and mealworms corresponding to each skink were dried to constant mass at 65 °C and weighed. Dried samples were burnt in a WGR-1 adiabatic calorimeter (Changsha Instrument, China), and data on energy density were automatically downloaded to a computer. The assimilation efficiency (AE) was calculated as $100 \times (I-F-U)/I$ (Ji et al., 1993), where $I =$ total energy ingested, $F =$ energy in feces and $U =$ energy in urates. The apparent digestive coefficient (ADC) was calculated as $100 \times (I-F)/I$ (Waldschmidt et al., 1986).

Statistical analyses

We used the Statistica software package (version 5.0 for PC) to analyze the data. Prior to all statistical analyses, the data were tested for normality using the Kolmogorov–Smirnov test and for homogeneity of variances using the Bartlett's test. Log_e (data on swimming stamina) or arcsine (percentage data) transformation was performed to satisfy the assumptions of parametric analyses. We used repeated-measures ANOVA, two-way ANOVA, two-way ANCOVA and Tukey's *post hoc* tests to analyze the corresponding data. All values are presented as mean ± SE, and the significance level is set at $\alpha = 0.05$.

Results

Locomotor performance

Within each temperature treatment swimming stamina was not correlated with body size (SVL or mass) in pregnant females, nonpregnant females or males (all $P > 0.124$). Data from males showed that the effect of body temperature on swimming stamina was very pronounced (repeated-measures ANOVA; $F_{11,\ 209} = 13.57$, $P < 0.0001$), with the mean value generally increasing with increase in body temperature within the range 18–32 °C and then decreasing at higher temperatures (Fig. 1). The maximization of swimming endurance was achieved in males at body temperatures within the range of 30–36 °C (Fig. 1).

Swimming stamina was affected by reproductive condition (repeated-measures ANOVA; $F_{2,59} = 10.46$, $P < 0.0002$), and such an effect was repeatedly found at 26 and 30 °C (Fig. 1). The mean time taken to swim until exhaustion was shorter at 26 °C than at 30 °C (repeated-measures ANOVA; $F_{1,59} = 33.06$, $P < 0.0001$), and was shorter in pregnant females than in nonpregnant females and males (Tukey's *post hoc* test; both $P < 0.004$); nonpregnant females and males did not differ in swimming stamina (Tukey's *post hoc* test; $P = 0.649$). The reproductive condition × body temperature interaction was not a significant source of variation in swimming stamina (repeated-measures ANOVA; $F_{2,59} = 0.21$, $P = 0.808$).

Feeding performance

Within each treatment individual variation in all the examined traits was very evident (Table 1), but none of these traits was correlated with body size (all $P > 0.097$). Daily food intake, daily production of feces and daily production of urates were affected by reproductive condition and by body temperature, whereas ADC and AE were affected by reproductive condition but not by body temperature (Table 1). Overall, skinks ate less at 26 °C than at 30 °C, and pregnant females ate less than did nonpregnant females and adult males (Table 1). When removing the influence of variation in ingested energy using a two-way ANCOVA, we found that (1) energy in feces differed among the three skink categories ($F_{2,53} = 6.08$, $P < 0.005$) but not between the two-temperature treatments ($F_{1,53} = 0.84$, $P = 0.364$), with the adjusted mean value being smaller in pregnant females than in nonpregnant females and males (Tukey's *post hoc* test; both $P < 0.03$); and (2) energy in urates differed between the two temperature treatments ($F_{1,53} = 9.90$, $P < 0.003$) but not among the three skink categories ($F_{2,53} = 1.65$, $P = 0.166$), with the adjusted mean value being smaller at 26 °C than at 30 °C. The reproductive condition × body temperature interaction was significant for fecal energy ($F_{2,53} = 15.13$, $P < 0.0001$), but not for uric energy ($F_{2,53} = 2.27$, $P = 0.113$). Overall, both ADC and AE were lower at 26 °C than at 30 °C (Table 1).

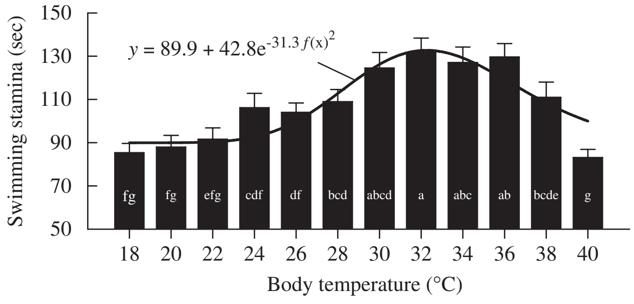

Fig. 1. Mean values (+SE) for swimming stamina of adult males ($n = 20$) at different body temperatures. Means with different letters differ significantly (Tukey's *post hoc* test, $\alpha = 0.05$; $a > b > c > d > e > f > g$). The curve is generated from a fit of a 4-parameter peak curve on the original data; the relevant function, where $f(x) = \log_e(x/32.2)$, is given in the figure.

Discussion

Swimming stamina was reduced in pregnant females but did not differ between nonpregnant females and males (Fig. 2). These results indicate that, as in a wide variety of squamate reptiles including other scincid lizards (Cooper et al., 1990; Qualls and Shine, 1997; Olsson et al., 2000; Wapstra and O'Reilly, 2001; Shine, 2003; Lin and Ji, 2005), nonscincid lizards (Bauwens and Thoen, 1981; Van Damme et al., 1989; Sinervo et al., 1991; Miles et al., 2000; Husak, 2006) and snakes (Seigel et al., 1987; Webb, 2004; Winne and Hopkins, 2006), pregnancy impairs locomotor performance in *M. multifasciata*. Data from an earlier study of *M. multifasciata* show that nearly all females larger than 90 mm SVL can reproduce and, in the wild, they usually give birth between May and June (Ji et al., 2006a). Accordingly, females (SVL >91 mm) collected for the present study in May should be either at the late gestation stages or at the early postpartum stages. Thus, the lack of the difference in swimming stamina between nonpregnant females and males provides evidence that the effect of pregnancy on swimming stamina does not persist after parturition in *M. multifasciata*. Compared with data pooled for nonpregnant females and males at the same body temperature, swimming stamina of pregnant females was reduced by about 27% at 26 °C and by about 23% at 30 °C (Fig. 2). The degree of locomotor impairment associated with pregnancy was noticeably greater at 26 °C than at 30 °C. This difference may be

Table 1. Daily food intake, daily production of feces, daily production of urates, ADC and AE of pregnant females, nonpregnant females and adult males at two body temperatures

	26°C			30°C			Effects		
	Pregnant females	Nonpregnant females	Adult males	Pregnant females	Nonpregnant females	Adult males	Temperature $F_{1,54}$	Skink category $F_{2,54}$	Interaction $F_{2,54}$
N	10	10	10	10	10	10			
Daily food intake ($J\,g^{-1}\,d^{-1}$)	151.3±11.8 103.0–219.4	258.6±18.5 161.5–374.9	267.1±22.5 139.0–364.5	208.1±14.9 129.9–301.6	385.6±18.1 294.7–469.8	486.4±37.9 241.9–646.4	87.57*** 26 < 30	34.82*** PF^b, NPF^a, AM^a	1.70^{NS}
Daily production of feces ($J\,g^{-1}\,d^{-1}$)	13.9±1.6 7.5–22.5	23.2±2.5 9.2–39.1	30.4±2.8 13.8–45.0	15.6±1.3 9.6–23.3	38.9±2.0 31.3–50.6	34.5±2.2 19.1–43.6	24.60*** 26 < 30	17.22*** PF^b, NPF^a, AM^a	1.87^{NS}
Daily production of urates ($J\,g^{-1}\,d^{-1}$)	9.9±0.9 6.4–13.7	16.8±1.4 8.1–22.8	16.1±1.3 9.7–22.1	13.7±0.9 9.4–17.2	26.7±1.8 16.5–34.8	31.7±2.2 20.6–41.1	82.06*** 26 < 30	11.71*** PF^b, NPF^a, AM^a	1.34^{NS}
ADC (%)	90.8±0.9 85.3–94.2	91.0±0.6 88.1–93.6	88.6±0.7 84.6–91.4	92.5±0.5 88.8–94.8	89.9±0.5 86.8–91.7	92.9±0.2 91.8–94.2	18.34*** 26 < 30	0.05^{NS}	3.56*
AE (%)	84.3±1.3 75.7–88.9	84.5±0.7 80.7–88.1	82.6±0.7 77.7–85.5	85.9±0.6 82.2–88.2	83.0±0.4 80.6–84.9	86.4±0.5 84.6–89.6	4.34* 26 < 30	1.61^{NS}	6.07**

F values correspond to single effects and factor interactions in two-way ANOVAs with body temperature and animal category (reproductive condition) as the factors. PF: pregnant females; NPF: nonpregnant females; AM: adult males. Symbols immediately after *F* values represent significance levels: NS $P > 0.05$; *$P < 0.05$; **$P < 0.001$; and ***$P < 0.0001$. Means with different superscripts differ significantly (Tukey's *post hoc* test, $\alpha = 0.05$, $a > b$).

ecologically important because *M. multifasciata* is an active forager often found near shallow water bodies and relies heavily on swimming performance to avoid capture or predation (Huang, 1999; Ji et al., 2006a). Our data suggest that reproductive costs resulting from locomotor impairments are more pronounced at lower body temperatures in *M. multifasciata*, and the increased reproductive costs at low body temperatures partly explain why females never select body temperatures lower than 27 °C when pregnant (Ji et al., 2007).

It has been reported for a wide variety of lizards that daily food intake generally increases with increase in body temperature because of the increased metabolic rates and food-processing rates at higher temperatures (e.g. Waldschmidt et al., 1986; Van Damme et al., 1991; Ji et al., 1996; Du et al., 2000; Chen et al., 2003; Xu and Ji, 2006). Similarly, in the present study, daily food intake was greater at 26 °C than at 30 °C (Table 1). Pregnant females ate much less than did nonpregnant females and males (Table 1), primarily because their available body volumes were highly packed by developing embryos. This result supports the earlier conclusion from snakes that the physical constraint on food intake caused by body volume during pregnancy confers reproductive costs to the female (Ji et al., 1997, 2001; Lourdais et al., 2002). Nonpregnant females did not differ from males in daily food intake, suggesting that the effect of pregnancy on feeding performance does not persist after parturition. Compared with data pooled for nonpregnant females and males at the same body temperature, daily food intake of pregnant females was reduced by about 42% at 26 °C and by about 52% at 30 °C (Table 1). The degree of feeding impairment associated with pregnancy was much greater at 30 °C than at 26 °C, suggesting that feeding costs of reproduction are greater in females maintaining higher body temperatures when pregnant.

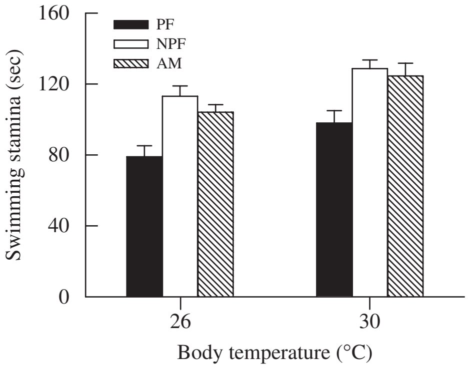

Fig. 2. Mean values (+SE) for swimming stamina of pregnant females ($n = 20$), nonpregnant females ($n = 22$) and adult males ($n = 20$) at two different body temperatures. PF: pregnant females; NPF: nonpregnant females; and AM: adult males.

The values of ADC and AE are determined by activities of digestive enzymes, food passage time and type and amounts of food consumed (Xu and Ji, 2006 and included references). Within a certain range, increased body temperature increases activities of digestive enzymes, but reduces the duration that food is exposed to these enzymes as food passage time is shortened (Harwood, 1979). This unique mechanism results in thermal insensitivity of ADC and AE in all lizards studied so far (Xu and Ji, 2006 and included references). Similarly, in the present study, both ADC and AE were less sensitive to variation in body temperature, as indicated by the fact that the differences in ADC and AE between the two temperature treatments, though statistically significant, were actually very slight (Table 1). Moreover, the existence of significant reproductive condition × body temperature interactions for ADC and AE revealed that results would not be repeatable at different temperatures. In combination with the results that both ADC and AE did not differ among the three skink categories, we conclude that ADC and AE of *M. multifasciata* are less sensitive to variation in body temperature as well as reproductive condition.

Data from adult males show that body temperatures within the range 30–36 °C maximize swimming stamina (Fig. 1). Interestingly, this range matches the range of body temperatures selected by nonpregnant females (29.7–35.2 °C) and adult males (30.2–35.7 °C; Ji et al., 2007). Such a match is unlikely to come up by chance but suggests that adults of *M. multifasciata* with the opportunity of thermoregulation typically maintain body temperatures optimal for locomotor performance. Pregnant females, however, select lower body temperatures falling within the range of 27.6–30.8 °C (Ji et al., 2007). Given that embryos of *M. multifasciata* develop successfully at temperatures ranging from 26 to 32 °C (Ji et al., 2007), why do pregnant females select body temperatures of about 29 °C, but not at any other lower or higher levels? The answers presumably lie in the following three aspects. First, pregnant females benefit very little from selecting body temperatures higher than 29 °C in terms of the reduced gestation length, because the mean gestation length decreases much less dramatically from 29 to 32 °C (<5 days) than from 26 to 29 °C ($\sim$3 weeks; Ji et al., 2006a). Thus, shifting selected body temperatures to about 29 °C allows females to produce good-quality offspring in a relatively short gestation time. Second, females should avoid selecting lower body temperatures, because the prolonged gestation time (and thus, the prolonged exposure of pregnant females to the effects of adverse factors) and the increased locomotor impairments at low body temperatures may substantially increase reproductive costs. Third, pregnant females should avoid selecting higher body temperatures, because the increased energetic costs associated with the increased metabolic rates and the increased feeding impairments at higher body temperatures may also increase reproductive costs.

In combination, our data validate the hypothesis that the maximization of reproductive benefits can be achieved in pregnant females by shifting thermal preferences towards the levels optimal for embryonic development and at the same time minimizing reproductive costs to a large extent.

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