Sexual Dimorphism and Female Reproduction in the Many-Lined Sun Skink (*Mabuya multifasciata*) from China

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ABSTRACT.—We studied sexual dimorphism and female reproduction in Many-Lined Sun Skinks (*Mabuya multifasciata*) from a population in Hainan (southern China). The smallest reproductive female was 90 mm snout–vent length (SVL). The largest male was 117 mm SVL and the largest female was 116 mm SVL. To measure the potential influence of gestation temperature on female reproduction, pregnant females were maintained under five thermal conditions until they gave birth. Parturition began in early May, and females produced up to two litters per breeding season. Litter size, litter mass, and offspring size (mass) were all positively correlated with female SVL. Litter size ranged from 2–7, and it was independent of relative fecundity (litter size relative female SVL). We did not detect a trade-off between body size and offspring number. Gestation temperature affected parturition date but not litter size, litter mass, neonate mass, or relative litter mass. Females at higher (average) gestation temperatures gave birth to young earlier than did those at lower temperatures. The detrimental effects of extreme ambient temperatures on offspring body size could be buffered through maternal thermoregulation.

Sexual dimorphism in body shape as well as overall body size is widespread among animals (Darwin, 1871; Andersson, 1994). Sexual selection, acting through female choice or male contest competition, is the most frequently cited explanation for the evolution of sexual dimorphism. Nonetheless, other factors such as natural selection, acting to reduce intersexual resource competition, fecundity selection, and differential mortality between the sexes, are increasingly reported as alternative causes of sexual dimorphism (Slatkin, 1984; Shine, 1989; Shine et al., 2002). These explanations are not always mutually exclusive because a sexually dimorphic trait initially induced by sexual selection may result in a shift in resource use between the sexes (Shine, 1991; Vincent et al., 2004). For example, male Blue-Tailed Skinks (Eumeces elegans) are the larger sex because of male contest competition and as a result, larger individuals can eat larger prey (Du and Ji, 2001; Zhang and Ji, 2004). Therefore, sexual dimorphism may be the net outcome of many selective pressures that often differ between the sexes in strength and sometimes, in direction. Because variation in sexual dimorphism is often associated with variation in female reproductive output (Cooper and Vitt, 1989; Shine et al., 1998), data on female reproduction, therefore, are very useful for revealing the origins of the phenomenon.

The Many-Lined Sun Skink (Mabuya multifasciata) ranges from southern China (Taiwan, Hainan, Guangdong, and Yunnan), Myanmar, Thailand, and Indochina to India, south to West Malaysia, Singapore, Indonesia, the Philippines, Indoaustralian Archipelago, and New Guinea (Zhao and Adler, 1993). This relatively large bodied, terrestrial skink, shows a preference for open sunny spaces (especially disturbed areas), forest edges, and riverbeds. Despite its wide geographic distribution, the ecology of *M*. multifasciata remains poorly known. Previous studies on sexual dimorphism and reproduction only presented limited descriptive data (Huang, 1999). Consequently, we studied life-history traits such as between-sex differences in body size and head size, and relationships among offspring size, litter size, and female size, for a population of M. multifasciata in Ledong (18°45'N, 109°10'E), Hainan, southern China. Based on morphological measurements taken for adult lizards collected from the field and for females that gave birth to young both in the laboratory and in a field enclosure, we present data on sexual dimorphism and female reproduction. Because reproducing females were exposed to very different thermal environments, we examined the influence of gestation temperature on female reproduction. Gestation

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temperature has previously been demonstrated to influence various offspring traits (Robert and Thompson, 2001; Lourdais et al., 2004; Wapstra et al., 2004). In the Yellow-Bellied Water Skink (*Eulamprus heatwolei*), for example, gestation temperature affects not only the sexual phenotype but also the body size of offspring (Langkilde and Shine, 2005).

Our study aims were as follows: (1) to evaluate sexual dimorphism in morphological characters such as body size and head size; (2) to examine the effects of gestation temperature on female reproduction; and (3) to investigate the relationships among offspring size, litter size, and maternal size.

MATERIALS AND METHODS

A total of 314 adult skinks were collected by hand during June 2002 and March 2004. Most of these were released at their point of capture following the collection of morphological data. Measurements to the nearest 0.1 mm were taken for each skink using Mitutoyo digital calipers, including SVL, tail length (TL), head length (HL; from the snout to the anterior edge of tympanum), and head width (HW; posterior end of the mandible) (Ji and Du, 2000; Ji et al., 2002).

In early March 2004, 140 females were palpated to evaluate their reproductive condition; five were also dissected to determine their state of ovulation. The remaining females were randomly allocated to five thermal conditions (temperature treatments) until parturition, to measure the influence of gestation temperature on female reproductive traits such as timing of parturition, litter size, litter mass, and offspring size. Females in three of the five treatments were maintained in three controlled temperature rooms, thereby maintaining their mean body temperatures at 26, 28, and 30°C, respectively. Cloacal temperature was taken for each female using a WMZ-3 electronic thermometer (Shanghai Medical Instrument, China) to verify that the mean body temperatures were controlled at the anticipated levels. Females in the fourth treatment (hereafter the TR [thermoregulation] treatment) were maintained in a room where temperatures never exceeded 20°C. A 275-W light bulb suspended (20 cm above the cage floor) above one end of each 1 \times 0.6×0.5 m cage holding the females created a thermal gradient ranging from 18-60°C during the photophase (14:10 light: dark). Body temperatures selected by females on the thermal gradients varied from 26.2–31.4°C, with a mean of 29.5°C (± 0.4 SE; indicative of selected body temperature; Ji et al., 1995). Females in the fifth treatment (hereafter the NAT [natural] treatment) were maintained in a 5

 \times 5 \times 1 m field enclosure built in Hainan, near the site where the skinks were collected. Females in the field enclosure had the opportunity of behaviorally regulating their body temperature. In the laboratory-kept animals, the lower and upper levels of constant body temperature were fixed at 26°C and 30°C, respectively, because these temperatures were close to the lower limit (26.2°C) and the average level (29.5°C) of body temperatures selected by females in the laboratory thermal gradient. Between eight to 10 females were housed together in the first four treatments in a 1 \times $0.6\times0.5~m^3$ glass cage, which had a substrate consisting of 100 mm of moist soil, debris, and grasses. All females were provided with mealworms (Tenebrio molitor) and water enriched with vitamin and minerals (Nekton-Rep, Nekton-product).

We checked the cages at least twice daily for newborns and immediately measured and weighed them after birth. Females giving birth during the same period were isolated from each other using dividers that created $30 \times 30 \times 30$ cm chambers so that newborns could be allocated accurately to the mother. Postpartum females were individually measured for SVL and weighed. Of the 135 females, 116 gave birth to young that were all well developed, whereas the remaining females produced abnormal litters with various numbers of dead young, stillborns, or unfertilized eggs. Abnormal litters, which were found in each temperature treatment, were excluded from analyses. We calculated relative litter mass (RLM) by dividing litter mass by the postpartum female mass (Shine, 1992), and relative fecundity (litter size relative to female SVL; Olsson and Shine, 1997) by using the residuals derived from the regression of loge (litter size) on log_e (maternal SVL).

All data were tested for normality using the Kolmogorov–Smirnov test, and for homogeneity of variances using Bartlett's test. Log_e-transformation was performed when necessary to satisfy the assumptions for using parametric tests. All values are presented as mean \pm SE, and the significance level was set at $\alpha = 0.05$.

RESULTS

The largest male and female were 117 and 116 mm SVL, respectively (Fig. 1). The mean SVL was significantly greater in adult males (107 \pm 0.2 mm) than in adult females (102 \pm 0.2 mm; ANOVA, $F_{1,312} = 71.05$, P < 0.0001); thus, males were the larger sex (Fig. 1). The rate at which head length increased with SVL was greater in adult males than in adult females (ANCOVA, $F_{1,310} = 8.89$, P < 0.003), but the rate at which head width increased with SVL did not differ



FIG. 1. Frequency distributions of SVL of adult Mabuya multifasciata (124 males, 189 females) showing sexual size dimorphism. The curves in the figure are generated from a fit of the normal distribution.

significantly between male and female adults (ANCOVA, $F_{1,310} = 0.79$, P = 0.374; Fig. 2). The mean values of residuals derived from the regressions of loge (HL) and loge (HW) on loge (SVL) were both significantly greater in adult males (HL, $F_{1,312} = 327.99$, P < 0.0001; HW, $F_{1,312}$ = 139.64, P < 0.0001). Thus, male adults had relatively larger heads than females (Fig. 2).

The smallest reproductive female was 90 mm SVL. Females in Hainan have the potential to produce two litters per breeding season since five of the eight postpartum females dissected had enlarged yolked follicles that would form the next litter. Ambient temperatures experienced by females in the field enclosure varied daily and seasonally, with the minimum, maximum, and the mean temperatures being 14.0, 37.0, and 27.5°C, respectively. Overall, females gave birth to young between mid-April and late June (Fig. 3). However, parturition dates differed significantly among treatments ($F_{4,111} = 21.07$, P



Ln (Snout-vent length) (mm)

FIG. 2. Linear regressions of head length and head width on adult SVL in Mabuya multifasciata. Males: solid dots; females: open dots.

< 0.0001), with females at higher (average) gestation temperatures giving birth to young earlier than females at lower temperatures (Fig. 3). Females under different thermal conditions differed in SVL and postpartum body mass, but they did not differ in litter size, litter mass, offspring size (neonate mass), and relative litter mass when controlling for the effects of body size on these examined traits (Table 1).

When pooling data from different treatments, we found that litter size ($r^2 = 0.15$, $F_{1,114} = 19.58$, P < 0.0001), litter mass ($r^2 = 0.22$, $F_{1,114} = 32.06$, P < 0.0001), and neonate mass ($r^2 = 0.09$, $F_{1,114} = 10.65, P < 0.002$) were all positively correlated with maternal SVL (Fig. 4) and that neonate mass was independent of relative fecundity ($r^2 = 0.01$, $F_{1,114} = 0.98$, P = 0.325).

DISCUSSION

Sexual Dimorphism.—As in many other vertebrates (Selander, 1972; Shine, 1979; Greenwood and Wheeler, 1985; Parker, 1992), the sexes differed in head size as well as overall body size



Month

FIG. 3. Duration of pregnancy of females maintained under different temperatures. Thermal treatments were females whose mean body temperatures were controlled at 26 (N = 21), 28 (N = 25), and 30°C (N = 27), respectively; TR: females (N = 13) maintained in the laboratory thermal gradient created by heating lights under a cycle of 14:10 light:dark; NAT: females (N = 35) maintained in a field enclosure. Numbers in the horizontal bars are the mean days after capture, but before parturition.

in *M. multifasciata*. Male *M. multifasciata* had larger heads than females of the same body length, which is consistent with the results reported for numerous other species of lizards worldwide (e. g., Cooper and Vitt, 1989; Braña, 1996; Ji et al., 2002; Lin et al., 2004; Zhang et al., 2005). The pattern of sexual size dimorphism (SSD) in *M. multifasciata* is opposite to that reported for *Sphenomorphus indicus* (Ji and Du, 2000) and *Phrynocephalus vlangalii* (Zhang et al., 2000)

2005) two viviparous lizards, in that males are the larger sex. Interestingly, the mean value for RLM is much smaller in *M. multifasciata* than in *S. indicus* (0.33; Ji and Du, 2000) and *P. vlangalii* (0.40; Zhang et al., 2005), and the proportion of variation in litter mass (reproductive output) that can be explained by female size (SVL) is also much smaller in *M. multifasciata* (22%) than in *S. indicus* (40%; Ji and Du, 2000) and *P. vlangalii* (49%; Zhang et al., 2005). What can be inferred from these comparisons is that the selective pressure toward increased female size is comparatively low in *M. multifasciata*.

SSD is believed to evolve in lizards mainly because of between-sex differences in reproductive success relating to adult body size (Cooper and Vitt, 1989: Hews, 1990: Mouton and Van Wyk, 1993). Theoretically, fecundity selection favors large females and sexual selection favors large males. The two selective pressures could cancel each other out and, consequently, result in a lack of SSD between males and females. For example, selection via male contest competition is the ultimate factor resulting in increased male size in *Eumeces chinensis* (Lin and Ji, 2000) and E. elegans (Du and Ji, 2001), whereas selection acting on fecundity or litter mass is the main cause for increased female size in S. indicus (Ji and Du, 2000) and P. vlangalii (Zhang et al., 2005). Less pronounced male contest competition (thus, potentially lower selective pressure toward increased male size) as well as less pronounced physical constraints from maternal body size on reproductive output (thus, poten-

TABLE 1. Reproductive characteristics of pregnant *Mabuya multifasciata* maintained under different temperature regimes. Data are mean \pm SE and range. *F*-values of one-way ANOVA (for maternal SVL) or one-way ANCOVA (using female SVL as the covariate for postpartum body mass, litter size, litter mass, and neonate mass, and postpartum body mass as the covariate for relative litter mass) are indicated. Means corresponding to the temperature treatments with different superscripts differed significantly (Tukey's test, $\alpha = 0.05$, ^a > ^b).

	Temperature treatments					Statistical analyses and the
	26	28	30	TR	NAT	comparisons
N	21	25	27	13	35	
Snout-vent length (mm)	104.4 ± 1.2 96.2–113.2	$\begin{array}{r} 104.0\pm1.0\\ 93.0113.8\end{array}$	$\begin{array}{r} 103.8 \pm 1.0 \\ 94.7 111.8 \end{array}$	$\begin{array}{r} 103.1 \pm 0.8 \\ 99.8 107.7 \end{array}$	$\begin{array}{r} 100.5 \pm 0.8 \\ 90.1 110.0 \end{array}$	$\begin{array}{l} F_{4,\ 111} = 3.13, P = 0.018 \\ 26^{\rm ab},\ 29^{\rm a},\ 30^{\rm ab},\ {\rm TR}^{\rm ab}, \\ {\rm NAT}^{\rm b} \end{array}$
Postpartum body mass (g)	25.0 ± 1.2 17.9–33.7	27.0 ± 1.0 16.7–36.7	$\begin{array}{r} 27.0 \pm 0.8 \\ 20.3 35.7 \end{array}$	26.0 ± 1.2 19.7–34.3	$\begin{array}{r} 22.5 \pm 0.7 \\ 15.7 30.6 \end{array}$	$\begin{array}{l} F_{4, \ 110} = 3.41, P = 0.011 \\ 26^{\rm b}, 28^{\rm ab}, 30^{\rm a}, {\rm TR}^{\rm ab}, \\ {\rm NAT}^{\rm b} \end{array}$
Litter size	4.1 ± 0.3 2-6	4.5 ± 0.3 2–7	4.5 ± 0.3 2–7	4.2 ± 0.2 3-6	4.1 ± 0.2 2-6	$F_{4,\ 110} = 0.54, P = 0.706$
Litter mass (g)	4.35 ± 0.30 2.10-7.10	$\begin{array}{r} 4.66 \pm 0.31 \\ 2.12 - 8.30 \end{array}$	$\begin{array}{r} 4.54 \pm 0.27 \\ 1.936.99 \end{array}$	$\begin{array}{r} 4.23 \pm 0.26 \\ 2.91 6.36 \end{array}$	$\begin{array}{r} 4.10 \pm 0.21 \\ 1.54 6.33 \end{array}$	$F_{4,\ 110} = 0.36, P = 0.838$
Neonate mass (g)	1.05 ± 0.02 0.87-1.23	1.04 ± 0.03 0.66 - 1.27	1.01 ± 0.03 0.80-1.43	1.02 ± 0.02 0.87 - 1.13	1.00 ± 0.02 0.77-1.40	$F_{4,\ 110} = 0.82, P = 0.515$
Relative litter mass	0.18 ± 0.01 0.07-0.28	$\begin{array}{c} 0.18 \pm 0.01 \\ 0.08 0.28 \end{array}$	$\begin{array}{c} 0.17 \pm 0.01 \\ 0.09 0.28 \end{array}$	$\begin{array}{c} 0.16 \pm 0.01 \\ 0.12 0.23 \end{array}$	$\begin{array}{c} 0.19 \pm 0.01 \\ 0.06 0.30 \end{array}$	$F_{4,\ 110} = 0.22, P = 0.925$

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FIG. 4. Linear regressions of litter size, litter mass and neonate mass on female SVL in *Mabuya multifasciata*.

tially lower selective pressure toward increased female size) explains why adults are monomorphic in *Calotes versicolor* (Ji et al., 2002), *Eremias brenchleyi* (Xu and Ji, 2003), *Eremias multiocellata* (Li et al., 2006), and *Takydromus septentrionalis* (Ji et al., 1998; Zhang and Ji, 2000). Female *M. multifasciata* are the smaller sex, primarily because reproductive output is relatively low in this species.

Female Reproductive Characteristics.—It was not surprising that female *M. multifasciata* maintained at higher average temperatures gave birth to young earlier than did those at lower

temperatures because high gestation temperatures generally result in faster embryonic development and thus, earlier parturition dates (Robert and Thompson, 2001; Lourdais et al., 2004; Wapstra et al., 2004). In the TR treatment, females could elevate body temperatures to an average level of 29.5°C during the light phase, but cooled to room temperature ($\leq 20^{\circ}$ C) during the dark phase. Thus, the overall mean gestation temperature in the treatment should be lower than 29.5°C, but presumably close to 28°C, as the mean interval after capture but before parturition in the TR treatment was almost the same as that in the 28°C treatment. Females in the field enclosure had the opportunity of experiencing extreme temperatures, at which they had little control over their body temperatures. Birth dates were later in the NAT treatment than in the TR treatment, suggesting that opportunities of regulating body temperature were less ample in the field enclosure than in the laboratory thermal gradient.

Litter size or clutch size is determined soon after vitellogenesis in reptiles (Sinervo, 1994; Ji and Du, 2000). Therefore, as expected, litter size did not vary among treatments, having already been determined when the females were collected from the field. It is worth noting, however, that neonate mass did not differ significantly among treatments (Table 1). In oviparous reptiles, embryos developing at extremely low or high temperatures often produce lighter or smaller hatchlings, primarily because of the increased embryonic use of energy at these temperatures (Ji and Braña, 1999; Ji and Zhang, 2001; Ji et al., 2003). The effects of embryonic temperature on hatchling phenotypes reported for oviparous species have also been found in viviparous species (Robert and Thompson, 2001; Lourdais et al., 2004; Wapstra et al., 2004). In this study, only embryos developing in the field enclosure had the opportunity of experiencing extreme temperatures since ambient temperatures varied from 14-37°C. The consistency of neonate mass across temperature treatments suggests that the effects of extreme ambient temperatures on neonate mass is effectively buffered through maternal thermoregulation in *M. multifasciata*.

Our data showed that maternal size was the main determinant of reproductive investment in *M. multifasciata*, with larger females producing more, as well as larger, offspring. A trade-off between size and number of offspring, although widespread in numerous organisms (Smith and Fretwell, 1974; Bernardo, 1996), was not detected in this study. Specifically, neonate mass was not negatively correlated with litter size when female SVL was held constant. Another lizard species, *Leiolepis reevesii*, also lacks the

size-number trade-off, primarily because fecundity (2–5 eggs per clutch) is low relative to maternal size (up to 112 mm SVL; Lin et al., 2004). Females *M. multifasciata* also have low fecundity relative to their body size. Therefore. we speculate that there may be a link between the existence of the size-number trade-off and size-specific fecundity.

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