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Sexual dimorphism, female reproduction and egg incubation in the oriental leaf-toed gecko (*Hemidactylus bowringii*) from southern China

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Abstract

We studied sexual dimorphism, female reproduction and egg incubation of the oriental leaf-toed gecko (*Hemidactylus bowringii*) from a population in southern China. The largest male and female in our sample were 60 and 57 mm snout-vent length (SVL), respectively. Males are the larger sex; sexual dimorphism in head size and tail length (TL) is evident in juveniles and adults, with males having larger heads as well as longer tails than females. Oviposition occurred between late May and late July. Females switched from laying two eggs early in the breeding season to 1–2 eggs later in the season. Clutch mass and egg mass were both independent of female SVL, whereas relative clutch mass was negatively correlated with female SVL. The previous conclusion that female *H. bowringii* lay a single clutch of eggs per breeding season is unlikely to be true. Thermal environments experienced by *H. bowringii* eggs affect incubation length as well as morphological and locomotor phenotypes of hatchlings. Hatchlings from eggs incubated at 30 °C were larger (SVL, tail length and body mass) and performed better in the racetrack than their counterparts from eggs incubated at 24 °C. Temperatures suitable for embryonic development are relatively high in *H. bowringii*, primarily as a consequence of the adaptive response to warm environments in southern China.

Keywords: Gekkonidae; Sexual dimorphism; Reproduction; Egg incubation; Hatchling phenotype

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Introduction

Sexual dimorphism in morphology as well as coloration is widespread among animals (Woolbright, 1983; Greenwood and Wheeler, 1985; Cooper and Vitt, 1989; Winquist and Lemon, 1994). Sexual dimorphism is the net outcome resulting from a balance of many selective pressures differing between the sexes in strength and/or in direction, because sexual selection (acting via female choice or male–male contest for mating opportunities), fecundity selection (leading to larger body size or body volume in females) and other factors such as natural selection acting to reduce intersexual resource competition and differential mortality between the sexes due to

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differences in longevity all can be the potential causes of sexual dimorphism (Shine, 1989; Hews, 1990; Andersson, 1994; Olsson et al., 2002).

Reproductive output is associated with morphological traits in lizards (Vitt and Congdon, 1978; Cooper and Vitt, 1989; Shine et al., 1998) and, thus, data on female reproduction can help us understand the origins of sexual dimorphism. Although the degree of sexual dimorphism may differ among species, it seems to be generalizable in lizards that sexual dimorphism becomes increasingly pronounced during ontogeny (Ji and Du, 2000; Lin and Ji, 2000; Ji et al., 2002a; Xu and Ji, 2003; Zhang and Ji, 2004; Zhang et al., 2005). Sexual dimorphism occurs at hatching in some species (Braña and Ji, 2000; Zhang and Ji, 2000; Pan and Ji, 2001; Ji et al., 2002b; Xu and Ji, 2003), but not in others (Ji and Du, 2000; Lin and Ji, 2000; Zhang and Ji, 2004; Zhang et al., 2005). Thus, to reveal when and how sexual dimorphism arises, we need to measure the traits of interest for individuals at different ages. To obtain morphological data on hatchlings, we often need to incubate eggs under either controlled or natural conditions.

Of some 80 species of *Hemidactylus* geckos (Carranza and Arnold, 2006), four can be found in China (Zhou and Liu, 1999). The oriental leaf-toed gecko (*Hemidactylus bowringii*) studied here ranges from India to Sikkim, Burma to southern China (Fujian, Guangdong, Hainan, Taiwan, Guangxi and Yunnan) and Ryukyu (Zhou and Liu, 1999). Although there has been some information on morphological traits as well as reproductive cycles of the species (Zhang et al., 1999, 2000; Zhou and Liu, 1999), there is little quantitative data on topics such as sexual dimorphism, female reproduction and egg incubation. There has been no detailed examination of the reproductive ecology of *H. bowringii*, although incidental information indicates that this gecko produces a single clutch of 1–2 eggs per breeding season between May and August, with mating activities occurring mostly in June (Zhang et al., 1999, 2000; Zhou and Liu, 1999).

To obtain more detailed information, we studied a population of *H. bowringii* in Zhaoqing (23° 02′N, 112° 27′E), Guangdong, southern China. Based on morphological measurements taken for geckos collected from the field and hatchlings from eggs incubated in the laboratory, we present data on sexual dimorphism, female reproduction and egg incubation for the population. Our study aims were (1) to test for the prediction that the evolution of sexual dimorphism is promoted by between-sex differences in reproductive success relating to adult morphological traits; (2) to investigate the relationships among egg size, reproductive output and maternal size; and (3) to examine the effects of incubation temperature on hatchling phenotypes.

Materials and methods

A total of 200 geckos having no evidence of caudal autotomy were collected during June 2004 and August 2005. Geckos larger than 45 mm snout-vent length (SVL) were considered as adults, because females larger than this size could lay eggs. Most of these geckos were released at their point of capture following the collection of morphological data. Measurements were taken for each gecko using Mitutoyo digital calipers, including SVL, tail length (TL), head length (HL; from the snout to the anterior edge of the tympanum), and head width (HW; posterior end of the mandible).

Forty-one adult females collected in May 2005 were used for the collection of data on earlier clutches laid before mid-June, and 31 adult females collected in June 2005 were used for the collection of data on later clutches. All of these females were housed individually in 20 × 15 × 10 cm (length × width × height) mesh cages, which were placed in a room where temperatures were never outside the range of 24–32 °C. Females were exposed to a natural daylight cycle, and were fed mealworms (head length *Tenebrio molitor*) and water enriched with vitamins and minerals. Eggs were collected, measured for length and width, weighed and numbered within a few hours after being laid. Post-oviposition females were measured (for SVL, TL, HL and HW) and weighed, and were then released to the site where they were originally collected. Clutch mass was calculated as the total mass of eggs in a clutch, and relative clutch mass (RCM) was calculated by dividing clutch mass by the post-oviposition mass.

A total of 36 eggs (18 clutches) laid in early June were incubated individually in covered plastic jars (50 ml) that contained known amounts of vermiculite and water to produce approximately −12 kPa water potential (1 g water/1 g vermiculite; Ji and Braña, 1999). These jars were equally assigned to two Shellab incubators (Sheldon MFG Inc., USA) inside which temperatures were controlled at 24 °C and 30(±0.3) °C, respectively; eggs from the same clutch were placed in different incubators. These two temperatures were chosen because the annual mean values of minimal and maximal air temperatures in Zhaoqing during May and June are ~24 and 30 °C, respectively. We moved jars among shelves daily according to a predetermined schedule to minimize any effects of thermal gradients inside the incubator.

The incubation length, measured as the number of days to pipping, was recorded for each egg. Wet body mass, SVL, TL, HL and HW were taken for each hatchling. All hatchlings were used to evaluate the effects of incubation temperature on locomotor performance and morphological traits. Because locomotor performance is thermally sensitive in reptiles, we conducted all trials at the body temperature of 30 °C, which was controlled by placing hatchlings in an incubator at the correspondent temperature for ~30 min prior to testing. Locomotor performance was assessed by chasing the hatchlings along a 2 m racetrack with one side transparent, which allowed videoing with a Panasonic NV-DS77 digital video camera. The tapes were later examined with a computer using MGI VideoWave III software (MGI Software Co., Canada) for sprint speed in the fastest 15-cm interval and the maximal distance traveled without stopping (hereafter the maximal length).

All data were tested for normality (Kolmogorov–Smirnov test) and homogeneity of variances (Bartlett test). Parametric analyses were used to analyze data when the assumptions for these analyses were met; otherwise, nonparametric analyses were used. Throughout this paper, values are presented as mean ± 1 standard error, and the significance level is set at $\alpha = 0.05$.

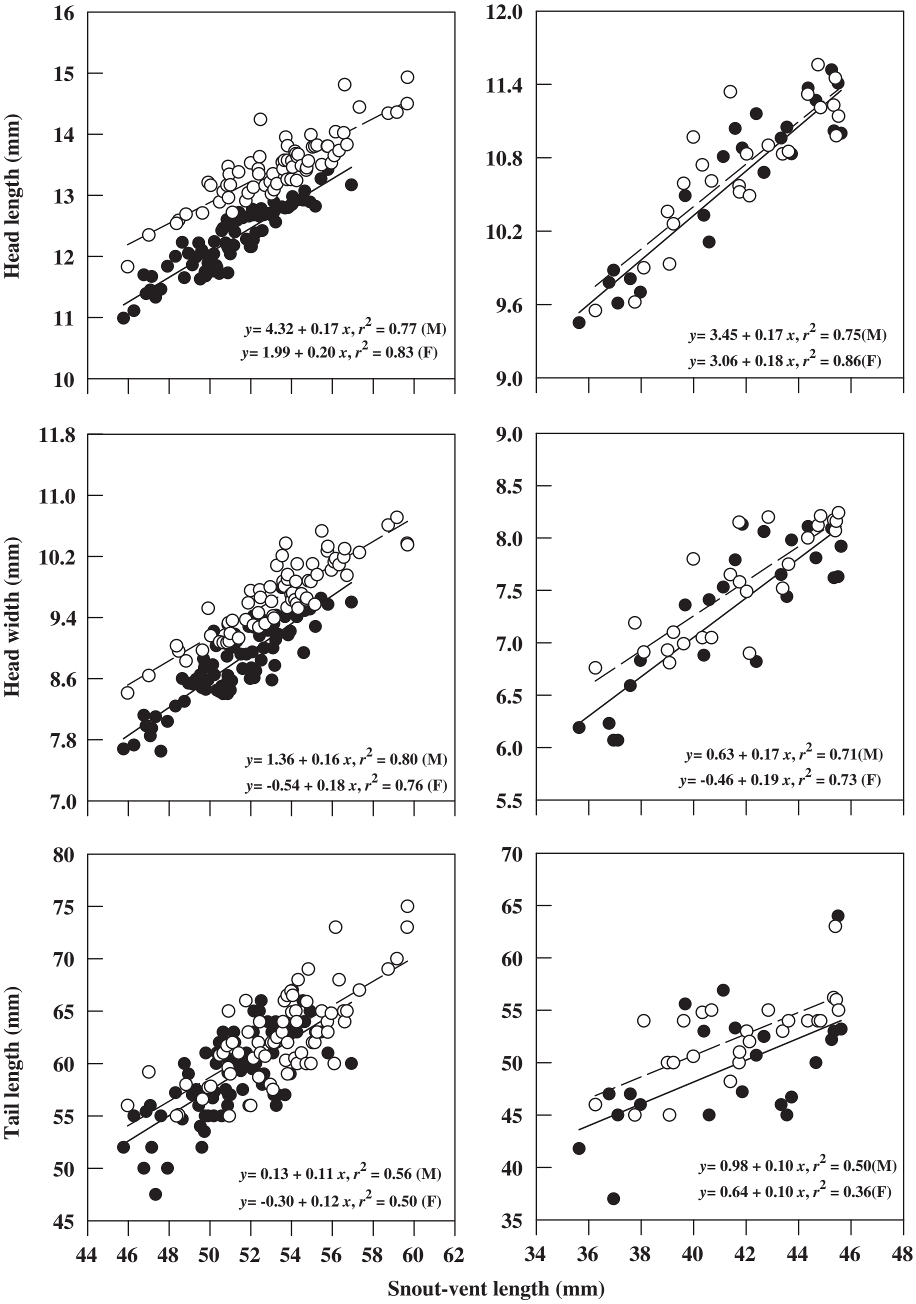

Fig. 1. Linear regressions of head length, head width and tail length on snout-vent length for juveniles and adults of *H. bowringii*. Solid dots: females; open dots: males; plots on the left side: adults; plots on the right side: juveniles. The regression equations and coefficients for females (F) and males (M) are given in each plot.

Table 1. Results of two-way ANCOVA (with age and sex as the factors, and SVL as the covariate) on head length, head width and tail length of juvenile and adult *H. bowringii* collected from the field

Variables	Effects		
	Age	Sex	Age × Sex
Head length	$F_{1,\ 195} = 12.07$, $P < 0.001$; J > A	$F_{1,\ 195} = 100.69$, $P < 0.0001$; M > F	$F_{1,\ 195} = 74.56$, $P < 0.0001$
Head width	$F_{1,\ 195} = 0.09$, $P = 0.761$; J = A	$F_{1,\ 195} = 56.84$, $P < 0.0001$; M > F	$F_{1,\ 195} = 13.95$, $P < 0.0003$
Tail length	$F_{1,\ 195} = 5.80$, $P = 0.017$; J > A	$F_{1,\ 195} = 12.51$, $P < 0.0006$; M > F	$F_{1,\ 195} = 1.62$, $P = 0.204$

J: juveniles; A: adults; M: males; F: females.

Table 2. Descriptive statistics for reproductive characteristics of female *H. bowringii*

Variables	Earlier clutches ($N = 41$)	Later clutches ($N = 31$)	*F* values and significance levels
Snout-vent length (mm)	51.6 ± 0.4 (45.7–57.2)	51.2 ± 0.4 (45.8–55.5)	$F_{1,\ 70} = 0.26$, $P = 0.610$
Post-oviposition body mass (g)	2.34 ± 0.05 (1.62–3.00)	2.25 ± 0.04 (1.93–2.73)	$F_{1,\ 69} = 1.34$, $P = 0.250$
Clutch size	2	1.8 ± 0.1 (1–2)	$F_{1,\ 70} = 9.57$, $P < 0.003$
Clutch mass (mg)	557.3 ± 11.3 (327.8–672.8)	527.9 ± 22.7 (248.4–737.6)	$F_{1,\ 70} = 1.55$, $P = 0.217$
Egg mass (g)	278.7 ± 5.6 (163.9–336.4)	293.1 ± 5.5 (245.7–368.8)	$F_{1,\ 70} = 3.21$, $P = 0.078$
Egg length (mm)	9.1 ± 0.1 (7.4–9.8)	9.0 ± 0.1 (8.3–10.1)	$F_{1,\ 70} = 0.17$, $P = 0.678$
Egg width (mm)	7.5 ± 0.1 (6.3–8.2)	7.7 ± 0.1 (6.7–8.4)	$F_{1,\ 70} = 2.42$, $P = 0.124$
Relative clutch mass	0.24 ± 0.005 (0.15–0.29)	0.24 ± 0.01 (0.11–0.38)	$F_{1,\ 70} = 0.11$, $P = 0.743$

Data are expressed as mean ± 1 standard error (range). *F* values of ANCOVA (for post-oviposition body mass, with female SVL as the covariate) or ANOVA (for all other variables) and significance levels are given in the table.

Results

Sexual dimorphism

The largest male and female measured 59.7 and 56.9 mm SVL, respectively. The mean SVL was greater in adult males (53.4 ± 0.3 mm, $N = 69$) than in adult females (51.3 ± 0.3 mm, $N = 81$; ANOVA, $F_{1,\ 148} = 25.51$, $P < 0.0001$); thus, males are the larger sex.

The rates at which HL, HW and TL increased with SVL did not differ between the sexes of the same age (category) and between juveniles and adults of the same sex (ANCOVA, all $P > 0.05$; Fig. 1). Males had larger heads (both HL and HW) as well as longer tails than females of the same SVL; SVL-specific HL and TL were both greater in juveniles than in adults, whereas SVL-specific HW did not differ between juveniles and adults (Table 1). Between-sex differences in head size (both HL and HW) and TL were not found in hatchlings (ANCOVA, all $P > 0.274$); thus, *H. bowringii* is one of those species where sexual dimorphism does not occur at hatching.

Female reproduction

Females collected in May laid eggs between late May and mid-June, and those collected in June laid eggs between late June and late July. Clutch mass and egg mass were both independent of female SVL in either the earlier or the later period of the breeding season (all $P > 0.379$), and females collected in May and June did not differ in SVL (Table 2). Females switched from laying two eggs early in the breeding season to 1–2 eggs later in the season, and the seasonal shift in mean clutch size was statistically significant (Table 2). Post-oviposition body mass, clutch mass, egg mass, egg shape and RCM remained remarkably constant during the breeding season (Table 2). RCM was negatively correlated with female SVL in both the earlier and the later period of the breeding season (both $P < 0.02$), and did not vary seasonally when the influence of variation in female SVL was removed (ANCOVA, $F_{1,\ 69} = 0.35$, $P = 0.559$). Data pooled for earlier and later clutches showed once again that RCM was negatively correlated with female SVL ($F_{1,\ 70} = 14.10$, $P < 0.0004$; Fig. 2).

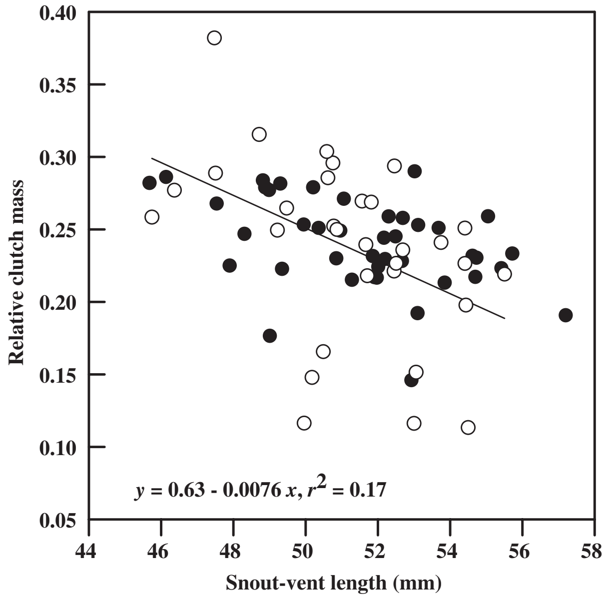

Fig. 2. Linear regression of relative clutch mass on female size (snout-vent length) for *H. bowringii*. Solid dots: earlier clutches; open dots: later clutches. The regression equation and coefficient are given in the figure.

Egg incubation and hatchling phenotypes

Eggs incubated at 24 and 30 °C differed in incubation length (ANOVA, $F_{1,\ 28} = 2101.68$, $P < 0.0001$), but not in hatching success ($G = 0.13$, $df = 1$, $P > 0.50$; Table 3). The mean incubation length was shortened by 35.4 days at 30 °C compared to 24 °C.

Within each of the two treatments, the examined hatchling variables were all positively correlated with egg mass (all $P < 0.05$), which was therefore used as the covariate in all ANCOVAs. Eggs incubated at 30 °C produced heavier and larger (both SVL and TL) hatchlings than did those incubated at 24 °C (Table 4). Hatchlings incubated at 30 °C overall had larger heads than did those incubated at 24 °C, although the adjusted mean values of HW did not differ between the two treatments (Table 4).

Neither sprint speed nor the maximal length was correlated with hatchling SVL (all $P > 0.185$), so we used ANOVA with incubation temperature as the factor to analyze data. Sprint speed ($F_{1,\ 28} = 5.12$, $P = 0.032$) and the maximal length ($F_{1,\ 28} = 7.48$, $P = 0.011$) were both greater in hatchlings from eggs incubated at 30 °C than in their counterparts from eggs incubated at 24 °C (Fig. 3).

Discussion

Our data show that between-sex differences in head size as well as TL were evident in juveniles and adults but not in hatchlings (Fig. 1). The finding that adult males have larger heads than females of the same SVL is consistent with the results reported for other saurian species studied worldwide, although the ways through which sexual dimorphism in head size arises vary among species. For example, females of *Takydromus septentrionalis* (northern grass lizard) increasingly sacrifice head growth for rapid growth in SVL to realize the greater potential reproductive output from a larger body volume, whereas males exhibit an increasingly rapid growth of the head (Zhang and Ji, 2000). In *Eremias brenchleyi* (Ordos racerunner), however, sexual dimorphism in head size arises mainly because of the increasingly rapid growth of the head in males (Xu and Ji, 2003). Sexual dimorphism in head size arises in *H. bowringii* in a way differing from those reported for the above two species, because the rates at which head size increased with SVL did not differ between the sexes of the same age and between juveniles and adults of the same sex (Fig. 1). Our finding that juveniles and adults of the same sex exhibit isometric growth of the head is consistent with the result reported for *Calotes versicolor* (oriental garden lizard) in which the selective pressure for increased female body volume due to decreased head size is relatively low (Ji et al., 2002a).

Juvenile and adult males possess longer tails than females of the same SVL in *H. bowringii*, presumably because males need additional tail space to accommodate hemipenes. Interestingly, however, between-sex difference in TL is more pronounced in juveniles than in adults (2.5 vs. 1.2 mm difference in intercepts between the sexes; Fig. 1). Thus, accommodation of hemipenes might be one but not the exclusive cause of sexual dimorphism in TL in *H. bowringii*.

The evolution of sexual size dimorphism (SSD) in lizards is associated with 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. For example, selection via male-male competition is the ultimate factor leading to increased male size in *Eumeces*

Table 3. Effects of incubation temperature on duration of incubation and hatching success

Incubation temperature (°C)	Incubated eggs	Duration of incubation (d)	Hatching success (%)
24	18	77.8 ± 0.6 (74.2 – 80.5)	77.8 (14/18)
30	18	42.4 ± 0.5 (38.0 – 47.3)	88.9 (16/18)

Data on duration of incubation are expressed as mean ± 1 standard error (range).

Table 4. Effects of incubation temperature on size and morphology of hatchlings of *H. bowringii*

Variables	Incubation temperature (°C)		*F* values and significance levels
	24 ($N = 14$)	30 ($N = 16$)	
Egg mass (mg)	308.4 ± 8.6 (240.7–355.9)	298.1 ± 7.4 (247.4–349.4)	$F_{1,\,28} = 0.83$, $P = 0.371$
Hatchling mass (mg)	216.2 ± 3.6 (199.3–237.5)	225.1 ± 4.9 (178.3–250.2)	$F_{1,\,27} = 5.83$, $P = 0.023$; $30 > 24$
Snout-vent length (mm)	20.0 ± 0.2 (18.7–22.0)	20.0 ± 0.3 (18.3–22.9)	$F_{1,\,27} = 5.51$, $P = 0.027$; $30 > 24$
Tail length (mm)	18.7 ± 0.2 (17.5–20.2)	19.9 ± 0.4 (17.4–23.3)	$F_{1,\,27} = 52.98$, $P < 0.0001$; $30 > 24$
Head length (mm)	5.7 ± 0.1 (5.2–6.3)	5.7 ± 0.1 (4.9–6.3)	$F_{1,\,27} = 5.53$, $P = 0.026$; $30 > 24$
Head width (mm)	4.4 ± 0.03 (4.2–4.6)	4.4 ± 0.05 (4.1–4.8)	$F_{1,\,27} = 0.13$, $P = 0.717$

Date are expressed as mean ± 1 standard error. *F* values of ANOVA (for egg mass) or ANCOVA (for all other variables, with egg mass as the covariate) and significance levels are given in the table.

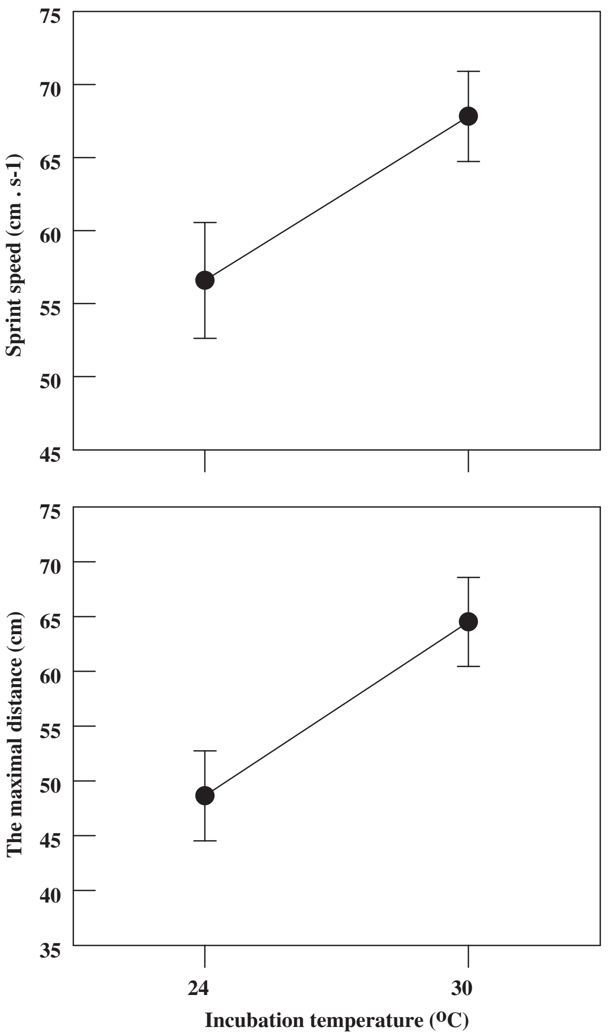

Fig. 3. Mean values (±1 standard error) for locomotor performance of hatchlings of *H. bowringii* derived from eggs incubated at 24 and 30 °C.

chinensis (Chinese skink; Lin and Ji, 2000) and *Eumeces elegans* (blue-tailed skink; Du and Ji, 2001), whereas selection acting on reproductive output is the main cause for increased female size in *Sphenomorphus indicus* (brown forest skink; Ji and Du, 2000) and *Phrynocephalus vlangalii* (Zhang et al., 2005). Less pronounced male–male competition as well as less pronounced physical constraints from maternal body size on reproductive output explains why adults are monomorphic in *C. versicolor* (Ji et al., 2002a), *Eremias multiocellata* (multi-ocellated racerunner; Li et al., 2006), *Eremias brenchleyi* (Xu and Ji, 2003), and *Takydromus septentrionalis* (Zhang and Ji, 2000).

The pattern of SSD in *H. bowringii* is opposite to that reported for *Gekko japonicus* (Japanese gecko; Ji et al., 1991). The two species differ in three important aspects: (1) RCM is greater in *G. japonicus* (>0.28; Ji et al., 1991) than in *H. bowringii* (0.24; Table 2); (2) female SVL explains a substantial proportion of variation in clutch mass (reproductive output) in *G. japonicus* (43.3%; Ji et al., 1991) but not at all in *H. bowringii*; and (3) RCM is negatively correlated with female SVL in *H. bowringii* but not in *G. japonicus* (Ji et al., 1991). What can be inferred from these differences is that the selective pressure leading to increased female size is comparatively low in *H. bowringii*.

Female *H. bowringii* were previously reported to lay a single clutch of eggs per breeding season (Zhou and Liu, 1999; Zhang et al., 2000). Our data show that the species is unlikely to be one of the single-clutched lizards for two reasons. First, the breeding season (from May to August) is long enough for females laying eggs early in the breeding season to prepare the next clutch. Second, if females do lay a single clutch of eggs per season, why do many females (large ones in particular) lay eggs so late in the season? In lizards, larger females often lay eggs earlier than smaller ones. Accordingly, female *H. bowringii* laying eggs early in the breeding season should be on average larger than those laying eggs later in the season if they lay only one clutch of eggs per season. In our sample, however, neither the range nor the mean of SVLs differs between females producing earlier and later clutches (Table 2). The lack of seasonal shifts in maternal size indicates that female *H. bowringii* have the potential to lay more than one clutch per season.

Thermal environments experienced by *H. bowringii* eggs affect incubation length as well as morphological and locomotor phenotypes of hatchlings. Hatchlings from eggs incubated at 30 °C were larger and performed much better in the racetrack than those from eggs incubated at 24 °C (Fig. 3). HL relative to egg mass was greater in hatchlings incubated at 30 °C (Table 4), but the trait did not differ between the two temperature treatments when the influence of variation in hatchling SVL was removed (ANCOVA, $F_{1,\ 27} = 0.30$, $P = 0.586$). Therefore, the greater HL of hatchlings incubated at 30 °C is primarily attributed to greater SVL. In contrast, TL was greater in hatchlings incubated at 30 °C even when the influence of variation in hatchling SVL was removed (ANCOVA, $F_{1,\ 27} = 61.40$, $P < 0.0001$).

The mean incubation length is shortened by 35.4 days at 30 °C compared to 24 °C in *H. bowringii*. Thus, the ecological advantages, such as increased growth period prior to the first winter, decreased chance of microbial contamination and decreased mechanical damage due to the decreased incubation length for eggs incubated at the higher temperature, can be very significant in the species. Because the incubation temperature of 24 °C has noticeable adverse effects on morphological and locomotor phenotypes of hatchlings, we conclude that the low limit of temperatures suitable for incubation of *H. bowringii* eggs should be higher than 24 °C. Temperatures suitable for embryonic development differ among lizards using different habitats (Lu et al., 2006). As in other lizards living in relatively warm habitats (Ji and Zhang, 2001; Ji et al., 2002b; Du et al., 2003), temperatures suitable for embryonic development are relatively high in *H. bowringii*, primarily as a consequence of the adaptive response to warm environments in southern China.

Acknowledgements

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