

Differences in body size and female reproductive traits between two sympatric geckos, *Gekko japonicus* and *Gekko hokouensis*

Yong-Pu ZHANG^{1,2}, Wei-Guo DU^{1*} and Lin-Jun ZHU¹

¹ Hangzhou Key Laboratory for Animal Science and Technology, Hangzhou Normal University, 310036 Hangzhou, Zhejiang, People's Republic of China; *e-mail: dwghz@126.com

² College of Life and Environmental Sciences, Wenzhou University, 325027 Wenzhou, Zhejiang, People's Republic of China

Received 8 October 2008; Accepted 18 December 2008

A b s t r a c t. We determined the differences in body size and female reproductive traits between two closely-related species of Asian geckos, *Gekko japonicus* and *G. hokouensis*. Snout-vent length and body mass of adults were greater in *G. japonicus* than *G. hokouensis*, and in both species, females were larger than males. Relative head size (length and width) did not show between-species divergence, but was larger in males than in females. Female *G. japonicus* was larger, and laid eggs earlier in the reproductive season than *G. hokouensis*. Both species produced an invariant clutch size of two eggs in our samples, but other reproductive traits such as egg size, clutch mass and relative clutch mass differed significantly between the species. *G. japonicus* produced larger eggs and, had greater clutch mass and relative clutch mass than did *G. hokouensis*. This inter-specific divergence in reproductive traits was partly attributable to the difference in maternal body size, but also stemmed from some other intrinsic factors such as genetic differences and maternal effects.

Key words: gecko body size, reproductive trait, inter-specific divergence

Introduction

Inter-specific comparison is a powerful method to elucidate the evolution of life histories, and has been used in many studies involving a variety of lineages (Dunham et al. 1988, Shine & Schwarzkopf 1992, Stearns 1992). Comparative studies indicate widespread variations in life-history traits among species, such as body size at maturity, the number and size of eggs (offspring), growth rates and longevity (Stearns 1992, Shine 2005). The inter-specific variations in life histories can be caused by genetic determinants (Dunham et al. 1988, Stearns 1992) as well as ecological factors such as climate and food availability (Madsen & Shine 2000, Du et al. 2005b, Du 2006). Given the significant effects of environmental factors on life histories, comparative studies need to be carefully designed and conducted to avoid the background noise arising from environmental differences. For example, common garden experiments in which different species are kept in a common environment to minimize the environment-induced differences have been used to eliminate this kind of noise (Aday et al. 2003, Du et al. 2005b). Accordingly, the differences in life histories detected in a common garden experiment would largely reflect intrinsic (e.g. genetic variation and maternal effect) differences among species rather than environmental effects.

Reproductive traits may affect population dynamics and sustainability, and thus lie at the core of life-history studies (Stearns 1992, Shine 2005). An extensive literature

*Corresponding author

on life-history evolution recognizes that maternal body size accounts for a large quantity of variation in reproductive traits, but the relationship between reproductive traits and maternal body size may differ considerably both within and among species. For instance, clutch size is more closely related to body size and more variable than egg size for most reptilian species (Shine & Seigel 1996, Du et al. 2005b, Shine 2005). However, in some particular lineages such as anoles and geckos, clutch size is consistently one or two, and thus egg size is obviously more variable than clutch size (Shine & Greer 1991). Therefore, it is reasonable to assume that the invariant-clutch-size species would adopt different reproductive strategies from their counterparts with variable clutch size. Surprisingly, detailed data on reproductive traits and strategies in invariant-clutch-size species is scarce, and only recently has scientific attention on these species increased (Kratovichil & Frynta 2006, Kratovichil & Kubicka 2007).

Gekko japonicus and *G. hokouensis* are mainly distributed in eastern China and Japan, and occur sympatrically or even syntopically in some regions (Zhou et al. 1982, Ota et al. 1989). Pope (1928) named a specimen from Jiangxi, China as a subspecies called *G. japonicus hokouensis*, which was morphologically different from *G. japonicus*. Zhou et al. (1982) updated this classification and named *G. japonicus hokouensis* as a species of *Gekko hokouensis*. Recently, further biochemical and molecular evidence confirmed that *G. hokouensis* is an independent species (Shen et al. 1996, Toda et al. 2000, Han et al. 2001). The classification has been the main focus of studies concerning these two species for decades, but comparisons on other interesting topics such as life history, which would yield insight into the divergence of the species (Schlichting 2004), is rather limited. Body size and female reproductive output have been reported in *G. japonicus* from mainland China and in *G. hokouensis* from Ryukyu Archipelago and Taiwan (Ota et al. 1988, Ji et al. 1991, Xu & Ji 2001, Okada et al. 2002), but as yet no comparative data on life-history traits of sympatric populations of the two species has been recorded.

In this study, we collected quantitative data on body size and conducted a common garden experiment to determine reproductive life-histories in *G. japonicus* and *G. hokouensis* from Zhejiang, eastern China. Here we present a detailed inter-specific comparison of reproductive life-histories, and provide new evidence to support the ecological divergence of these two species, in addition to the genetic differences reported previously (Han et al. 2001).

Materials and Methods

G. japonicus and *G. hokouensis* are small nocturnal geckos, mainly inhabit houses or shacks in human habitations. Females lay 1–2 clutches of 2 eggs in May to August (Zhao et al. 1999). In late April 2006, we captured non-gravid females and adult males of *Gekko japonicus* and *G. hokouensis* by hand or noose from Yueqing county, Wenzhou city of eastern China, and transferred them to our laboratory at Hangzhou Normal University. Immediately after they arrived, the geckos were measured snout-vent length (SVL), head length (distance between the snout and the anterior edge of the tympanum), head width (posterior end of the mandible), and axilla-groin distance (distance between fore limb and hind limb) using a digital caliper (± 0.01 mm) and weighed body mass (BM) using a Mettler balance (± 0.001 g). In the laboratory, the animals were housed in mesh cages ($60 \times 15 \times 20$ cm³), the bottom of which was lined with several folds of paper to supply shelters for geckos. Each cage contained 5–6

females and 3–4 males, and was kept in a room with a constant temperature of 23 ± 1 °C and a light cycle of 12L:12D (0630 on and 1830 off). A heat source was provided underneath the cages between 0800 and 1600 hours to provide a thermal gradient from 23 °C to 40 °C, which enabled the geckos to regulate their body temperatures voluntarily. Food (larvae of *Tenebrio molitor*) and water (containing mixed vitamins and minerals) were provided *ad libitum*.

Female gravidity was visually determined through the semi-transparent abdomen of geckos. Females with large oviductal eggs were moved to individual plastic cages lined with paper, where they remained until oviposition. Each cage was checked twice per day for freshly-laid eggs. The eggs were weighed (± 0.001 g) and their total combined mass was recorded as clutch mass, and mean egg mass was calculated by dividing clutch mass with clutch size. The length and width of each egg was measured using the digital caliper (± 0.01 mm). After laying eggs, females were returned to their original location of collection in early August.

Relative clutch mass (RCM) was calculated as the ratio of clutch mass to maternal post-laying mass (Shine 1992). The normality of data and the homogeneity of variances were tested using the Kolmogorov–Smirnov test and Bartlett’s test, respectively. We used two-way ANOVA to detect the inter-specific and between-sex difference in snout-vent length and body mass. To compare the differences in relative head length and width, we employed a two-way ANCOVA with snout-vent length as the covariate. For reproductive traits, we used a Mann-Whitney U test to compare the inter-specific difference in female oviposition date, and t-tests to detect the inter-specific differences in maternal SVL and body mass. Inter-specific differences in egg size and clutch mass were evaluated with ANCOVAs, in which female SVL was used as the covariate. An ANCOVA on clutch mass using maternal body mass as the covariate was conducted to compare RCMs between the two species. We also used an ANCOVA on egg width with egg length as the covariate to compare egg shape.

Results

Difference in adult morphology

Snout-vent length and body mass showed significant differences between the species as well as the sexes (Table 1). *G. japonicus* was larger and heavier than *G. hokouensis*, and in both species, females were larger than males (Fig. 1a,b). *G. japonicus* also had a longer tail than *G. hokouensis* (Fig. 1c). When SVL was controlled using ANCOVAs, head length and width did not differ between species, but differed significantly between males and females (Table 1), with larger head size in males than in females in both species (Fig. 2a,b). For abdomen length, however, neither inter-specific or between-sex differences were found (Table 1, Fig. 2c).

Difference in female reproductive traits

Median oviposition date of *G. japonicus* females was significantly earlier than that of *G. hokouensis* females (2 June vs 4 July; Mann-Whitney U test $Z = -2.95$, $P < 0.01$). The minimum SVL of reproductive females in our samples were 61.5 mm for *G. japonicus* and 57.5 mm for *G. hokouensis*, and overall reproductive females were larger in *G. japonicus* than in *G. hokouensis* in terms of mean SVL and body mass (Table 2).

Both species produced two rigid-shelled eggs in each clutch, but other traits with regard to reproductive output exhibited considerable inter specific differences. *G. japonicus*

Table 1. The results of two-way ANOVA and ANCOVA analyses on inter-specific and between-sex differences on morphology in geckos. A two-way ANOVA was applied to snout-vent length and body mass. A two-way ANCOVA with snout-vent length as the covariate was used for analyzing head length and width. Significant results are shown in bold. The analysis of homogeneity-of-slope indicated that the continuous predictor variable (SVL) did not have different effects on independence variables (head length and width) between the two populations (all $P > 0.22$).

	Species	Sex	Interaction
Snout-vent length	$F_{1,71} = \mathbf{22.59}$ $P < \mathbf{0.0001}$	$F_{1,71} = \mathbf{20.44}$ $P < \mathbf{0.0001}$	$F_{1,71} = 1.38$ $P = 0.24$
Body mass	$F_{1,71} = \mathbf{30.22}$ $P < \mathbf{0.00001}$	$F_{1,71} = \mathbf{11.13}$ $P < \mathbf{0.01}$	$F_{1,71} = 3.22$ $P = 0.08$
Relative head length	$F_{1,70} = 2.98$ $P = 0.09$	$F_{1,70} = \mathbf{7.87}$ $P < \mathbf{0.01}$	$F_{1,70} = 0.66$ $P = 0.42$
Relative head width	$F_{1,70} = 0.00005$ $P = 0.99$	$F_{1,70} = \mathbf{6.83}$ $P = \mathbf{0.01}$	$F_{1,70} = 0.006$ $P = 0.94$
Axilla-groin distance	$F_{1,70} = 0.51$ $P = 0.48$	$F_{1,70} = 1.57$ $P = 0.21$	$F_{1,70} = 0.10$ $P = 0.76$

produced larger eggs (egg mass and size) and, had greater clutch mass and RCM than did *G. hokouensis*. These between-species differences were still evident even after the effect of female size (SVL) had been statistically removed using ANCOVAs (Table 2). In these

Table 2. Maternal size and reproductive output in *Gekko japonicus* and *G. hokouensis*. Inter-specific differences in body size and mass were analyzed using Student's *t*-tests, and data on these two traits are indicated as mean \pm standard error. An analysis of covariance was used to compare the between-species differences in reproductive traits with maternal SVL as the covariate. Data are expressed as adjusted mean \pm standard error. An ANCOVA on clutch mass with maternal body mass as the covariate was conducted to test the between-species difference in relative clutch mass. Significant results are shown in bold. The analysis of homogeneity-of-slope indicated that the continuous predictor variable (SVL or body mass) did not have different effects on independence variables (reproductive traits) between the two populations (all $P > 0.22$).

	<i>Gekko japonicus</i>	<i>Gekko hokouensis</i>	
Sample size	21	16	
Snout-vent length (mm)	65.73 \pm 0.89	62.78 \pm 0.61	$t = \mathbf{2.57}$ $df = \mathbf{35}$ $P = \mathbf{0.01}$
Body mass (g)	4.66 \pm 0.26	3.85 \pm 0.17	$t = \mathbf{2.45}$ $df = \mathbf{35}$ $P = \mathbf{0.02}$
Clutch size	2	2	-
Egg mass (g)	0.621 \pm 0.021	0.497 \pm 0.024	$F_{1,34} = \mathbf{13.69}$, $P < \mathbf{0.001}$
Egg length (mm)	13.28 \pm 0.18	12.60 \pm 0.20	$F_{1,34} = \mathbf{6.07}$, $P = \mathbf{0.02}$
Egg width (mm)	9.52 \pm 0.12	8.70 \pm 0.14	$F_{1,34} = \mathbf{18.60}$, $P < \mathbf{0.001}$
Clutch mass (g)	1.241 \pm 0.042	0.993 \pm 0.048	$F_{1,34} = \mathbf{13.70}$, $P < \mathbf{0.001}$
Relative clutch mass	0.283 \pm 0.014	0.256 \pm 0.011	$F_{1,34} = \mathbf{13.45}$, $P < \mathbf{0.001}$

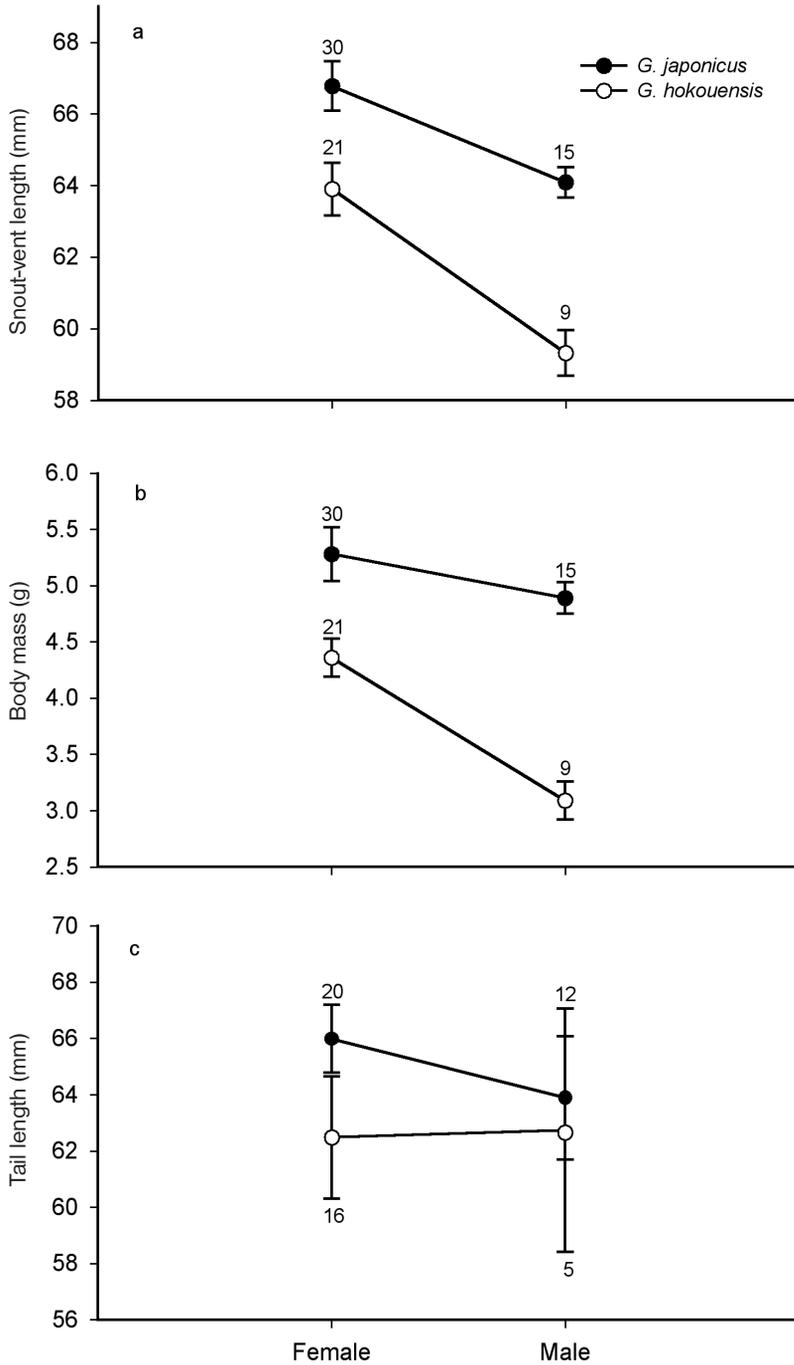


Fig. 1. Snout-vent length (a), body mass (b), and tail length (c) of adult females and males in *Gekko japonicus* and *G. hokouensis*. Graphs show mean values and associated standard errors. Numbers above or below the error bars in the graphs are sample sizes. See Table 1 for statistical details.

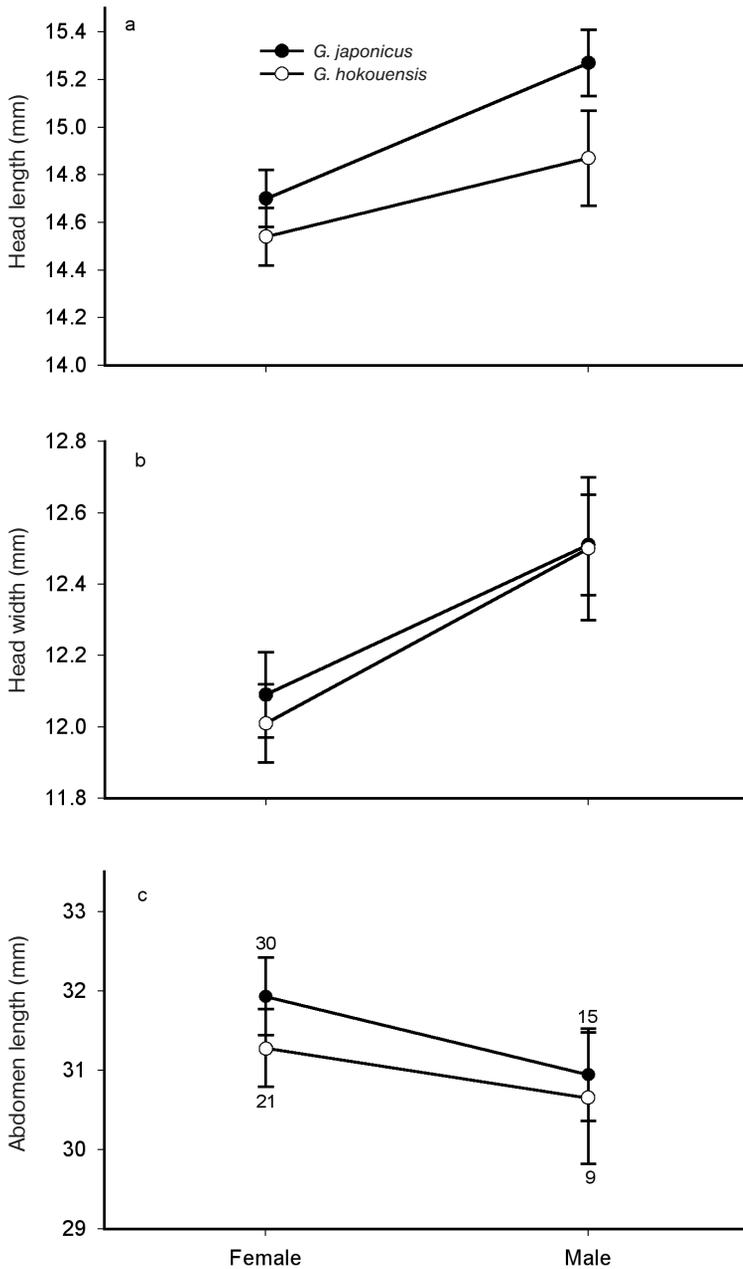


Fig. 2. Head size (a, b), and abdomen length (c) of adult females and males in *Gekko japonicus* and *G. hokouensis*. Graphs show adjusted mean values and associated standard errors. Numbers above or below error bars in the lower graph are sample sizes, and apply to the upper graphs within this Figure. See Table 1 for statistical details.

two species, egg length (EL) was positively correlated with egg width (EW) ($R = 0.814$, $t_{21} = 6.43$, $P < 0.00001$). Egg shape did not differ significantly between the two species (the homogeneity of slope: $F_{1,19} = 0.73$, $P = 0.40$; main effect: $F_{1,34} = 2.91$, $P > 0.05$).

Discussion

This study indicates that *G. japonicus* and *G. hokouensis* differ significantly in a wide range of life-history traits, including adult body size, egg mass, clutch mass and relative clutch mass. In addition to the genetic difference revealed by a previous study (H a n et al. 2001), these results provide new evidence on the ecological divergence of these two species: (1) *G. japonicus* is larger in body size, and produces larger eggs than *G. hokouensis*; and (2) *G. japonicus* invests more reproductive effort than *G. hokouensis* in terms of RCMs.

Body size is not only determined by genetic component, but also significantly affected by environmental factors such as food availability and inter-specific competition (B o b a c k 2003, S e a r s & A n g i l l e t t a 2004). The mean SVL of *G. japonicus* may differ among populations in mainland China and Japan, ranging from 62 to 66 mm (J i et al. 1991, X u & J i 2001, I k e u c h i 2004). Similarly, *G. hokouensis* also differ in body size among populations, with larger SVL in mainland population (62.8 mm, this study) than island populations from Ryukyu Archipelago and Taiwan (less than 58 mm) (O t a et al. 1988, O k a d a et al. 2002). These results suggest that (1) the difference in body size between species not only happens to sympatric populations as in our study, but also exists among allopatric populations, and therefore (2) the body size difference is not likely a simple result of competition between the sympatric populations of these two species.

The between-species difference in egg size is partly attributable to maternal body size, given the positive relationship between maternal body size and egg size. This phenomenon has been reported in another population of *G. japonicus* (X u & J i 2001) as well as numerous other lizard species (S h i n e 1992, K r a t o c h v í l & K u b i č k a 2007). Nonetheless, maternal body size variation cannot entirely account for between-species difference in egg size, because such differences were still evident even after the effect of maternal body size had been removed using statistical methods. The between-species difference in relative clutch mass provides further evidence that additional factors other than female body size may account for the variation in reproductive output. In our experiment, the collected female geckos were non-gravid and laid eggs one month later. The between-species difference in reproductive output arising from environmental differences (e.g. temperature, food availability) should have been largely reduced owing to this common garden method. Therefore, other than female body size, additional factors that may cause inter-specific differences in life histories would likely be genetic and/or maternal effects. Of course, we cannot exclusively attribute the inter-specific differences to intrinsic factors, as it is virtually impossible to completely eliminate environmental influence on reproductive traits. For example, female reproduction may be affected by previous life experience such as changes in food availability and thus levels of energy storage (J i & W a n g 1990, D o u g h t y & S h i n e 1998). However, in multiple-clutch species such as the geckos in this study (X u & J i 2001, O k a d a et al. 2002), food availability and energy storage are more likely to affect clutch frequency rather than reproductive traits such as egg size and clutch mass (D u 2006).

Like most other geckos, *G. japonicus* and *G. hokouensis* both typically produce invariant clutches of two eggs. The reproductive output of *G. japonicus* in our population is similar to that of Hangzhou population reported by X u & J i (2001) in terms of egg size and relative clutch mass. The difference in egg size corresponding to differences in maternal body size in these two species is consistent with the conclusion drawn by an allometric analysis that egg size is positively related to female body size in geckos (K r a t o c h v í l & K u b i č k a 2007).

Relative clutch mass, a body-size independent parameter of reproductive output, has been widely used in inter- and intra-specific comparisons on life histories of reptiles (Williams 1966, Vitt & Congdon 1978, Dunham et al. 1988, Shine 1992, Angilletta et al. 2001). Relative clutch mass is regarded as an indicator of reproductive investment, and differs between species (Vitt & Congdon 1978). For example, lizards have lower RCMs than do snakes (Seigel & Fitch 1984, Shine 1992), and RCMs are lower in “wide-foraging” lizards than in “sit-and-wait” lizards (Vitt & Congdon 1978). *G. japonicus* is a “sit-and-wait” species, whereas *G. hokouensis* adopts an intermediate strategy between “sit-and-wait” and “wide-foraging” (Werner et al. 1997). Our finding that *G. japonicus* has a larger RCM than *G. hokouensis* fits well with the RCM-foraging mode hypothesis mentioned above. RCMs are lower in lizards with invariant clutch size such as geckos and anoles than in species with a variable clutch size (Shine 1992). Compared with the geckos reported by Shine (1992), however, our species have much higher RCMs (Means: 0.276 vs 0.11). High RCMs are not unusual; some other species from different lineages of geckos have high RCMs too, for example, *Hemidactylus bowringii* (0.24; Xu & Ji 2007), *Oedura lesueurii* (0.320) (Dougherty 1997), and *Gehyra dubia* (0.214; Dougherty 1996). Thus, species with low and invariant clutch size such as gekkonid lizards may not necessarily have low RCMs, because some geckos can increase their clutch mass proportionally to female size by enlarging egg size (Kračhvíl & Kubíčka 2007).

Both *G. japonicus* and *G. hokouensis* show sexual dimorphism in body and head sizes, which is rather common in geckos as well as other lizards (Du & Ji 2001, Olsson et al. 2002, Xu & Ji 2007). In these two species, females are larger than males and, adult males have larger heads than females (Figs 1, 2). This pattern of sexual size dimorphism is consistent among populations of these species (Ji et al. 1991, Okada et al. 2002), and has also been reported in some but not all geckos (How et al. 1986, Dougherty & Shine 1995, but see Xu & Ji 2007). The larger body size in adult females could be a result of delayed maturation (How et al. 1986), but this is not the case in *G. hokouensis* as suggested by a mark and recapture study (Okada et al. 2002). An alternative explanation is fecundity selection that favors larger female body size (Olsson et al. 2002, Du et al. 2005a). The positive relationship between female body size and clutch mass in *G. japonicus* provides a support to this explanation (Xu & Ji 2001). Sexual dimorphism in head size may arise due to between-species difference in growth rate of head; for example, some lizards show faster head growth in males (Zhang & Ji 2000, Du & Ji 2001). Larger heads might be advantageous for males in male-male competition, copulation or predation (Via & Stewart 1989, Webb & Shine 1994).

Acknowledgements

We thank Lin-Jun Zhu, Hua-Yu Hu for their assistance in the laboratory and field, and Hidetoshi Ota, Melanie Elphick and anonymous reviewers for their suggestive comments on the manuscript. This work was supported by a grant from the local government of Zhejiang Province for the Key Discipline of Zoology.

LITERATURE

Aday D.D., Wahl D.H. & Philipp D.P. 2003: Assessing population-specific and environmental influences on bluegill life histories: A common garden approach. *Ecology* 84: 3370–3375.

- Angilletta M.J., Sears M.W. & Winters R.S. 2001: Seasonal variation in reproductive effort and its effect on offspring size in the lizard, *Sceloporus undulatus*. *Herpetologica* 5: 365–375.
- Boback S.M. 2003: Body size evolution in snakes: Evidence from island population. *Copeia* 2003: 81–94.
- Doughty P. 1996: Allometry of reproduction in two species of gekkonid lizards (*Gehyra*): Effects of body size miniaturization on clutch and egg sizes. *J. Zool.* 240: 703–715.
- Doughty P. 1997: The effects of “fixed” clutch sizes on lizard life-histories: Reproduction in the Australian velvet gecko, *Oedura lesueurii*. *J. Herpetol.* 31: 266–272.
- Doughty P. & Shine R. 1995: Life in 2 dimensions: Natural history of the southern leaf-tailed gecko, *Phyllurus platurus*. *Herpetologica* 51: 193–201.
- Doughty P. & Shine R. 1998: Reproductive energy allocation and long-term energy stores in a viviparous lizard (*Eulamprus tympanum*). *Ecology* 79: 1073–1083.
- Du W.G. 2006: Phenotypic plasticity in reproductive traits induced by food availability in a lacertid lizard, *Takydromus septentrionalis*. *Oikos* 112: 363–369.
- Du W.G. & Ji X. 2001: Growth, sexual size dimorphism and female reproductive of blue-tailed skinks, *Eumeces elegans*. *Zool Res.* 22: 279–286.
- Du W.G., Ji X. & Shine R. 2005a: Does body-volume constrain reproductive output in lizards? *Biol Lett.* 1: 98–100.
- Du W.G., Ji X., Zhang Y.P., Xu X.F. & Shine R. 2005b: Identifying sources of variation in reproductive and life-history traits among five populations of a Chinese lizard (*Takydromus septentrionalis*, Lacertidae). *Biol. J. Linn. Soc.* 85: 443–453.
- Dunham A.E., Miles D.B. & Reznick D.N. 1988: Life history patterns in squamate reptiles. In: Gans C. & Huey R.B. (eds), *Biology of the Reptilia. A.R. Liss, New York*: 441–522.
- Han D.M., Zhou K.Y. & Wang Y.Q. 2001: Phylogeny of the species of Chinese Gekkonid lizards (Gekkonidae: Lacertilia) inferred from 12SrDNA DNA sequences. *Acta Zool. Sin.* 47: 139–144.
- How R.A., Dell J. & Wellington B.D. 1986: Comparative biology of eight species of *Diplodactylus* gecko in western Australia. *Herpetologica* 42: 471–482.
- Ikeuchi I. 2004: Male and female reproductive cycles of the Japanese gecko, *Gekko japonicus*, in Kyoto, Japan. *J. Herpetol.* 38: 269–274.
- Ji X. & Wang P.C. 1990: Annual cycles of lipid contents and caloric values of carcass and some organs of the gecko, *Gekko japonicus*. *Comp. Biochem. Physiol. A.* 96: 267–271.
- Ji X., Wang P.C. & Hong W.X. 1991: The reproductive ecology of the gecko, *Gekko japonicus*. *Acta Zool. Sin.* 37: 185–192.
- Kratochvíl L. & Frynta D. 2006: Egg shape and size allometry in geckos (Squamata : Gekkota), lizards with contrasting eggshell structure: why lay spherical eggs? *J. Zool. Syst. Evol. Res.* 44: 217–222.
- Kratochvíl L. & Kubička L. 2007: Why reduce clutch size to one or two eggs? Reproductive allometries reveal different evolutionary causes of invariant clutch size in lizards. *Func. Ecol.* 21: 171–177.
- Madsen T. & Shine R. 2000: Silver spoons and snake body sizes: prey availability early in life influences long-term growth rates of free-ranging pythons. *J. Anim. Ecol.* 69: 952–958.
- Okada S., Izawa M. & Ota H. 2002: Growth and reproduction of *Gekko hokouensis* (Reptilia: Squamata) on Okinawajima Island of the Ryukyu Archipelago, Japan. *J. Herpetol.* 36: 473–479.
- Olsson M., Shine R., Wapstra E., Ujvari B. & Madsen T. 2002: Sexual dimorphism in lizard body shape: The roles of sexual selection and fecundity selection. *Evolution* 56: 1538–1542.
- Ota H., Crombie R.I., Lue K.-Y. & Chen S.-H. 1988: A record of *Gekko hokouensis* (Reptilia: Sauria) from Lanyu Island, Taiwan, with notes on its variation. *J. Taiwan Mus.* 41: 7–14.
- Ota H., Lue K.-Y., Chen S.-H. & Brown W.C. 1989: Taxonomic status of the Taiwanese gekko, with comments on the synonymy of *Luperosaurus amissus* Taylor. *J. Herpetol.* 23: 76–78.
- Pope C.H. 1928: Four new snakes and a new lizard from south China. *Am. Mus. Nov.* 325: 1–4.
- Schlichting C.D. 2004: The role of phenotypic plasticity in diversification. In: DeWitt T.J. & Scheiner S.M. (eds), *Phenotypic plasticity: Functional and conceptual approaches. Oxford University Press, Oxford*: 191–200.
- Sears M.W. & Angilletta M.J. 2004: Body size clines in *Sceloporus* lizards: Proximate mechanisms and demographic constraints. *Integrative and Comparative Biology* 44: 433–442.
- Seigel R.A. & Fitch H.S. 1984: Ecological patterns of relative clutch mass in snakes. *Oecologia* 61: 293–301.
- Shen J.W., Lu P.H. & Chen Y.F. 1996: The comparative study on LDH isozymes of six tissues of three species of *Gekko*. *J. Nanjing Norm. Univ. (N.S.)*. 19: 45–47.
- Shine R. 1992: Relative clutch mass and body shape in lizards and snakes: Is reproductive investment constrained or optimized. *Evolution* 46: 828–833.

- Shine R. 2005: Life-history evolution in reptiles. *Ann. Rev. Ecol. Evol. Syst.* 36: 23–46.
- Shine R. & Greer A.E. 1991: Why are clutch sizes more variable in some species than in others. *Evolution* 45: 1696–1706.
- Shine R. & Schwarzkopf L. 1992: The evolution of reproductive effort in lizards and snakes. *Evolution* 46: 62–75.
- Shine R. & Seigel R.A. 1996: A neglected life-history trait: Clutch-size variance in snakes. *J. Zool.* 239: 209–223.
- Stearns S.C. 1992: The evolution of life histories. *Oxford University Press, Oxford.*
- Toda M., T. H. & Ota H. 2000: Discovery of sympatric cryptic species within *Gekko hokouensis* (Gekkonidae: Squamata) from the Okinawa Islands, Japan, by use of allozyme data. *Zool. Scrip.* 30: 1–11.
- Via L. & Stewart J.R. 1989: The manifestation and significance of sexual dimorphism in anguid lizards: a case study of *Barisia monticola*. *Can. J. Zool.* 67: 68–72.
- Vitt L.J. & Congdon J.D. 1978: Body shape, reproductive effort, and relative clutch mass in lizards: resolution of a paradox. *Am. Nat.* 112: 595–608.
- Webb J.K. & Shine R. 1994: Feeding habits and reproductive biology of Australian pygopodid lizards of the genus *Aprasia*. *Copeia* 1994: 390–398.
- Werner Y.L., Okada S., Ota H., Perry G. & Tokunaga S. 1997: Varied and fluctuating foraging modes in nocturnal lizards of the family Gekkonidae. *Asiatic Herpetol. Res.* 7: 153–165.
- Williams G.C. 1966: Adaptation and Natural Selection. *Princeton Monographs, Princeton.*
- Xu D.D. & Ji X. 2007: Sexual dimorphism, female reproduction and egg incubation in the oriental leaf-toed gecko (*Hemidactylus bowringii*) from southern China. *Zoology* 110: 20–27.
- Xu X.F. & Ji X. 2001: Female reproduction and influence of incubation temperature on duration of incubation and hatching traits in the gecko, *Gekko japonicus*. *Chin. J. Ecol.* 29: 8–11.
- Zhang Y.-P. & Ji X. 2000: Ontogenetic changes of sexual dimorphism in head size and food habit in grass lizard, *Takydromus septentrionalis*. *Zool. Res.* 21: 181–186.
- Zhao E.M., Zhao K.T. & Zhou K.Y. 1999: Fauna Sinica Reptilia Vol. 2 Squamata. *Chinese Science Press, Beijing.*
- Zhou K.Y., Liu Y.Z. & Li D.J. 1982: Three new species of *Gekko* and remarks on *Gekko hokouensis* (Lacertiformes, Gekkonidae). *Acta Zootax. Sin.* 7: 438–446.