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Sexual Dimorphism and Female Reproductive Characteristics in the Oriental Garden Lizard, *Calotes versicolor*, from Hainan, Southern China

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ABSTRACT.—Males and females of the oriental garden lizard (*Calotes versicolor*) from a population in Hainan, southern China, differed in head size at hatching: males had larger heads than females. This dimorphism was slightly more pronounced in adults than in hatchlings. Hatchlings had larger heads but shorter tails relative to snout-vent length (SVL) than subadults and adults. When SVL was held constant, tail length of subadults and adults of the same sex was similar. Adult lizards were not sexually dimorphic in body size (SVL), but males possessed longer tails than females at the same SVL throughout their size range. The smallest and largest reproductive females in our sample were 78.9 and 103.8 mm SVL, respectively. Females in our laboratory (Hangzhou, eastern China) laid multiple clutches from April to June. Clutch size, clutch mass, and egg mass varied from 3 to 14 (mean = 9.0) eggs, 1.58 to 6.47 (mean = 4.65) g, and 0.45 to 0.61 (mean = 0.52) g, respectively. Clutch size and clutch mass were both positively correlated with female SVL. Egg mass was not correlated with female SVL even when clutch size was held constant using a partial correlation analysis. Clutch size was not correlated with female condition when female SVL was held constant. Egg length, egg width, and clutch size were not correlated with each other when the remaining variable was held constant. Egg mass was not correlated with clutch size when female SVL was kept constant. Larger-sized *C. versicolor* females increased reproductive output primarily through production of more eggs (and hence heavier clutches).

Agamid lizards of the genus *Calotes* occur throughout the Oriental region and the Sunda Islands (Malayan Peninsula, and the islands of Sumatra, Borneo, Palawan, and Java). Of some 20 species represented in the genus, the oriental garden lizard *Calotes versicolor* is the most widespread, ranging from southeastern Iran to Afghanistan and Nepal, India to Sri Lanka, Burma to Indochina, southern China to Peninsular Malaysia and Sumatra (Boulenger, 1912; Smith, 1935; Erdelen, 1986; Zhao and Adler, 1993). *Calotes versicolor* is a fascinating arboreal lizard with brilliant male breeding coloration, ability to change that coloration, and capacity to adapt to environments altered by human activities. The lizard is thought to be extremely successful in some parts of its range, such as Singapore Island, where the introduced *C. versicolor* has to some extent displaced a native agamid lizard, the green crested lizard *Bronchocela cristatella* (Diong et al., 1994). Despite its wide geographic distribution and the fact that it is taxonomically and zoogeographically well known (e.g., Pope, 1935; Smith, 1935; Moody, 1980; Erdelen, 1986; Zhao and Adler, 1993; Diong and Lim, 1998), the biology and ecology of *C. versicolor* in east

Asia remain poorly studied. Several investigators have conducted studies on female reproduction, but they only presented descriptive data (e.g., Asana, 1931; Iyer, 1942; Minton, 1966; Pandha and Thapliyal, 1967; Indurkar and Sabnis, 1977; Erdelen, 1986; Diong et al., 1994). Geographical variation in clutch size, timing of reproduction, and length of breeding season have been noted (Erdelen, 1986); however, no detailed data exist on egg size for any studied population. Consequently, life-history traits such as the relationships among egg size, clutch size, and female size are unclear in this species. Almost no data are available on *C. versicolor* found in Hainan, southern China, where it is one of the most conspicuous lizard species.

This paper provides data on sexual dimorphism and female reproductive characteristics gathered from a population of *C. versicolor* in Tongshi (18°47'N, 109°30'E), Hainan. We pay particular attention to (1) ontogenetic changes in ecologically important morphological characters such as tail length, head length, and head width; (2) sexual dimorphism in these characters; and (3) the relationships among egg size, clutch size, and female size.

MATERIALS AND METHODS

Lizards were collected by hand or noose from March to May 1999. The annual average tem-

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TABLE 1. Mean \pm SE of morphometric traits of *Calotes versicolor*. Range in parentheses, and N = number of lizards measured. All length units are in millimeters and mass units in grams.

Group	N	Snout-vent length	Body mass	Tail length	Head size		Relative head size (%)	
					Head length	Head width	HL/SVL	HW/SVL
Hatchling females	33	24.6 \pm 0.2 (22.3–27.1)	0.57 \pm 0.01 (0.42–0.78)	44.9 \pm 1.0 (36.0–59.5)	7.1 \pm 0.05 (6.6–7.9)	5.5 \pm 0.04 (5.0–5.9)	28.7 \pm 0.2 (26.2–31.2)	22.5 \pm 0.2 (21.2–24.6)
Hatchling males	40	24.0 \pm 0.2 (19.4–27.1)	0.58 \pm 0.01 (0.40–0.84)	46.2 \pm 1.0 (32.8–59.5)	7.1 \pm 0.07 (5.9–7.9)	5.6 \pm 0.04 (4.9–6.1)	29.5 \pm 0.1 (28.1–31.6)	23.2 \pm 0.2 (21.4–26.2)
Subadult females	14	69.6 \pm 2.0 (53.4–77.8)	5.8 \pm 0.5 (2.7–7.5)	207.0 \pm 8.0 (143.5–239.0)	16.2 \pm 0.4 (13.0–17.7)	11.1 \pm 0.3 (8.8–12.4)	23.3 \pm 0.2 (22.3–24.6)	16.0 \pm 0.2 (14.9–17.3)
Subadult males	16	75.6 \pm 0.7 (69.1–78.4)	7.8 \pm 0.4 (4.8–9.9)	232.1 \pm 3.3 (206.0–254.0)	17.3 \pm 0.2 (15.2–18.8)	11.8 \pm 0.2 (10.1–12.4)	22.9 \pm 0.2 (21.9–24.3)	15.6 \pm 0.2 (14.5–16.4)
Adult females	76	89.8 \pm 0.8 (78.9–103.8)	15.1 \pm 0.6 (7.7–25.9)	259.1 \pm 2.4 (217.0–303.0)	19.6 \pm 0.2 (17.7–22.7)	13.9 \pm 0.1 (12.1–16.9)	21.9 \pm 0.08 (20.4–23.9)	15.5 \pm 0.07 (14.4–16.9)
Adult males	117	90.1 \pm 0.5 (79.1–104.9)	16.0 \pm 0.4 (8.7–29.4)	272.8 \pm 1.7 (220.0–321.0)	20.5 \pm 0.1 (18.0–23.9)	14.8 \pm 0.1 (12.4–17.1)	22.8 \pm 0.05 (21.1–24.0)	16.4 \pm 0.05 (14.9–17.7)

perature and rainfall in Tongshi, where our lizards were collected, are approximately 23°C and 2000 mm, respectively. Captured lizards with intact tails were transported by air to our laboratory in Hangzhou, Zhejiang (eastern China), where they were sexed, weighed, measured, and marked (toe-clipping) individually for future identification. Females larger than 78 mm were palpated to assess their reproductive condition. Captured lizards were housed in 3 \times 1.5 \times 2.2 m³ (length \times width \times height) wire enclosures, inside which temperatures were never below 23°C. At no time were there more than 15 lizards in a single enclosure. Lizards were exposed to a natural light cycle and some direct sunlight. Supplementary heating with suspended lamps, dishes of water, horticultural shrubs and trees, and hiding places were provided so that lizards had ample opportunities for behavioral thermoregulation during the photophase. Each enclosure contained six plastic boxes (200 \times 300 mm²) of moist soil and vermiculite which served as artificial egg-laying sites. We fed lizards mealworms (*Tenebrio molitor*), commercial worms, and water enriched with vitamins and minerals.

Enclosures were checked at least twice every day for eggs and more frequently when females were seen to dig oviposition chambers at the egg-laying sites in the enclosures. All freshly laid eggs were measured and weighed immediately to minimize changes in egg mass at oviposition caused by loss or gain of water. Eggs were incubated at four constant temperatures ranging from 24–33°C. Detailed data on hatchling characteristics will be reported elsewhere.

Each lizard was measured for snout-vent length (SVL), tail length (TL), head length (HL, from the snout to the anterior edge of tympanum), head width (HW, taken at the posterior end of the mandible), and body mass. Individ-

uals larger than 78.9 mm SVL were considered adults, because only females larger than this size laid eggs. Data on clutch size were also derived from females with yolked follicles or oviductal eggs that died in captivity or were dissected. We calculated relative clutch mass (RCM) using two methods: RCM1 was calculated by dividing clutch mass by the female postoviposition mass (Shine, 1992), and RCM2 by dividing clutch mass by the total female (clutch plus body) mass (Vitt and Price, 1982; Seigel and Fitch, 1984). Female condition was estimated using the residuals derived from the regression of log (female postpartum mass) on log (female SVL; van Damme et al., 1992).

All data were tested for normality (Kolmogorov-Smirnov test) and homogeneity of variances (Bartlett test), and log_e-transformed when necessary to satisfy conditions for parametric tests. We used one-way ANOVA to test for the difference in body size (SVL) between male and female adults. We used one-way ANCOVA with SVL as the covariate to test for differences in head size (head length and width) and tail length between males and females. Homogeneity of slopes was checked prior to testing for differences between adjusted means. A partial correlation analysis was employed to examine relationships between the selected pairs of variables while holding other variables constant. Values are presented as mean \pm 1 SE.

RESULTS

Sexual Dimorphism.—The largest male and female were 104.9 and 103.8 mm SVL (N = 223), respectively (Table 1). *Calotes versicolor* in our sample did not show sexual dimorphism in SVL (ANOVA, $F_{1,191}$ = 0.18, P = 0.670; Table 1), but males attained longer tails than did females at the same SVL throughout the size range (ANCOVA, P < 0.05 for all comparisons; Fig. 1).

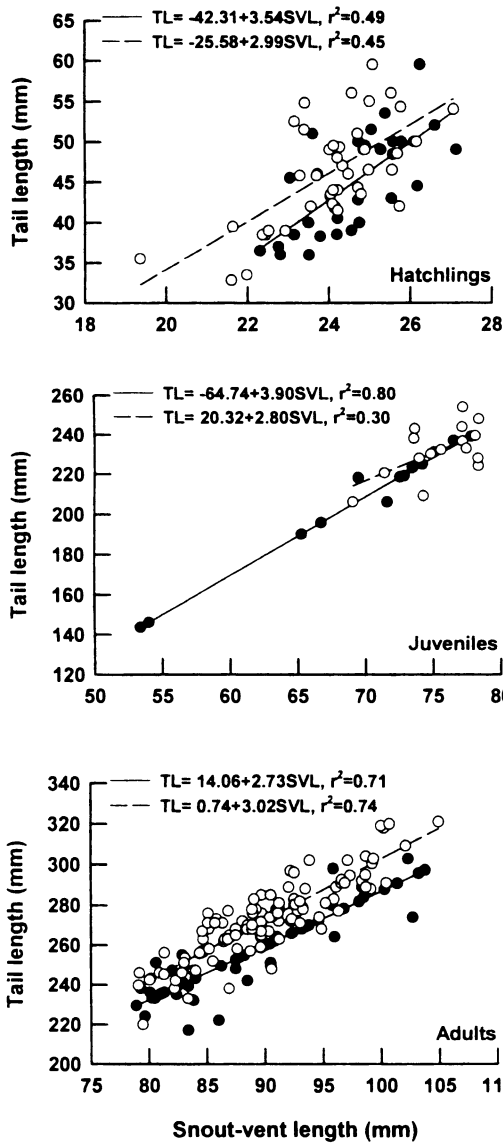


FIG. 1. Linear regressions of tail length on SVL for *Calotes versicolor* at different ontogenetic stages. The solid dots and lines indicate females, and the open dots and dash lines indicate males.

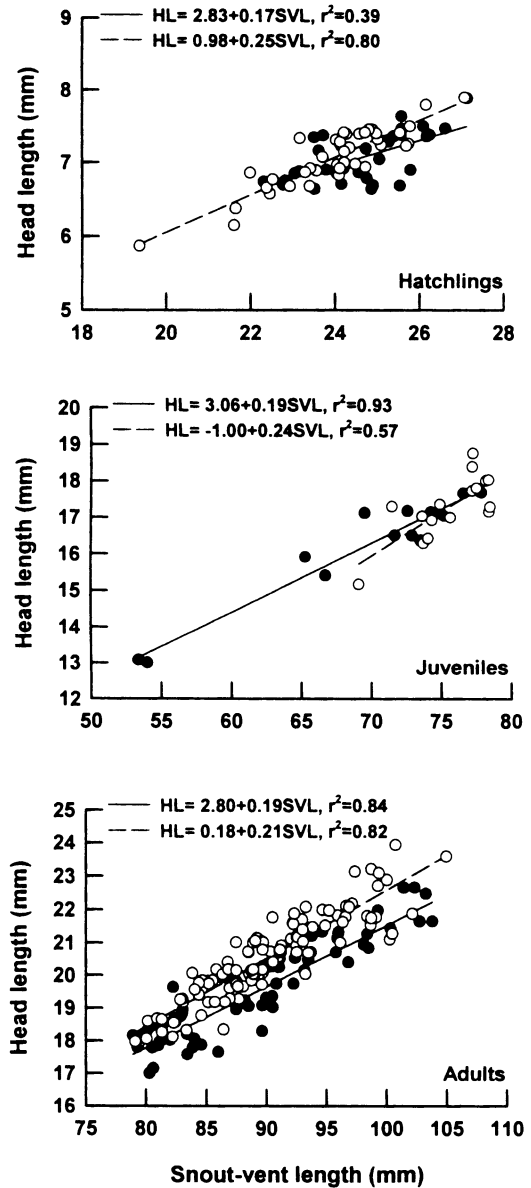


FIG. 2. Linear regressions of head length on SVL for *Calotes versicolor* at different ontogenetic stages. The solid dots and lines indicate females, and the open dots and dash lines indicate males.

Head length, head width, and tail length exhibited allometric growth for both sexes (Log_e-transformation, ANCOVA, all $P < 0.003$).

Males and females differed in relative head size (ANCOVA; HL: $F_{1,70} = 6.70, P = 0.012$; HW: $F_{1,70} = 8.29, P = 0.005$) at hatching, with males having larger heads than females (Table 1, Figs. 2–3). This sexual dimorphism was slightly more pronounced between adults (adjusted HL males/females = 1.04; adjusted HW males/females = 1.06) than between hatchlings (adjust-

ed HL males/females = 1.02; adjusted HW males/females = 1.02). However, no significant sexual dimorphism in head size (ANCOVA; HL: $F_{1,27} = 0.19, P = 0.667$; HW: $F_{1,27} = 0.55, P = 0.463$) was found in subadults, presumably because of the limited sample size and the smaller head-size difference between males and females.

Hatchlings had larger heads but shorter tails relative to SVL than did subadults and adults

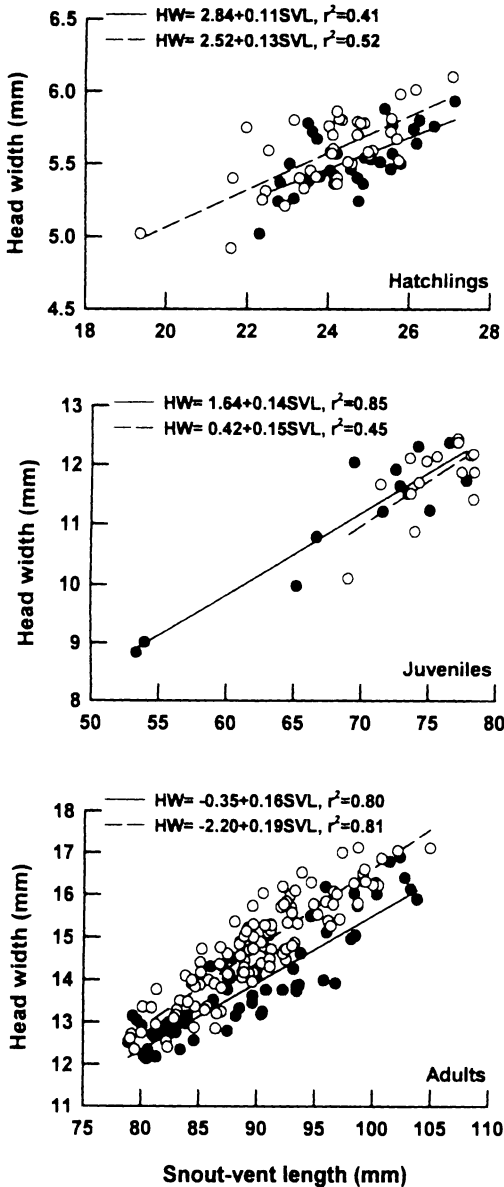


FIG. 3. Linear regressions of head width on SVL for *Calotes versicolor* at different ontogenetic stages. The solid dots and lines represent females, and the open dots and dash lines represent males.

(Table 1). When SVL was held constant, tail length and head size of subadults and adults of the same sex were similar (Log_e-transformation, ANCOVA, difference between adjusted means, $P \geq 0.07$ for all comparisons).

Female Reproductive Characteristics.—The smallest and largest reproductive females in our sample were 78.9 and 103.8 mm SVL, respectively. All females larger than 78.9 mm SVL had yolke follicles or oviductal eggs when they

were collected, indicating that they were reproductive individuals. Twenty females laid one clutch of eggs in our laboratory between April and June. *Calotes versicolor* from Hainan may lay multiple clutches of eggs, because all dissected postoviposition females ($N = 15$) had yolke follicles that would form the next clutch. Table 2 summarizes data on female reproductive characteristics.

Clutch size as determined by counting the number of yolke follicles, and oviductal eggs did not differ from that determined by counting the number of freshly laid eggs (ANCOVA, $F_{1,63} = 1.65, P = 0.204$); thus, the corresponding data were pooled. Both clutch size ($r^2 = 0.48, F_{1,64} = 57.97, P < 0.0001$) and clutch mass ($r^2 = 0.48, F_{1,18} = 27.05, P < 0.0001$) were positively correlated with female SVL (Fig. 4). We did not find a linear relationship between egg mass and female SVL ($r^2 = 0.03, F_{1,18} = 0.58, P = 0.455$).

We employed a partial correlation analysis to test for the relationships among (1) clutch size, female SVL, and female condition; (2) egg length, egg width, and clutch size; and (3) egg mass, clutch size, and female SVL. Clutch size was not correlated with female condition when female SVL was held constant ($r = -0.03, t = 0.14, df = 18, P = 0.891$). Egg length, egg width, and clutch size were not correlated with each other when the remaining variable was held constant ($P = 0.158$ for all cases). Egg mass was not correlated with clutch size when female SVL was held constant ($r = -0.12, t = 0.48, df = 18, P = 0.636$), and egg mass was not correlated with female SVL when clutch size was held constant ($r = 0.20, t = 0.84, df = 18, P = 0.411$).

Female *C. versicolor* in our sample increased reproductive output mainly through increasing clutch size (and hence clutch mass). No trade-off between egg number and egg size was evident.

DISCUSSION

It has been suggested that an arboreal species of lizard should tend to have a relatively long tail because it is used as a balancing organ. Unlike lizards that use tail autotomy as a mechanism to escape from predators, arboreal lizards rarely lose tails because tail loss may result in a marked decrease in survivorship (e.g., Ballinger, 1973; Vitt, et al., 1977; Arnold, 1984; Fox et al., 1990; Brown et al., 1995). Data on the tail of *C. versicolor* are consistent with these ideas. Tails of *C. versicolor* are impressively long, constituting approximately 65% of the total length in hatchlings and 75% of the total length in subadults and adults (Table 1). The relative tail length is shorter in hatchlings, suggesting that embryos and posthatching individuals differentially allocate resources to the growth of tail. A long tail

TABLE 2. Descriptive statistics for female reproductive characteristics of *Calotes versicolor*. All length units are in millimeters and mass units in grams.

	N	Mean \pm SE	Range
Body mass ^a	20	15.0 \pm 0.8	9.9–25.9
Snout–vent length ^b	65	90.4 \pm 0.9	78.9–103.8
Clutch size ^b	65	9.0 \pm 0.3	3–14
Egg length	20	14.5 \pm 0.2	13.3–16.2
Egg width	20	8.0 \pm 0.1	7.4–8.5
Egg mass	20	0.52 \pm 0.01	0.45–0.61
Clutch mass	20	4.65 \pm 0.29	1.58–6.47
Relative clutch mass			
RCM1	20	0.314 \pm 0.017	0.160–0.466
RCM2	20	0.236 \pm 0.010	0.138–0.318

^a The body mass refers to the postoviposition body mass.

^b The data on female SVL and clutch size include those from the dissected females that contained yolked follicles or oviductal eggs.

may be less important as a balancing organ for *C. versicolor* hatchlings, and this hypothesis, although untested, is supported by the observation that juveniles are seldom found on trees because they forage and bask mostly at ground level (Diong et al., 1994). In contrast, subadults and adults spend a considerable amount of time

on tree trunks for foraging and thermoregulatory activities, as well as in a head-down survey posture to hunt prey. In these arboreal activities, the lizard uses its long tail as a balancing organ. Thus, the ontogenetic changes in perch use probably explain the shorter relative tail length in hatchlings.

Our data suggest that *C. versicolor* embryos allocate relatively more resources to the growth of ecologically significant morphological characters than to characters less directly tied to early survival and growth of hatchlings. As a consequence of this allocation pattern, *C. versicolor* hatchlings noticeably have relatively larger heads but shorter tails than adults. Head size is generally positively correlated with body size, and a larger head is thought to be associated with an increased ability of a predator to eat larger prey items (e.g., Schoener et al., 1982; Shine, 1991; Barden and Shine, 1994). There is growing evidence that lizards capture increasingly larger prey during ontogeny, although larger individuals usually do not exclude smaller items from their diet (e.g., Castilla et al., 1991; Pérez-Mellado et al., 1991; Webb and Shine, 1994). Moreover, according to optimal foraging models, a foraging predator tends to increase the rate of net energy intake by consuming larger prey items so as to maximize net energy gain (Schoener, 1971; Pyke et al., 1977; Stephens and Krebs, 1986). Thus, the relatively larger head should be ecologically important for *C. versicolor* hatchlings to increase their ability to use larger prey and potentially increase early survival and growth.

Previous work on *C. versicolor* in Singapore demonstrated the existence of sexual dimorphism in size with males larger than females, but the authors did not indicate whether "size" referred to SVL or to total length (Diong et al., 1994). In the present study, *C. versicolor* appar-

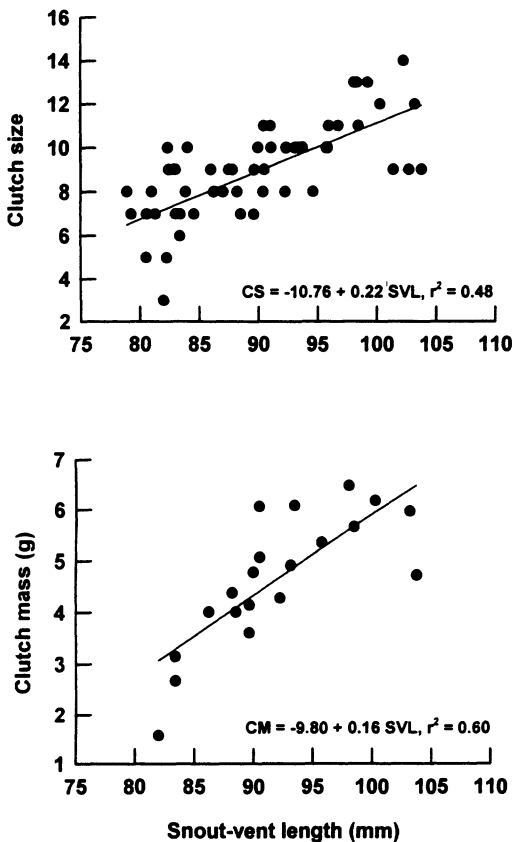


FIG. 4. Linear regressions of clutch size and clutch mass on female SVL for *Calotes versicolor*.

ently did not exhibit sexual dimorphism in SVL. The lack of dimorphism presumably is true for *C. versicolor* in nature, because we measured a large number of adults (117 males and 76 females; Table 1), which were randomly collected from the field. Males are, however, still the larger sex because of their longer tails, which effectively increase their total length. The sexual dimorphism in tail length is present at hatching and is preserved across the size range into adult life. That male hatchlings have longer tails than do female hatchlings has also been recorded in some other lizards, for example, *Eremias brenchleyi*, *Podarcis muralis*, and *Takydromus wolteri* (Braña and Ji, 2000; XJ, unpubl. data), but the ecological advantages and determinants of this dimorphism are unclear.

Between-sex differences in head size are widespread among lizards, with males having larger heads than do females in nearly all saurian species studied to date. *Calotes versicolor* also shares this feature. It is noteworthy, however, that this dimorphism arises in lizards of different species at different ontogenetic stages. *Calotes versicolor*, as in *P. muralis* (Braña and Ji, 2000) and *Takydromus septentrionalis* (Zhang and Ji, 2000), exhibits this dimorphism at hatching. In contrast, *Eumeces chinensis* (Lin and Ji, 2000) and *Sphenomorphus indicus* (Ji and Du, 2000) only show this head-size dimorphism on approaching adult size at maturity.

Sexual dimorphism in head size may arise in different species of lizards in very different ways. For example, females of *E. chinensis* and *T. septentrionalis* increasingly sacrifice head growth for rapid growth in SVL to realize the greater potential reproductive output from a larger body size, whereas males exhibit an increasingly rapid growth of the head (Ji et al., 1998; Lin and Ji, 2000; Zhang and Ji, 2000). *Podarcis muralis* and *S. indicus* represent an alternative case: the sexual dimorphism in head size arises only because females sacrifice head growth for rapid growth in SVL (Braña, 1996; Ji and Du, 2000). *Calotes versicolor* differs from the above species in that subadults and adults of the same sex apparently exhibit isometric head growth. Broadly speaking, the difference in head size between the sexes could be attributed to selection for success in female reproduction. However, this hypothesis is unlikely in *C. versicolor*, because between-sex difference in head size in the species is small and hence contributes little, if any, to increased body volume. Moreover, as mentioned below, reproductive output is apparently not constrained by the body volume in *C. versicolor*. Thus, we conclude that there is low selection pressure for increased female head size in *C. versicolor*.

Our dataset on female reproduction is prelim-

inary as the data are measurements of reproductive output carried over a short time period that does not cover the whole breeding season. Given that reproductive output and egg composition may differ considerably among clutches in multiple-clutched lizards, data without detailed descriptions of each clutch may be less informative (Ji and Braña, 1999, 2000). Nonetheless, our data are sufficient to reveal three interesting trends.

First, eggs of *C. versicolor* may be well optimized for size, presumably as a consequence of their adaptive responses to local environments. Previous studies predict that, if eggs of reptiles are not optimized, the egg size should vary as a function of maternal size (SVL) and clutch size (e.g., Ford and Seigel, 1989; Doughty and Shine, 1997; Ollsson and Shine, 1997; Ji et al., 1997, 2000; Lin and Ji, 2000). However, in this study, we found no evidence of the predicted trade-off (an inverse relationship) between egg size and clutch size, and variation in egg size associated with maternal SVL. Thus, our results, although not completely conclusive because other untested potential causes might contribute to variation in egg size, offer support for the assertion that *C. versicolor* produces optimally sized eggs.

Second, reproductive output of *C. versicolor* is influenced by maternal body volume but at some optimal level rather than maximal level. Here we use information on egg shape of *C. versicolor* to substantiate this claim. If reproductive output of a given species is at a high or maximal level, then reproductive females should tend to produce as large a clutch as they can (Qualls and Shine, 1995; Ji et al., 2000). This may be reflected in egg shape, because more rounded eggs are always associated with larger or heavier clutches in species in which the reproductive output is highly constrained by the maternal body volume (Ji and Braña, 2000; Ji et al., 2000). The lack of relationships among egg width, egg length, and clutch size indicates that eggs are less crowded together in the oviduct, suggesting that *C. versicolor* produces clutches that do not completely fill the available body volume. The lack of physical constraints from body volume on reproductive output is a particularly interesting result, given that *C. versicolor* is an arboreal lizard in which survivorship may increase if females remain fairly agile because of a lower physical burden of carrying the clutch. In fact, the reduced reproductive output per episode coupled with presumed increase in agility (and hence survivorship) may enhance lifetime reproductive success in arboreal lizards. Thus, our results reinforce the idea that adaptations to particular habitats may place constraints on reproductive output in lizards (Vitt, 1981). In *C. versicolor*, the total clutch mass accounted for

23.6% of the total female mass (Table 2), which means that each reproductive event relieves a female of almost one-quarter of its mass.

Third, *C. versicolor* in Hainan does not reproduce continuously although it might have the potential to do so. *Calotes versicolor* in warmer regions such as Sri Lanka has been reported to reproduce continuously (Erdelen, 1986), but it is very unlikely for our lizards to adopt this reproductive tactic. Wild populations of *C. versicolor* in Hainan are seldom active during the coldest months of the year, from December to February. Moreover, the risk of failure of egg incubation or the extremely long incubation period may prevent lizards from laying eggs in cold months. For example, *C. versicolor* eggs incubated at 24°C need approximately 82 days to complete embryonic development, and hatching success at the temperature is low (approximately 43%; Ji et al., in press).

Our results provide evidence showing differential allocation of resources to head and tail growth during ontogeny and additionally suggest the relative importance of these shifts to survivorship at different ontogenetic stages. Our results further support the observation that lizards in a particular habitat-type produce optimal-sized offspring at some optimal, rather than maximal level. Although the latter conclusion is based on egg shape and the correlation of egg size with maternal size and clutch size, the results are convincing. We hypothesize from our results that the reduced female reproductive output per episode potentially increases lifetime reproductive success associated with the increased survivorship in arboreal lizards.

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