

Tail loss affects fecundity but not offspring traits in the Chinese skink *Eumeces chinensis*

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Abstract We used the Chinese skink *Eumeces chinensis* as a model animal to study the effects of tail loss on reproductive investment and offspring traits. A total of 147 wild-captured adult females were divided into four groups according to their tail conditions. Tail breaks occurred most frequently in the proximal portion of the tail and least frequently in the distal portion, with the middle portion in between. This finding suggests that tail breaks occurring in nature often entails substantial energetic costs in *E. chinensis* where the tail is a major site of energy storage. The proportion of females that laid eggs was higher in females with intact or completely regenerated tails than in those with broken tails. Following whole-tail autotomy, the clutch size was reduced by 17%, and the clutch mass was reduced by 14%. Females undergoing substantial tail autotomy reduced reproductive investment, and they did so by reducing the number but not the size of eggs produced. None of the egg and hatchling traits was affected by tail loss. Comparing our data with those reported for other oviparous and viviparous skinks allows us to draw two general conclusions: one is that fecundity (clutch or litter size) is affected by tail loss in all species so far studied, whereas offspring size is affected by tail loss in some species, but not in others; the other is that the reduction in fecundity following tail loss is more evident in species lacking abdominal fat bodies [*Current Zoology* 58 (2): 228–235, 2012].

Keywords Scincid lizard, Costs of tail autotomy, Fecundity, Offspring size, Morphology, Locomotor performance

For lizards using the mechanism of tail autotomy, tail loss offers a direct survival benefit, but entails several costs. For example, tailless lizards are more susceptible to starvation due to the loss of stored energy, and often have to reduce growth rates and reproductive investment due to diversion of energy away from other functions to tail regeneration (Taylor, 1986; Wilson and Booth, 1998; Chapple and Swain, 2002; Chapple et al., 2002; Goodman, 2006). Tailless lizards may also have reduced abilities to escape from predators (Fox and McCoy, 2000; Kelehear and Webb, 2006; see also Lu et al., 2010), modified foraging tactics (Martín and Salvador, 1993a), activity patterns (Martín and Avery, 1998; Zhao et al., 2008) and microhabitat use (Ballinger, 1973; Martín and Salvador, 1992), decreased home range size (Martín and Salvador, 1993b; Salvador et al., 1995) and diminished social status (Tokarz, 1985; Fox et al., 1990).

Skinks are among lizards that use tail autotomy to evade predatory attacks, with high frequencies (for both sexes combined) of tail breakages already reported for

several species such as *Eumeces obsoletus* (67%–70%; Fitch, 2003), *Lampropholis guichenoti* (67%; Downes and Shine, 2001), *Mabuya multifasciata* (57%; Sun et al., 2009), *M. frenata* (82%; Van Sluys et al., 2002), *Niveoscincus metallicus* (78%; Chapple and Swain, 2002), and *Sphenomorphus indicus* (77%; Sun et al., 2007). Like many other lizard taxa (Congdon et al., 1974; Derickson, 1976; McConnachie and Whiting, 2003; Lin and Ji, 2005), skinks carry a substantial portion of their total energy reserves in the form of fatty tissue in the tail (Ji et al., 1994; Chapple et al., 2002; Chapple and Swain, 2002; Lin et al., 2006; Sun et al., 2007, 2009). The reduction in reproductive investment following tail autotomy has been reported for lizards where the production of offspring is heavily dependent on caudal lipid reserves (Smyth, 1974; Dial and Fitzpatrick, 1981; Taylor, 1986; Doughty and Shine, 1998; Wilson and Booth, 1998). However, tail breakages occurring in nature may not always have severe energetic consequences and thus significantly reduce the amount of energy allocated to reproduction. For example, 76%

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of tail breaks result in no more than 10% of loss of lipid reserves in the tail of *N. metallicus* (Chapple and Swain, 2002). The reduction in fecundity (litter size) following a recent tail break is not related to the position of tail break in *N. metallicus* (Chapple et al., 2002), while in *L. guichenoti*, fecundity is not affected by tail loss even when reproductive females undergo whole-tail autotomy (Taylor, 1986). Moreover, if females have already undergone maximal, or close to maximal, autotomy before they reach reproductive age, then the influence of autotomy on fecundity will be much less than if maximal autotomy is experienced frequently in reproductively active females. The reproductive cost associated with tail autotomy is an interesting topic, but still remains poorly known in lizards. For example, we know little about what particular reproductive parameters [fecundity (clutch or litter size), total reproductive investment (clutch or litter mass), and offspring size (hatchling or neonate mass)] are more likely to be affected by tail loss and how often tail breaks occurring in nature entail substantial reproductive costs.

In this study, we used the Chinese Skink *Eumeces chinensis*, a medium-sized (up to 134 mm snout-vent length, SVL), oviparous scincid lizard, as a model animal to examine the effects of tail loss on female reproductive traits. The skink is one of the most abundant lizard species in southeastern China (Huang, 1999). Females larger than 85 mm SVL are able to produce a single clutch of 7-30 eggs per breeding season, with larger females generally producing more and larger eggs than do smaller ones (Lin and Ji, 2000; Ji et al., 2002). Tail breaks often entail substantial energetic costs in both sexes of the skink (Lin et al., 2006). Nearly 40% of the total lipids are stored in the tail, which is therefore a major site of energy storage (Ji et al., 1994). In the population under study, approximately 73% of adults

(73.9% males, and 71.9% females) have regenerated or injured tails, with approximately 49% of tail breaks occurring in the proximal portion of the tail (Lin et al., 2006). Neither the frequency of autotomy nor the frequency distribution of locations of the tail break differs between male and female adults (Lin et al., 2006). Our study aims are as follows: (1) to assess the possible reproductive costs associated with tail loss, (2) to identify reproductive traits more likely affected by tail loss, and (3) to draw some general conclusions on the effects of tail loss on overall reproductive performance by comparing data among skinks so far studied.

1 Materials and Methods

We collected adults larger than 85 mm snout-vent length (SVL) in late March 2004 from a previously studied population in Lishui (28°46'N, 119°92'E), East China. All captured skinks were transported to our laboratory in Hangzhou, where they were checked for signs of previous tail loss. Of the 147 adult females, 108 (~73%) had autotomized some portion of the tail at least once. We individually measured the skinks ($n = 39$) with intact tails for SVL and tail length (TL), and the skinks with regenerated tails ($n = 108$) for SVL, regenerated tail length (RTL) and stump length (SL, from the vent to the site of tail break). We followed Chapple et al. (2002) to estimate the relative tail length and relative position of tail break for each skink with a regenerated tail, and established a linear regression equation ($TL = 1.72SVL - 19.85$; $r^2 = 0.57$, $F_{1,37} = 49.55$, $P < 0.0001$) of TL against SVL for the females never undergoing tail autotomy to estimate the original tail length (OTL) of the skinks with signs of tail loss. We then calculated the relative tail length by RTL/OTL, and the relative position of the tail break by SL/OTL (Fig. 1).

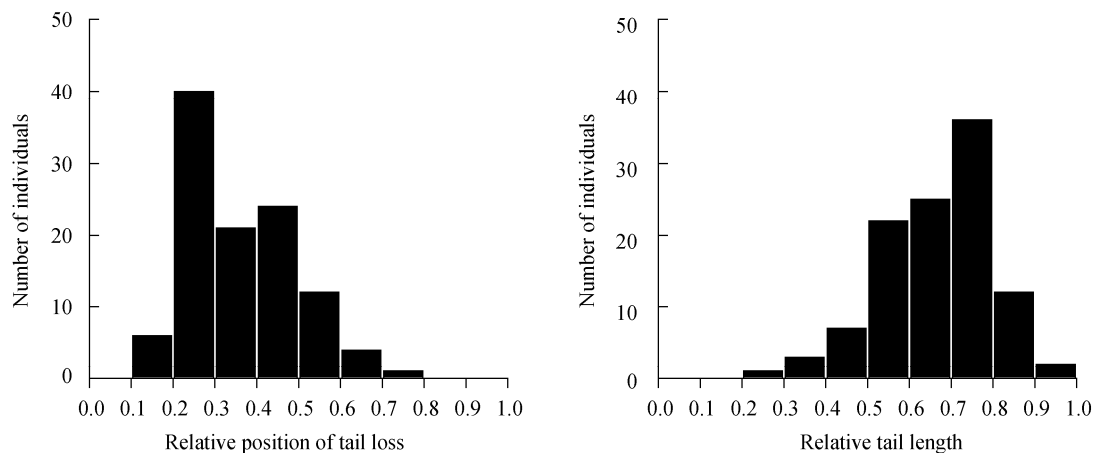


Fig. 1 Frequency distributions of relative positions where tail autotomy occurred and relative regenerated tail lengths. Data are based on 108 female adults of *E. chinensis* collected from a population in Lishui.

Females were assigned to one of the four groups according to their tail conditions: Group 1, females ($n = 33$; hereafter G1 females) with intact or completely regenerated tails (RTL/OTL $> 90\%$); Group 2, females ($n = 46$; hereafter G2 females) underwent tail loss in the middle or distal portion of the tail, with SL/OTL values of 30–70% and RTL/OTL values of 60–90%; Group 3, females ($n = 40$; hereafter G3 females) underwent tail loss in the proximal portion of the tail, with SL/OTL values of 10–30%, and RTL/OTL values of 20–70%; and Group 4, females ($n = 28$; hereafter G4 females) originally had intact or completely regenerated tails but underwent artificially proximal tail autotomy (~2 cm from the vent) soon after they arrived in our laboratory.

Between 15–18 adults (10–12 females and 5–6 males) were housed in one of the ten 150 × 150 × 60 cm (length × width × height) outdoor enclosures, and females of different groups were never housed in the same enclosure. Mealworm larvae *Tenebrio molitor*, house crickets *Achetus domestica* and water enriched with vitamins and minerals were provided *ad libitum*. Enclosures were checked at least twice daily for eggs as soon as the first female laid eggs. Females were isolated from each other using dividers that created 30 × 30 × 30 cm chambers if they laid eggs during the same time period in the same enclosure. Eggs were collected, weighed and measured for length and width less than 3 h post-laying. The viability of freshly laid eggs was judged by the presence of an embryonic disc using a spot light. Body mass, SVL and TL were taken for each post-oviposition female. All adults were released at their point of capture in mid-July.

Of the 147 adult females, 86 laid eggs. One egg from each clutch was dissected to assess the embryonic stage at oviposition sensu Dufaure and Hubert's (1961). The three egg components (embryo, yolk and eggshell) were dried separately to constant mass in an oven at 65 °C and weighed. Two or three viable eggs from each clutch were individually incubated in covered plastic jars (50 ml) with standardized amounts of vermiculite and water (1 g dried vermiculite: 2 g water). One-third of the egg was buried lengthwise in the substrate, with the surface near the embryo exposed to air inside the jar. These jars were placed in a room where temperature was controlled at 28 ± 0.5 °C, which falls within the range of optimal temperatures for embryonic development in *E. chinensis* (Ji and Zhang, 2001). Water was evenly added into substrates to compensate for evaporative losses and water absorbed by the egg.

Incubation length varied from 22–27 d. Hatchlings

were collected, weighed and measured for locomotor capacity, SVL and TL less than 6 h post-hatching. All locomotor trials were conducted at the body temperature of 28 °C, which was achieved by placing hatchlings in an incubator at the correspondent temperature for approximately 30 min prior to testing (Braña and Ji, 2000). Locomotor capacity was assessed by individually chasing down hatchlings along a 2 m racetrack with one side transparent, which allowed lateral filmation with a Panasonic NV-GS408 digital video camera. Hatchlings that refused to run were excluded from analyses. The tapes were later examined with a computer using MGI VideoWave III software (MGI Software Co., Canada) for sprint speed in the fastest 20 cm interval, the maximal distance traveled without stopping (hereafter the maximal length) and the number of stops in the race-track. All hatchlings were released to the site where their mothers were collected also in mid-July.

Data on hatchlings from the same clutch were pooled to avoid pseudo-replication. We used log-likelihood ratio test (*G*-test), linear regression analysis, Kruskal-Wallis test, one-way analysis of variance (ANOVA), one-way analysis of covariance (ANCOVA) and multivariate analysis of variance (MANOVA) to analyze data. Prior to parametric analyses, data were tested for normality using the Kolmogorov-Smirnov test, and for homogeneity of variances using the Bartlett's test (univariate level) or the Box's *M* test (multivariate level). The homogeneity of slopes was checked prior to examining differences in the adjusted means. All statistical analyses were performed with the Statistica software (version 6.0 for PC, Tulsa, OK, USA). Throughout this paper, values are presented as mean ± standard error (SE), and the significance level is set at $\alpha = 0.05$.

2 Results

2.1 Tail autotomy in females

Tail breaks at the extreme base (SL/OTL $< 10\%$) of the tail were absent. Of the 108 females with previous bouts of tail loss, 67 shed their tail in the proximal portion (SL/OTL greater than 10% but smaller than 30%) of the tail, 40 at the middle portion (SL/OTL greater than 30% but smaller than 70%), and one at the distal portion (SL/OTL greater than 70%) (Fig. 1). Frequencies of tail breaks occurring in the proximal, middle and distal portions of the tail differed significantly ($G = 84.50$, $df = 2$, $P < 0.0001$).

2.2 Female reproduction

Approximately 76% (25/33) of the G1 females, 57% (26/46) of the G2 females, 50% (20/40) of the G3 fem-

ales and 54% (15/28) of the G4 females laid eggs between early June and early July. The proportion of females that laid eggs was higher in the G1 group than in the other three groups, but the differences were not significant ($G = 5.85$, $df = 3$, $P > 0.10$). For females that laid eggs, mean values for SVL ($F_{3,82} = 1.84$, $P = 0.146$) and egg-laying date ($H_{3, n=86} = 5.52$, $P = 0.137$) did not differ among the four groups. Clutch size (Fig. 2A) and clutch mass (Fig. 2B) were positively related to female SVL within each of the four groups ($P < 0.05$ in all cases). Clutch size differed among the four groups (ANCOVA with female SVL as the covariate; $F_{3,81} = 2.75$, $P < 0.05$). When setting female SVL at 100 mm, mean clutch sizes for the G1, G2, G3 and G4 females were 16.4, 15.7, 15.0 and 13.6, respectively. Clutch mass also differed among the four groups (ANCOVA with female SVL as the covariate; $F_{3,81} = 2.96$, $P = 0.037$). When setting female SVL at 100 mm, mean clutch masses for the G1, G2, G3 and G4 females were

10.4, 10.5, 9.7 and 8.9 g, respectively. Egg size (mass), egg shape (length / width) and relative clutch mass were independent of female SVL within each group ($P > 0.32$ in all cases), and did not differ among the four groups (Wilks' $\lambda = 0.81$, $df = 12, 209$, $P = 0.144$) (Table 1).

2.3 Eggs and hatchlings

Embryonic stages at oviposition, varying from Dufaure and Hubert's (1961) stage 31 to 36, did not differ among the four groups ($H_{3, n=86} = 4.64$, $P = 0.200$). No egg component (water, yolk dry mass and eggshell dry mass) examined differed among the four groups (Wilks' $\lambda = 0.86$, $df = 9, 195$, $P = 0.192$, Table 2). Wet mass (Fig. 3A) and SVL (Fig. 3B) of hatchlings were positively related to initial egg mass ($P < 0.01$ in all cases), whereas sprint speed and the maximal length were not ($P > 0.35$ in all cases). No hatchling trait (wet mass, SVL, tail length and three locomotor variables) examined differed among the four groups (Wilks' $\lambda = 0.80$, $df = 18, 207$, $P = 0.531$, Table 3).

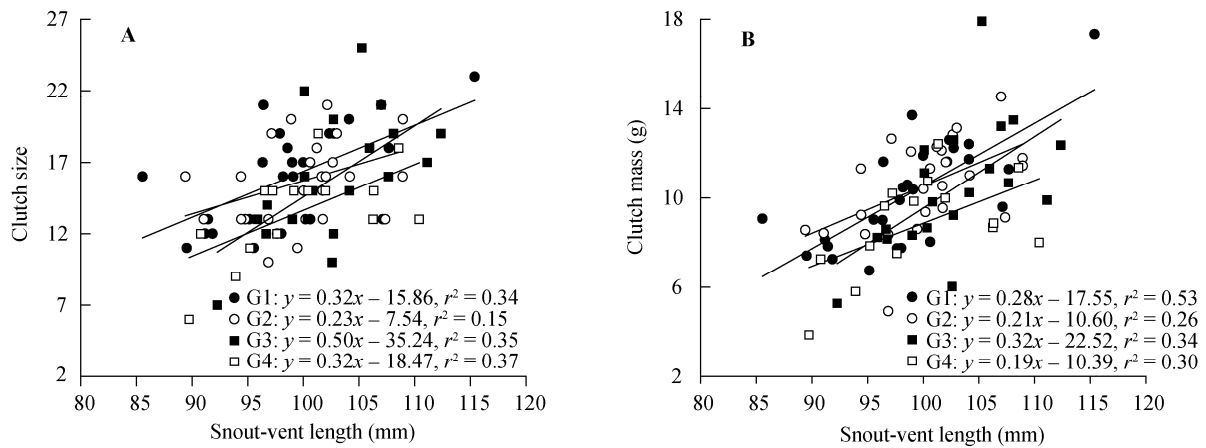


Fig. 2 Linear regressions of clutch size (A) and clutch mass (B) against female snout-vent length. Regression equations and coefficients are given in the figure.

Table 1 Reproductive traits of female *E. chinensis* assigned to four groups according to their tail conditions

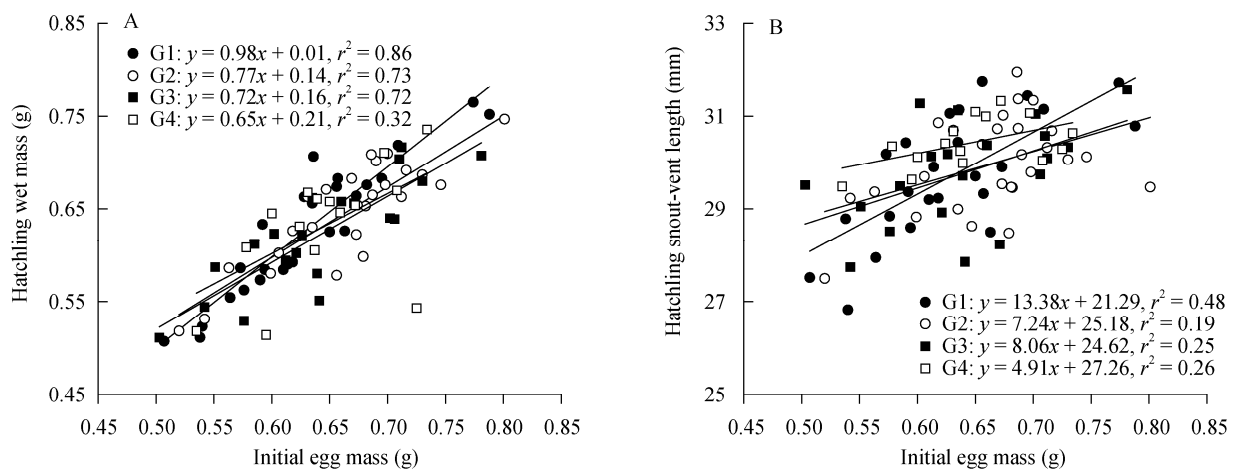
	G1 females	G2 females	G3 females	G4 females
<i>n</i>	25	26	20	15
Snout vent length (mm)	98.6 ± 1.3 85.6–115.4	100.3 ± 1.0 89.4–108.9	102.6 ± 1.2 92.3–112.4	99.7 ± 1.6 89.7–110.4
Post-oviposition mass (g)	18.7 ± 0.6 13.7–25.1	18.8 ± 0.5 12.9–24.3	18.6 ± 0.8 13.3–26.3	18.4 ± 0.8 13.8–24.9
Clutch size	15.9 ± 0.7 11–23	15.8 ± 0.6 10–21	15.9 ± 1.0 7–25	13.5 ± 0.9 6–19
Egg length (mm)	14.1 ± 0.2 12.7–16.5	14.4 ± 0.1 13.0–16.6	14.3 ± 0.1 13.3–15.6	14.3 ± 0.1 13.6–15.1
Egg width (mm)	9.0 ± 0.1 8.4–9.9	9.2 ± 0.1 8.2–10.1	9.1 ± 0.1 8.7–9.7	9.1 ± 0.1 8.8–9.3
Egg mass (g)	0.64 ± 0.02 0.52–0.82	0.67 ± 0.01 0.49–0.78	0.66 ± 0.01 0.55–0.77	0.65 ± 0.01 0.59–0.72
Clutch mass (g)	10.1 ± 0.5 6.7–17.3	10.6 ± 0.4 4.9–14.5	10.4 ± 0.6 5.3–17.9	8.8 ± 0.6 3.9–12.4

Data are expressed as mean ± SE and range. See text for definitions for G1, G2, G3 and G4 females.

Table 2 Embryonic stages and components of eggs laid by female *E. chinensis* with different tail conditions

	G1 females	G2 females	G3 females	G4 females
<i>n</i>	25	26	20	15
Egg mass (g)	0.64 ± 0.02 0.52–0.84	0.68 ± 0.01 0.55–0.84	0.65 ± 0.02 0.52–0.77	0.65 ± 0.02 0.47–0.78
Embryonic stage at oviposition	33.2 ± 0.2 32–35	32.7 ± 0.2 31–35	33.1 ± 0.3 31–36	33.4 ± 0.2 32–35
Eggshell dry mass (mg)	7.7 ± 0.2 6.2–9.6	7.7 ± 0.2 6.2–9.0	7.4 ± 0.2 6.0–9.9	7.2 ± 0.2 5.7–8.9
Yolk dry mass (mg)	222.9 ± 8.4 163.6–332.2	230.6 ± 5.0 181.2–283.1	219.8 ± 7.4 159.5–278.5	203.5 ± 8.0 147.7–286.0
Water content (mg)	399.8 ± 14.5 299.7–590.0	435.7 ± 12.1 320.3–548.4	415.4 ± 12.8 297.0–506.5	427.7 ± 19.6 270.2–564.3

Data are expressed as mean ± SE and range.

**Fig. 3** Linear regressions of wet mass (A) and snout-vent length (B) of hatchlings against egg mass at oviposition

Regression equations and coefficients are given in the figure.

Table 3 Size, mass, morphology and locomotor performance of hatchlings produced by female *E. chinensis* with different tail conditions

	G1 females	G2 females	G3 females	G4 females
<i>n</i>	25	26	20	15
Initial egg mass (g)	0.63 ± 0.01 0.51–0.79	0.66 ± 0.01 0.52–0.80	0.64 ± 0.02 0.50–0.78	0.65 ± 0.01 0.54–0.73
Hatchling wet mass (g)	0.63 ± 0.01 0.51–0.77	0.65 ± 0.01 0.52–0.75	0.62 ± 0.01 0.51–0.72	0.63 ± 0.02 0.51–0.74
Snout-vent length (mm)	29.7 ± 0.3 26.8–31.8	30.0 ± 0.2 27.5–32.0	29.8 ± 0.3 27.7–31.6	30.2 ± 0.3 27.9–31.3
Tail length (mm)	36.7 ± 0.5 31.4–40.9	37.6 ± 0.4 31.9–40.8	37.2 ± 0.6 31.4–41.7	38.1 ± 0.7 32.2–41.4
Number of stop	8.8 ± 0.6 4–14	9.1 ± 0.6 3–16	9.0 ± 0.7 2–15	8.3 ± 0.7 4–12
Maximum length (cm)	72.8 ± 6.6 21–160	65.2 ± 5.8 27–155	64.3 ± 7.2 26–165	77.5 ± 7.0 37–150
Sprint speed (cm/s)	53.8 ± 2.2 35.7–76.0	49.9 ± 1.8 31.7–73.5	50.7 ± 3.0 26.0–87.7	50.6 ± 1.8 35.7–62.5

Data are expressed as mean ± SE and range.

3 Discussion

Our results are in agreement with previous studies that female skinks reduce reproductive investment when undergoing substantial tail autotomy (Smyth, 1974;

Taylor, 1986; Doughty and Shine, 1998; Wilson and Booth, 1998; Chapple et al., 2002). Females of *E. chinensis* do so by reducing the number rather than the size of eggs, as revealed by the fact that the mean egg mass remained remarkably constant among the four

groups. The clutch size was reduced by 14% following whole-tail autotomy in *Morethia boulengeri* (Smyth, 1974), 17.5% in *Niveoscincus metallicus* (Chapple et al., 2002), 55%–100% in *Ctenotus taeniolatus* (Taylor, 1986), 42% in *Eulamprus tympanum* (Doughty and Shine, 1998), 75% in *Eulamprus quoyii* (Wilson and Booth, 1998) and 55% in *Hemiergis peronii* (Smyth, 1974). We found in the G4 females that the clutch size was reduced by 17% as compared with the G1 females. This proportion is similar to the values reported for *M. boulengeri* and *N. metallicus*, but lower than the values reported for *C. taeniolatus*, *E. tympanum*, *E. quoyii* and *H. peronii*. *Morethia boulengeri* (Smyth, 1974), *N. metallicus* (Chapple et al., 2002) and *E. chinensis* (Ji et al., 1994) possess abdominal fat bodies, whereas *C. taeniolatus* (Taylor, 1986), *E. tympanum* (Doughty and Shine, 1998), *E. quoyii* (Wilson and Booth, 1998) and *H. peronii* (Smyth, 1974) do not. The above comparisons allow us to draw two conclusions: one is that fecundity is affected by tail loss, and the other is that the reduction in fecundity following tail loss is more pronounced in skinks lacking abdominal fat bodies.

Caudal lipid stores are proximally concentrated in *E. chinensis* and, as in other skinks such as *N. metallicus* (Chapple and Swain, 2002), *E. tympanum* (Doughty et al., 2003), *Sphenomorphus indicus* (Sun et al., 2007) and *Mabuya multifasciata* (Sun et al., 2009), partial tail loss does not severely influence energy stores in *E. chinensis* (Lin et al., 2006). For example, individuals of *E. chinensis* that lose distally 75% of the tail still retain more than 60% of the total caudal lipids (Lin et al., 2006). However, as tail breaks occur more frequently in the proximal portion of the tail in adults collected from the field, tail loss occurring in nature often entails substantial energetic costs in *E. chinensis* (Lin et al., 2006). In this study, clutch size and clutch mass were significantly reduced in the G4 females but not in the G2 and G3 females, partly because the G4 females lost nearly all caudal lipids and were therefore more likely to divert energy away from reproduction to tail regeneration, and partly because *E. chinensis* is among skinks possessing abdominal fat bodies that can be used to fuel reproduction (Ji et al., 1994).

Tail autotomy results in a reduction in offspring (egg or neonate) size in *E. quoyii* (Wilson and Booth, 1998) and *N. metallicus* (Chapple et al., 2002). This effect was not detected in *E. chinensis*. Offspring size is an important life-history trait tightly linked to the fitness of both mothers and offspring (Stearns, 1992; Bernardo, 1996; Agrawal et al., 2001; Roff, 2002), and a positive correlation between offspring size and fitness has been de-

tected in a wide range of animal taxa (Ferguson and Fox, 1984; McGinley et al., 1987; Sargent et al., 1987; Mousseau and Fox, 1998; Janzen et al., 2000). Tail regeneration may have energetic priority over reproduction in relatively long-lived species (Maiorana, 1977; Bernardo and Agosta, 2005). Diversion of energy away from reproduction into tail regeneration reduces the amount of energy available for the production of offspring (Doughty and Shine, 1998; Chapple et al., 2002; Bernardo and Agosta, 2005; Bateman and Fleming, 2009). However, for relatively long-lived lizard species, stochastic fluctuations in the number of offspring caused by tail loss may not severely influence lifetime fecundity. In this study, the clutch size was reduced by 17% following whole-tail autotomy. This reduction in clutch size could have a less important role in influencing lifetime fecundity in *E. chinensis*, a relatively long-lived lizard species with a high probability of future reproductive success. The negative impact of reducing offspring size sometimes exceeds that of skipping reproduction (Bernardo and Agosta, 2005). Thus, reducing the number but not the size of offspring following tail loss could be a reproductive tactic in *E. chinensis* to avoid a decline in offspring fitness (and thus, inclusive maternal fitness). It has been reported for *E. chinensis* that egg size varies among populations, but not among years within a population (Lin and Ji, 2000; Ji et al., 2002). These observations suggest that, in a given population of *E. chinensis*, eggs are well optimized for size, which is less likely to vary with total reproductive investment.

As in other oviparous lizards, hatchling size (both SVL and body mass) is determined by egg mass at oviposition in *E. chinensis* (Ji and Zhang, 2001). The size of hatchlings is also affected by egg composition in lizards (Ji and Braña, 1999; Du et al., 2010). Other morphometric traits often are positively correlated with hatchling size in lizards, including *E. chinensis* (Ji and Zhang, 2001). Also as in other oviparous lizards, size, morphology and locomotor performance of hatchlings are affected by incubation condition in *E. chinensis* (Ji and Zhang, 2001). Given that neither egg size nor egg composition differed among the four groups, and that all eggs were incubated under identical conditions, it is therefore not surprising that none of the hatchling traits examined differed among the four groups.

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