

Maternal egg care enhances hatching success and offspring quality in an oviparous skink

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Abstract

Maternal egg-caring behavior can often be observed in oviparous scincid lizards. The expression of such behavior is predictably affected by the trade-off between its resultant costs and benefits for mothers and/or offspring, which has been investigated in only a few scincid species. Here, post-ovipositional *Plestiodon chinensis* females were treated to care for their egg clutches without interference, under simulated predation pressure, or to be care-deprived. Potential maternal costs and offspring benefits associated with egg-caring behavior were then evaluated by measuring changes in maternal body condition, egg mortality, and hatchling performance. Egg-caring behavior caused post-ovipositional females to participate less in outside-nest activity, eat less food, and show relatively poorer body conditions at egg hatching. By contrast, compared with care-deprived females, egg-caring females gained mass slightly faster, and achieved a similar body condition within a few months of hatching. Eggs that were cared for by their mothers were more likely to hatch and produced larger, faster-running and better-growing hatchlings with higher survival than uncared-for eggs. Simulated exposure to a potential predator had no distinct impact on maternal egg-caring behavior expression and offspring performance. These results indicated that marked benefits of offspring viability but minor maternal energy costs might play a decisive role in the occurrence of maternal egg-caring behavior in *P. chinensis*.

Key words: benefit-cost tradeoff, egg mortality, offspring fitness, parental care, *Plestiodon chinensis*

INTRODUCTION

Parents may influence the phenotype and performance of their offspring and thereby improve offspring fitness

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via a variety of ways (e.g., investing more energy into offspring, providing favorable environmental conditions for embryonic or larval development, and helping juveniles develop their survival skills) (Clutton-Brock 1991; Uller 2008; Smiseth *et al.* 2012; Burgess & Marshall 2014; Du *et al.* 2014; Klug & Bonsall 2014; Li *et al.* 2021). Parental care behavior is one of the most common forms of parental effort and occurs in various animal groups from arthropods to mammals (Queller 1997). Parental care behavior contributes substantially to better growth and survival in offspring (Eggert *et al.* 1998; Gubernick & Teferi 2000; Salomon *et al.* 2005; Langkilde *et al.* 2007), but entails potential fecundity and survival costs for mothers or fathers (Reynolds & Gross 1990; Klug &

Bonsall 2014; Dugas *et al.* 2016). Coexistent offspring benefits and parental costs associated with parental care behavior inevitably lead to a trade-off between them, which can conversely influence behavioral expression (Maestriperi 1994; Cain & Ketterson 2013; Klug & Bonsall 2014). Predictably, the evolution of parental care behavior would be favored when the benefits of this behavior evidently outweigh its costs (Zink 2003; Huang & Pike 2013; Klug & Bonsall 2014).

Despite being rare in reptiles, various categories of parental care can be found frequently in scincid lizards, which are generally performed by mothers (Shine 1988; While *et al.* 2015). In skinks, post-ovipositional females not only care for (and brood) their eggs, but also guard their eggs and hatchlings against potential predators (Hasegawa 1985; Somma 1987; Somma & Fawcett 1989; Vitt & Cooper 1989; O'Connor & Shine 2004). In these cases, maternal egg-caring behavior may serve a protective function against desiccation, pathogen infection, and other threats (Shine 1988; Lourdaïs *et al.* 2007; While *et al.* 2015). While offspring benefits associated with egg-caring behavior (such as reduced egg mortality, improved offspring quality) have been explored in some species (Somma & Fawcett 1989; Huang 2006; Huang & Pike 2013), the future survival and reproductive costs for caring females are rarely quantified, likely because it requires conducting long-term surveillance studies (Huang & Pike 2013). Energy costs indirectly evaluated via changes in maternal body conditions, that is normally estimated using body length and mass measurements, during (and after) the egg-caring period have been used to partially indicate maternal costs associated with egg-caring behavior, and showed to be detectable, but trivial, in some snake species (Shine *et al.* 1997; Stahlschmidt & DeNardo 2009a). Moreover, offspring benefits and maternal costs may be modulated under different environmental conditions (Shine 1988; Huang & Pike 2013). For example, high predation pressure may increase the survival costs of maternal egg attendance for females, but also increase the potential benefits to offspring. Generally, post-ovipositional females must make a choice to enhance care investment on their eggs, or directly abandon (even eat) their eggs when facing such a situation (Huang 2006; Klug & Bonsall 2007). Quantifying the benefits and costs of maternal care is rarely done in scincid species or populations (largely owing to the high difficulty of maternal cost measurement, see Huang & Pike 2013). Based on currently available data, we were still unable to fully understand the adaptive significance of egg-caring behavior in these species. Therefore, gathering more information from different species might be a necessary undertaking.

The Chinese skink, *Plestiodon* (formerly *Eumeces*) *chinensis*, is a medium-sized oviparous scincid lizard widely distributed in southeastern China, and can be found in a variety of habitats often not far from water bodies (Yang *et al.* 2020). In *P. chinensis*, oviposition normally occurs between late May and early July, with females larger than 85 mm snout-vent length (SVL) laying a single clutch of 7–30 pliable-shelled eggs (Lu *et al.* 2012, 2021). According to our laboratory observations, females from different populations across a wide geographical area (approximately north latitude from 24.8° to 29.5°, east longitude from 108.5° to 119.9°) often remain in the nest and coil around the eggs after oviposition (Lu *et al.* unpublished data), thereby providing a suitable system to evaluate the benefits and costs of maternal egg-caring behavior. In this study, we randomly assigned female *P. chinensis* into 1 of the 3 different treatments (females that cared for their eggs without interference or under simulated predation pressure, those that deprived of egg-caring) to evaluate care-induced maternal energy costs by measuring body mass and condition changes, as well as offspring benefits by measuring egg mortality and hatchling performance (e.g., size, locomotive ability, early growth, and survival). On the basis of previous results of maternal care in some reptilian species (Somma & Fawcett 1989; Shine 1988; Huang 2006; Huang & Pike 2013; Stahlschmidt & DeNardo 2009a), we predicted that: (1) offspring benefits (such as egg survival, hatchling size, survival, and growth) would be improved substantially under maternal egg-caring; and (2) maternal energy costs might not be necessarily evident but would increase under simulated predation pressure.

MATERIALS AND METHODS

Animal collection and husbandry

We collected adult *P. chinensis* larger than 85 mm SVL in late April 2018 in Guilin (25°26'N, 110°20'E), Guangxi Province, China, and transported them to our laboratory in Hangzhou Normal University. After being measured for SVL (from the tip of the snout to the anterior edge of the vent) to the nearest 0.01 mm with a Mitutoyo digital caliper and body mass to the nearest 1 mg on a Mettler-Toledo analytical balance, skinks were evenly assigned to 1 of 6 enclosures (in the outdoor courtyard, length × width × height: 200 × 160 × 60 cm, 7–9 females and 4–5 males in each enclosure) filled with moist sand covered with grass for acclimation to the laboratory environment. There was a large bird-proofing metal net over the

outdoor courtyard to prevent predators (but not light) from entering.

Experimental treatment

After 2 weeks, 24 females with intact or completely regenerated tails were selected and removed from the enclosures, and transferred individually into plastic terraria ($60 \times 50 \times 55$ cm) filled with ~ 15 cm of moist sand. These individuals were then assigned to different groups as follows: normally egg-caring females (i.e., control, $N = 10$), egg-caring females exposed to simulated predation pressure (hereafter snake-exposed females, $N = 8$), and care-deprived females ($N = 6$). A plastic transparent container (diameter = 25 cm, depth = 20 cm, with small holes on the sides for ventilation) containing a red-banded snake *Lycodon rufozonatus* and moist sand substrate was placed in each terrarium to simulate a predation risk environment for the snake-exposed group; a similar container with no snake was placed in each terrarium for other groups. Skinks could use visual cues in predator detection on account of container transparent visibility, although they might largely rely on olfactory cues (chemical cues from snake predators could flow out through the holes in the container). Terraria were placed in the outdoor courtyard, so that animals in the terraria could utilize natural sunlight to regulate their body temperature. The substrate in the terraria was kept evenly moist by spraying with distilled water every morning. Food (mealworms [*Tenebrio molitor* larvae] and house crickets [*Achetus domestica*]) was provided *ad libitum* once daily, and water enriched with vitamins and minerals was freely available. Several cameras were suspended above the terraria to record the activities of animals in the terraria. Afterward, we analyzed the video clips obtained from cameras using MGI VideoWave III software (MGI Software Co., Canada) to determine the duration of outside-nest activity within a day (daily mean time spent outside the nest).

A total of 22 females successfully produced a clutch of eggs between 2 June and 13 June. One female from the snake-exposed group and one from the care-deprived group did not lay eggs, and their corresponding data were excluded in subsequent analyses. The time of oviposition was recorded for each ovipositing female. If egg-caring female *P. chinensis* are disturbed greatly, they may eat the eggs (Lu *et al.* personal observation). In order to minimize the disturbance to post-ovipositional females and avoid the occurrence of infanticide, only one randomly selected egg was picked out cautiously from each clutch. The within-clutch variation of egg mass in *P. chinensis* is relatively small (mean value of coefficient variation

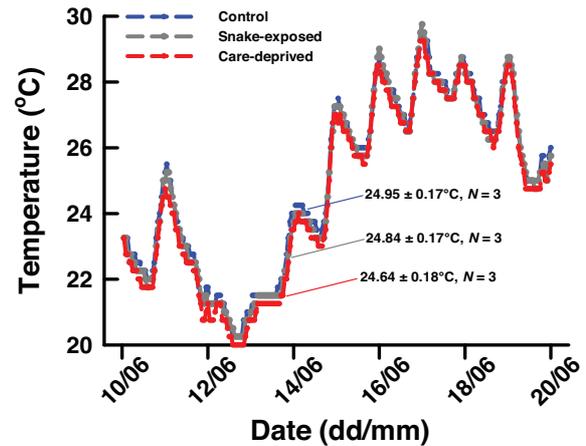


Figure 1 Temperatures in randomly-selected nests (during 10 days within the egg-caring period) recorded by iButton temperature loggers.

for within-clutch mass is approximately 5%, Lu *et al.* 2021). Therefore, to use the mass of one egg from each clutch to be representative of the clutch is a valid approach that captures among-clutch variation in egg size. These eggs were returned to their nest after being weighed. Thermocron iButton temperature loggers (DS1921, 711C, MAXIM Integrated Products/Dallas Semiconductor, Sunnyvale, USA) were carefully placed in several randomly selected nests ($N = 3$ in each group) at a similar depth to record the temperature every 1 h. Fluctuating temperature recorded over a 10-day period was presented in Fig. 1. The mean nest temperatures of control (mean \pm standard error: $24.95 \pm 0.17^\circ\text{C}$, paired-sample t -test, $t = 25.84$, $df = 239$, $P < 0.001$, $d = 0.115$) and snake-exposed ($24.84 \pm 0.17^\circ\text{C}$, $t = 16.65$, $df = 239$, $P < 0.001$, $d = 0.074$) groups were slightly higher than that of the care-deprived group ($24.64 \pm 0.18^\circ\text{C}$). Post-ovipositional females in the maternal-care-deprived group were removed from the terraria and transferred to other terraria with similar conditions, whereas those in other groups were left undisturbed and kept in their terraria. The daily food intake of post-ovipositional females was evaluated by providing 6 mealworms for each individual in the morning everyday (0730–0830). Eaten mealworms were counted and uneaten ones were removed from the terraria in the afternoon (1600–1700) over a 7-day period after oviposition.

Hatchling performance

Egg clutches were retained in their nests until hatching. The time of egg hatching was between 11 July and 19 July

for different clutches. Hatching success was calculated for each clutch. Newly hatched individuals were removed from terraria, and measured for SVL with a Mitutoyo digital caliper (0.01 mm precision), tail length (from the posterior edge of the vent to the tip of the tail) with a ruler (1 mm precision), and body mass on a Mettler-Toledo analytical balance (1 mg precision). Hatchling locomotor performance was estimated at a body temperature of 30°C, which is the optimal temperature for sprint speed in *P. chinensis* hatchlings (Lu *et al.* 2021). Hatchlings were individually housed in a terraria kept in a climate-controlled room maintained at 30 (± 0.5)°C for a minimum of 30 min prior to testing, then introduced at one end of a 2 m racetrack with one transparent side, and chased along the racetrack. The running performance of each hatchling was tested twice with a minimum of 30 min of rest (maintained in their terraria) between the 2 trials, and filmed laterally with a Panasonic HDC-SD900GK digital video camera (25 frames per second). Hatchlings that refused to run were excluded from subsequent analyses. The video clips were later examined on a frame-by-frame basis using the MGI VideoWave III software. The fastest 25 cm track interval was selected and its corresponding time was recorded for each hatchling. The sprint speed was defined as the maximum speed over a 25 cm interval. Following running trials, hatchlings were marked individually by toe-clipping, and then randomly moved into 1 of 6 outdoor enclosures (200 × 160 × 60 cm, 40–50 individuals in each enclosure, individuals from a single clutch were split into different enclosures). These enclosures were built in another courtyard with similar bird-proofing net over it. Small mealworms and house crickets were provided in excess and spread throughout the enclosure. Hatchlings in enclosures were recaptured, and re-measured for SVL and body mass on the 30th and 60th days after hatching to determine their early growth. After the measurement on the 60th day (approximately in late September), surviving individuals were released at the sites where their mothers were collected. Relative survival rate was calculated as the number of recaptured hatchlings divided by the total number of individuals in each group.

Female body condition after egg hatching

Post-ovipositional females were still kept in the terraria and provided food as before, and measured for SVL and body mass at 30-day intervals. For both females and hatchlings, we calculated their body condition as the residual from the linear regression of ln-transformed body mass against ln-transformed SVL.

Statistical analysis

The Kolmogorov–Smirnov test was used to determine normality of data (including the residuals from linear regression models) distribution, and Bartlett's test was used to confirm homogeneity of variances between groups. One-way analysis of variance (ANOVA) was used to examine differences in body size and condition, outside-nest activity duration, and food intake of females among groups. Mixed model ANOVA with maternal treatment as a fixed factor and clutch origin as a random factor was used to examine differences in hatchling traits (size and sprint speed) among groups. Repeated-measures ANOVA was used to examine differences in female (and hatchling) body size and condition changes among groups. The *G*-test was used to examine differences in egg hatching success and hatchling survival rate among groups. The values of Cohen's *d* for *t*-test, partial eta-square (η_p^2) for ANOVA, and Cramer's ϕ for *G*-test were presented as the measures of effect size, respectively. Generalized linear mixed model (GLMM) analysis with maternal treatment as a fixed factor and clutch origin as a random factor was also used to explore the potential confounding of other factors on egg hatching success (with hatching success as a binomial dependent variable) or hatchling survival (with hatchling survival as a binomial dependent variable, hatchling SVL and hatching date as independent variables). Values in this article were presented as mean \pm standard error (SE), and the significance level was set at $\alpha = 0.05$.

RESULTS

Pre-ovipositional body mass ($F_{2,19} = 0.10$, $P = 0.909$, $\eta_p^2 = 0.010$), SVL ($F_{2,19} = 0.29$, $P = 0.754$, $\eta_p^2 = 0.029$), and condition ($F_{2,19} = 0.24$, $P = 0.787$, $\eta_p^2 = 0.025$) of reproductive females did not differ significantly among different groups. Snake-exposed females spent less time on outside-nest activity than other groups prior to oviposition (~9% and 7% less than the mean duration of outside-nest activity of control and care-deprived females, respectively); egg-caring (control and snake-exposed) females spent a significantly shorter amount of time for outside-nest activity than care-deprived females after oviposition (~ 63 times and 39 times more than those of control and snake-exposed females respectively, Table 1). Consequently, egg-caring females had lower daily food intakes during the egg-caring period compared with care-deprived females (~83% decrease in daily food intake, Table 1). No death occurred in post-ovipositional females, but the change in body size (mass and SVL) was

Table 1 Descriptive statistics (expressed as mean \pm SE) for the duration of outside-nest activity and daily food intake of female *Plestiodon chinensis* in different treatment groups

		Treatment groups of females			Statistical analyses
		Control	Snake-exposed	Care-deprived	<i>F</i> -value, significance level and effect size
Duration of outside-nest activity (min)	Pre-oviposition	173.5 \pm 3.5	157.5 \pm 3.7	169.2 \pm 2.6	$F_{2,19} = 5.52, P = 0.013, \eta_p^2 = 0.368$
	Egg-caring period	2.9 \pm 0.9	4.6 \pm 1.4	184.7 \pm 4.9	$F_{2,19} = 240.37, P < 0.001, \eta_p^2 = 0.962$
Daily food intake (number of mealworms)		0.53 \pm 0.09	0.53 \pm 0.11	3.04 \pm 0.12	$F_{2,19} = 155.55, P < 0.001, \eta_p^2 = 0.942$

Table 2 Hatching success and incubation duration of eggs, and survival rate at the 30th and 60th day of hatchling of *Plestiodon chinensis* from different treatment groups

		Treatment groups of females			Statistical analyses
		Control	Snake-exposed	Care-deprived	<i>G</i> - (or <i>F</i> -) value, significance level and effect size
Egg hatching success		99.4% (160/161)	88.7% (94/106)	26.3% (20/76)	$G = 169.75, df = 2, P < 0.001, \varphi = 0.722$
Egg incubation length (days)		35.9 \pm 0.6	35.3 \pm 0.5	38.7 \pm 0.3	$F_{2,17} = 4.49, P = 0.027, \eta_p^2 = 0.345$
Hatchling survival at 30-day		25.0% (40/160)	18.1% (17/94)	5.0% (1/20)	$G = 6.11, df = 2, P = 0.047, \varphi = 0.136$
Hatchling survival at 60-day		23.75% (30/160)	14.83% (15/94)	0% (0/20)	$G = 7.80, df = 2, P = 0.020, \varphi = 0.129$

significant in each group throughout the experiment (all $P < 0.02$, Fig. 2). Egg-caring females had poorer body conditions than care-deprived females after egg caring (at egg hatching) ($F_{2,19} = 5.59, P = 0.012, \eta_p^2 = 0.371$). However, the former seemed to gain mass more quickly than the latter in the following 2 months ($F_{4,38} = 5.44, P < 0.01, \eta_p^2 = 0.364$). Consequently, no significant between-group differences in body mass ($F_{2,19} = 0.62, P = 0.547, \eta_p^2 = 0.062$) and condition ($F_{2,19} = 2.79, P = 0.087, \eta_p^2 = 0.227$) were found 2 months later (Fig. 2).

No significant difference among maternal treatment groups was found in the mass of randomly selected egg from each clutch ($F_{2,19} = 2.14, P = 0.146, \eta_p^2 = 0.183$). In this study, a total of 274 hatchlings were collected. The incubation length of care-deprived eggs was longer than that of eggs cared for by females (Table 2). Nearly all of the eggs hatched in the control group. The hatching success of care-deprived eggs was significantly lower than that of eggs cared for by females ($\sim 73\%$ and 62% lower than those of control and snake-exposed groups, respectively, Table 2, GLMM result, $F_{2,340} = 19.58, P < 0.001$). Hatchling body mass differed significantly among clutches (mixed model ANOVA with clutch origin as a random factor, $F_{17,254} = 26.77, P < 0.001, \eta_p^2 = 0.642$),

but not among treatment groups ($F_{2,17} = 1.81, P = 0.193, \eta_p^2 = 0.174$). Hatchling SVL was affected by both the experimental treatment ($F_{2,17} = 4.19, P = 0.033, \eta_p^2 = 0.329$) and clutch origin (mixed model ANOVA with clutch origin as a random factor, $F_{17,254} = 43.57, P < 0.001, \eta_p^2 = 0.745$). Hatchlings from eggs in the control group showed greater SVLs than those from care-deprived eggs ($\sim 7\%$ longer than the mean SVL of care-deprived group, Fig. 3). The sprint speed of hatchlings was also affected by the experimental treatment ($F_{2,22} = 3.67, P = 0.042, \eta_p^2 = 0.248$) and clutch origin ($F_{17,212} = 1.81, P = 0.028, \eta_p^2 = 0.127$). Hatchlings from eggs cared for by females ran faster than those from care-deprived eggs (control: 48.0 ± 0.9 cm/s; snake-exposed: 47.8 ± 1.0 cm/s; care-deprived: 38.0 ± 3.7 cm/s).

No hatchlings from care-deprived eggs survived 2 months after hatching. Therefore, the survival rate of hatchlings from care-deprived eggs was significantly lower than that of hatchlings from cared eggs (Table 2). However, when taking the effects of hatchling size variation and clutch origin into account, the difference in hatchling survival between different maternal treatments was not statistically significant (GLMM result: 30-day, $F_{2,269} = 0.67, P = 0.515$; 60-day, $F_{2,269} = 0.42,$

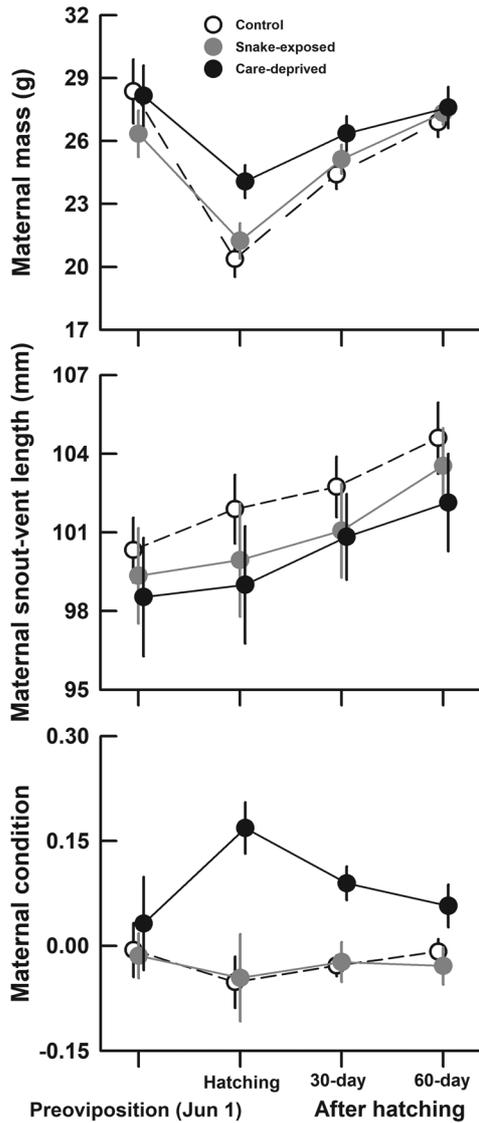


Figure 2 Changes in body mass, snout-vent length, and body condition of female *Plestiodon chinensis* in different treatment groups. Values are expressed as mean \pm SE.

$P = 0.657$). Repeated-measures ANOVAs showed that changes in hatchling mass (increased 4.4 times within 2 months, $F_{2,78} = 169.57$, $P < 0.001$, $\eta_p^2 = 0.813$) and SVL (increased 1.5 times within 2 months, $F_{2,78} = 581.12$, $P < 0.001$, $\eta_p^2 = 0.937$) were significant within 2 months after hatching, but did not differ between the control and snake-exposed groups (maternal treatment group \times test time interaction: mass, $F_{2,78} = 0.30$, $P = 0.744$, $\eta_p^2 = 0.008$; SVL, $F_{2,78} = 0.48$, $P = 0.620$, $\eta_p^2 = 0.012$, Fig. 3).

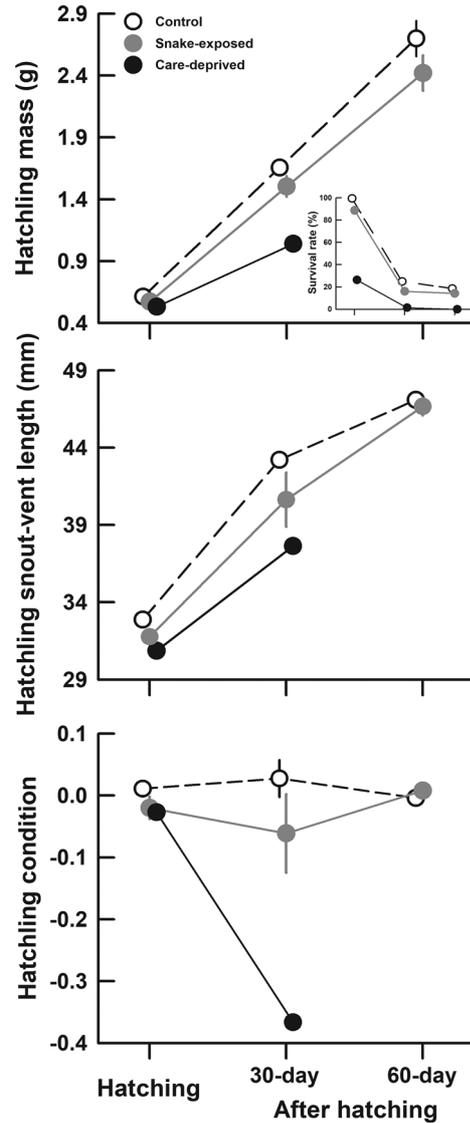


Figure 3 Changes in body mass, snout-vent length, and body condition of hatchling *Plestiodon chinensis* from different treatment groups. Values are expressed as mean \pm SE. No data on the body size and condition of hatchlings from care-deprived eggs on the 60th day after hatching were presented in graphs because none of them survived for 2 months. The inlaid small-graph showed the survival rate of eggs or hatchlings that was calculated as the number of surviving individuals divided by the total number of eggs produced in each treatment group.

DISCUSSION

As reported in other *Plestiodon* species (Hasegawa 1985; Somma & Fawcett 1989; Vitt & Cooper 1989), *P. chinensis* females stayed in their nest and exhibited

typical egg-caring behaviors after oviposition. Egg-caring behavior in *P. chinensis* decreased egg mortality, increased offspring quality (larger size and better performance) and survival. However, it also imposed several energy costs for post-ovipositional females, as manifested by decreased food intake during the egg-caring period, and poorer body conditions at egg hatching. Nearly no time spent for outside-nest activity during the egg-caring period would predictably reduce the food (and thus energy) intake of egg-caring females, resulting in mass loss and relatively poorer body condition at the end of this behavior. Interestingly, the energy cost associated with egg-caring behavior may not persist for a long time in this species, because the body mass and condition of egg-caring females became equal to those of care-deprived females within a few months after egg hatching in captivity. These results indicated that egg-caring-induced maternal energy costs (especially in single-clutched species within a reproductive season, such as *P. chinensis*) could be completely or partially balanced by increasing food intake in the subsequent period as long as the food is ample in their natural habitat. Similar results were also observed in other reptilian species. For example, mass loss during the egg-caring period is observable for post-ovipositional female *Eutropis* (formerly *Mabuya*) *longicaudata*, but it can be balanced after a subsequent foraging period (Huang 2007). The energy cost caused by egg-caring could be trivial even during the actual egg-caring period in some snake species, such as *Python regius* (less than 6% mass loss in egg-caring females, Aubret *et al.* 2005b). Certainly, other aspects of maternal costs (e.g., increased parasite load, and reduced future survival and reproductive output) may be entailed by egg-caring behavior (Huang 2007; Stahlschmidt *et al.* 2012). Whether those costs would occur in egg-caring *P. chinensis* females should be confirmed in future studies.

On the other hand, the benefits associated with maternal egg-caring behavior for offspring were remarkable. Similar to findings in other lizard species (e.g., *P. okadae*, Hasegawa 1985; *P. septentrionalis*, Somma & Fawcett 1989; *E. longicaudata*, Huang 2006; *Ptyodactylus oudrii*, Mateo & Cuadrado 2012), the mortality of *P. chinensis* eggs was markedly reduced when post-ovipositional females remained within their nests throughout the egg-caring period. Tongue licking of the eggs by caring females could frequently be observed in some scincid lizards (Evans 1959), and this behavior is believed to remove mold on the eggshell and increase the moisture for eggs. Therefore, infection protection and hydric modification associated with egg-caring could be important factors for reducing egg mortality in this species (Somma

& Fawcett 1989; Mateo & Cuadrado 2012). Nonexclusively, the presence of post-ovipositional females may produce a suitable thermal environment for egg incubation, and thus increase hatching success (Mateo & Cuadrado 2012). Maternal egg-caring behavior enhancing egg hatching success via nest thermal modification has also been found in some python species, such as *Liasis fuscus* and *Antaresia childreni* (Shine *et al.* 1997; Stahlschmidt & DeNardo 2009a). In addition, maternal egg-caring behavior enhanced nest temperatures because the temperature of randomly selected nests with the presence of post-ovipositional females was slightly higher than that of nests without females. As a result, eggs cared by post-ovipositional females had a shorter incubation length than uncared-for eggs.

In addition to reduced egg mortality, hatchlings from eggs cared for by post-ovipositional females were larger, running-faster, and more likely to survive in the next few months than those from care-deprived eggs, indicating a long-lasting positive impact of maternal care on offspring performance. The above results were consistent with our first prediction. Interestingly, between-group difference in hatchling survival was not significant after removing hatchling size and clutch effects, which indicated that lower survival was primarily associated with poorer hatchling quality (e.g., smaller size), resulting from relatively less maternal pre- and post-ovipositional investment even within each clutch. Improved offspring quality and survival are common types of care benefits for offspring, and have been documented in various species, including beetles, spiders, fish, and others (Eggert *et al.* 1998; Salomon *et al.* 2005; Schradin & Pillay 2005; Tinne *et al.* 2005). However, only a very limited number of studies focused on reptilian species show some inconsistencies. For example, eggs cared for by post-ovipositional females produce larger and better-performing (faster swimming and developing) hatchlings in the ball python, *Py. regius* (Aubret *et al.* 2005b), but produce smaller and poorer-performing hatchlings in the children's python, *A. childreni* (Stahlschmidt & DeNardo 2009b). Smaller and poor performing hatchlings were produced because coiling tightly around the eggs by females created a hypoxic incubation environment for developing embryos (Stahlschmidt & DeNardo 2008, 2009a). Such a situation was not likely to occur in *P. chinensis*, because the relatively stubby body of female skinks would not allow them to coil tightly around a whole clutch of eggs, as observed in snakes.

Predation pressure may affect the expression of maternal care in lizards (Huang *et al.* 2013; Cabezas-Cartes *et al.* 2018). Generally, egg-caring females may become

relatively more aggressive and enhance care investment (e.g., prolong the time of maternal care) when encountering potential predators (Huang & Pike 2013; Cabezas-Cartes *et al.* 2018). However, post-ovipositional females of *P. chinensis* rarely left their nests throughout the entire egg-caring period, and the time staying in the nest of snake-exposed females was not longer than that of control females. Moreover, there were no differences in hatchling size and sprint speed between the snake-exposed and control groups, which was inconsistent with our second prediction. These results might indicate a very limited impact of simulated exposure to a potential predator (such as *L. rufozonatus*) on female expression of maternal care and hatchling performance in *P. chinensis* under our specific conditions. Future studies should assess the generality of this result by conducting experiments under more realistic conditions or exposure to other predators.

In summary, maternal egg-caring behavior in *P. chinensis* reduced egg mortality, improved hatchling quality, and thus enhanced offspring fitness (larger, faster-running, and better-growing hatchlings often have a greater ability to forage and avoid predators, and hence greater chances to survive, Olsson & Madsen 2001; Warner & Shine 2005), although it also simultaneously entailed unavoidable energy costs for egg-caring females (a loss of mass during the egg-caring period). Interestingly, the energy cost of maternal care for post-ovipositional females might be minor relative to its resultant benefits for offspring (Aubret *et al.* 2005a; Huang 2007). An apparent benefit that outweighed its cost may play a decisive role in the occurrence of maternal egg-caring behavior in *P. chinensis*. From another point of view, maternal care allows egg-caring females to improve their fitness to some extent by increasing offspring fitness. Our study provided additional empirical evidence for the role of benefit-cost tradeoff in determining the evolution of parental care behavior in reptiles, and helped to improve our understanding of differential parental care behaviors across different animal taxa.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHOR CONTRIBUTIONS

W.D. and H.L. conceived and designed the study. J.W. and C.K. carried out the experiments. J.W. and H.L. performed data analyses and wrote the first draft of the manuscript. All authors contributed substantially to revisions.

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