RESEARCH ARTICLE

WILEY ZOOBIOLOGY

Impacts of maternal characteristics and temperature on juvenile survival in the crocodile lizard: Implications for conservation

Qiyu Li[1,2] | Shuyi Luo[3] | Chunsheng Yang[3] | Shuran Li[4] |
Jun Guo[3] | Jiasong He[3] | Yaohuan Chen[3] | Chengming Huang[1] |
Zhengjun Wu[5,6] | Weiguo Du[1]

[1] Key Laboratory of Animal Ecology and Conservation Biology, Institute of Zoology, Chinese Academy of Sciences, Beijing, People's Republic of China

[2] University of Chinese Academy of Sciences, Beijing, People's Republic of China

[3] Daguishan National Nature Reserve for Crocodile Lizards, Hezhou, Guangxi, People's Republic of China

[4] College of Life and Environmental Science, Wenzhou University, Wenzhou, Zhejiang, People's Republic of China

[5] Key Laboratory of Ecology of Rare and Endangered Species and Environmental Protection (Guangxi Normal University), Ministry of Education, Guilin, Guangxi, People's Republic of China

[6] Guangxi Key Laboratory of Rare and Endangered Animal Ecology, Guangxi Normal University, Guilin, Guangxi, People's Republic of China

Correspondence
Weiguo Du, Key Laboratory of Animal Ecology and Conservation Biology, Institute of Zoology, Chinese Academy of Sciences, Beijing 100101, People's Republic of China.
Email: duweiguo@ioz.ac.cn
Zhengjun Wu, Key Laboratory of Ecology of Rare and Endangered Species and Environmental Protection (Guangxi Normal University), Ministry of Education, Guilin 541004, Guangxi, People's Republic of China.
Email: wu_zhengjun@yahoo.com.cn

Captive breeding is an important conservation measure that may restore and enhance wild populations of rare and endangered species. Multiple anthropogenic hazards have brought the crocodile lizard, *Shinisaurus crocodilurus*, to the brink of extinction. We initiated a captive breeding program and quantified female reproductive traits, including reproductive timing, litter size, litter mass, and neonate size. To identify the internal and external factors affecting female reproductive function, we then analyzed how maternal age is related to body size, temperature, and female reproductive traits. We found that larger female crocodile lizards produced more offspring than smaller ones, as both litter size and litter mass were positively related to maternal body size. In contrast, neonate size was independent of maternal body size. Maternal reproductive output varied among different age groups. Young and old females had significantly smaller living litter size and mass than middle-aged females. Among captive females, one-third exhibited early parturition in autumn and winter instead of the following spring, a pattern probably associated with higher ambient temperatures in captivity. Although female reproductive output and neonatal body size did not differ between early- and normal-parturition females, offspring from the former group died earlier than those from the latter. Our study highlights the danger of climate change in hastening parturition, a phenomenon that could significantly hamper neonate survival and impede population recruitment.

KEYWORDS
captive breeding, climate warming, litter size, neonate size, reproductive timing, *Shinisaurus crocodilurus*

Qiyu Li and Shuyi Luo contributed equally to this work.

1 | INTRODUCTION

Captive breeding and the release of captive-bred individuals are widely-used conservation strategies that can restore and improve wild populations of endangered species, increasing the probability of long term persistence (Andrew, Georgina, & Leader-Williams, 1996; Griffiths & Pavajeau, 2008). Captive breeding provides endangered species with a safe environment through food supplementation, removal of predators, and health care. As a result, fecundity and survival rates in captivity are generally higher than those in the wild (Ricklefs, 1998, 2000; Ricklefs & Scheuerlein, 2001). However, captive breeding often causes behavioral and physiological changes, as well as a loss of genetic variability, which may limit eventual settlement success in nature (Charlesworth & Charlesworth, 1987; Kati, Dufrêne, Legakis, Grill, & Lebrun, 2004; Slade et al., 2014; Snyder et al., 1996). Therefore, producing healthy individuals and maintaining self-sustaining populations are essential to achieving the ultimate goal of captive breeding: reintroduction and population expansion of endangered species (Kleiman, 1980; Snyder et al., 1996).

Few attempts have been made to breed reptiles for conservation purposes (Hua et al., 2017; Schmidt, Espinoza, Connell, & Hughes, 2018), especially compared with the efforts devoted to endangered mammals (Nuss & Warneke, 2010; Smucny et al., 2004; Zhang, Swaisgood, & Zhang, 2004). Nonetheless, unlike many larger-bodied vertebrate species, most reptiles are well-suited to captive breeding and reintroduction programs given their small body size, relatively high fecundity, and low maintenance requirements (Shine, 2005; Hua et al., 2017; Schmidt et al., 2018).

Monitoring a species' reproductive traits is essential to a successful captive breeding program. Among females, reproductive traits are affected by a number of internal and external factors (e.g., age, body size, and environmental conditions) (Du, 2006; Ma, Sun, Li, Sha, & Du, 2014; Martin & Shepherdson, 2012; Wang, Zeng, Li, Bi, & Du, 2016). For example, older or larger females tend to produce more or larger offspring than younger, smaller females (e.g., Du, Ji, Zhang, Xu, & Shine, 2005; Forsman & Shine, 1995; Ji & Wang, 2005). Reptiles are ectothermic vertebrates, so environmental temperature may significantly affect their reproduction. For example, high temperatures experienced by the mother can speed up reproduction timing through enhancing embryonic development rate (Ma et al., 2014). Together, these changes can significantly affect reproductive output and even offspring traits (Wang et al., 2016). Therefore, the thermal environment is an important factor in the captive breeding of reptiles that determines reproductive success and offspring quality.

First reported from southern China (Ahl, 1930; Zhang, Zeng, & Zhou, 2002), the crocodile lizard (*Shinisaurus crocodilurus*) is the only living representative of the family Shinisauridae and a remnant reptile from the Pleistocene. Over 70 years later, the first Vietnamese subpopulation was reported in the Yen Tu Nature Reserve, Quang Ninh Province, northeastern Vietnam (Quyet & Ziegler, 2003). The species is now on the brink of extinction owing to habitat loss and fragmentation as a result of anthropogenic activity, including timber logging, illegal poaching for the pet trade industry, exploitation for medicine, and coal mining (Huang et al., 2008; van Schingen, Cuong The, et al., 2014). A field survey in 2004 estimated that only 950 individuals remained across eight wild populations in southern China, all with low genetic variability (Huang et al., 2008; Huang, Wang, Li, Wu, & Chen, 2014). In addition, a 2015 survey estimated that fewer than 150 mature individuals were present in Vietnam (van Schingen et al., 2016; van Schingen, Ihlow, et al., 2014). Ecological modeling predicts that climate change will cause all desirable habitats for crocodile lizards to vanish by 2081–2100 (Li et al., 2013). To prevent extinction, some legislation has been passed. For example, *S. crocodilurus* has been included as a Category I protected species in China since the 1980s and was listed on the CITES Appendix I in 2017 to comprehensively prohibit their trade worldwide.

The viviparous crocodile lizard is an ecological habitat specialist, preferring mountainous streams within evergreen broadleaf forests and bamboo forests (Zhang, 2002; Huang et al., 2008). For this species, the presence of a sand stream bed and vegetation coverage are the two main features that determine habitat selection (Wu, Dai, Nin, Huang, & Yu, 2012). Crocodile lizards have low body temperatures in the wild in April and May, ranging from 18.4 to 22.5 °C (Wang, Wu, Yu, Huang, & Zhong, 2008). The mean selected body temperature (24.31–26.56 °C) and resting metabolic rate (0.052–0.204 ml O_2 g^{-1} h^{-1}) are higher in juveniles (1–2 years old) and gravid females than in adult males and non-gravid females (Wang et al., 2009). Male crocodile lizards are polygynous while females are polyandrous, with multiple paternity common among offspring from the same mother (Huang et al., 2015). Most female crocodile lizards mate in spring and summer from April to July and have a long gravid period of 9–12 months, giving birth in the next spring from April to May (Yu et al., 2009; Zhang, 2002; Zhao et al., 1998). However, we have very little detailed data on reproductive life history for this species, largely due to the logistic difficulty of quantifying reproductive traits in wild populations.

Establishing a self-sustaining captive breeding population of *S. crocodilurus* may be an effective conservation approach to reduce the risk of extinction before the reintroduction phase can be achieved (Robert, 2009). To this end, in 2010, we initiated a captive breeding program for *S. crocodilurus* and monitored their reproductive life history in the Daguishan National Nature Reserve for Crocodile Lizards, Guangxi, China. In this study, we aimed to quantify the reproductive output (reproductive timing, litter size, litter mass, and neonate size) of female crocodile lizards, while identifying factors that affect reproductive traits. More specifically, we hypothesized that (i) litter size (mass) and neonate size would improve as age and body size increases; and (ii) warm conditions would speed up the timing of female reproduction. Finally, we explore the implications of our results for captive breeding and conservation of this critically endangered lizard species.

2 | MATERIALS AND METHODS

2.1 | Study site and experimental animals

Our study was performed in a national nature reserve (24°09′N, 111°81′E; elevation 97 m) for the crocodile lizard in Daguishan, Hezhou

City, Guangxi Province of China, founded in April 2005. This nature reserve is characterized by a humid subtropical monsoon climate with annual precipitation of 2000–2100 mm, and average annual temperature of 19–20 °C, with extreme low (−1 °C) and high (39–40 °C) temperatures (http://www.nmic.cn). The landscape of the nature reserve is evergreen broadleaf forest, with a large river system.

From 2014 to 2017, in a captive population, we measured the reproductive output of 54 female crocodile lizards, as well as the morphology and survival of their offspring. Subjects originated from a group of 53 individuals (25 males and 28 females) rescued from the local wild population. Captive adult lizards were raised in 2 × 3 m enclosures, with three females in each enclosure. Adult males were introduced into female enclosures during the reproductive season. Enclosures were built along the creek originally occupied by crocodile lizards, and water from the creek was diverted to the enclosures (Figure 1). The enclosure is partly covered by local vegetation, including tree species (*Ficus carica* Linn., Taxodiaceae, *Pinus*, *Citrus limon* (L.) Burm. f., *Citrus maxima*, *Melia azedarach* Linn., *Musa basjoo*, *Loropetalum chinense* var. *rubrum*) and liana (*Passiflora edulis Sims*, *Mucuna sempervirens* Hemsl.). Food (earthworms and *Tenebrio molitor* larvae) and water were provided *ad libitum* to the lizards twice a week.

From May to October 2017, we randomly set up thermochron i-Buttons (DS1921, MAXIM Integrated Products Ltd., TX; diameter, 15 mm; height, 6 mm) to measure hourly temperature in the outdoor enclosures (6 i-Buttons) and in the natural habitat (12 i-Buttons).

2.2 | Female reproductive output

In October, gravid females were housed individually in small enclosures (1 × 1 m) and monitored daily for neonates. Once emerged, the neonates were collected and their snout-vent length [SVL] (±0.01 mm) and body mass [BM] (±0.01 g) were measured. Some litters contained deceased neonates at parturition, and so we calculated both litter size (mass) and living litter size (mass), which included or excluded the deceased neonates, respectively. We

calculated the relative clutch mass (RCM) in two ways: RCM1 = litter mass/maternal postpartum body mass; RCM2 = litter mass/(maternal postpartum body mass + litter mass) (Schulte-Hostedde, Zinner, Millar, & Hickling, 2005). In this study, we only measured the SVL (n = 29, ±0.01 mm) and BM (n = 37, ±0.01 g) for some post-partum females.

2.3 | Offspring survival

The neonates were randomly assigned to small enclosures (1 × 1 m), with four individuals in each enclosure. We took photos of the tail color pattern of each neonate for individual identification. Once the offspring reached maturity, they were moved to large enclosures (2 × 3 m). Food (earthworms and larvae of *T. molitor*) and water were provided *ad libitum* to the lizards twice a week. The enclosures were checked daily, and the date when an individual was found dead was recorded. The survival of offspring was monitored for up to 3.5 years.

2.4 | Statistical analysis

All analyses were conducted with the software SPSS Statistics (version 20.0). Prior to analysis, we tested the normality and homogeneity of all variances. The difference in ambient temperature between the outdoor enclosures and wild habitat was tested using the Student's *t*-test. Linear regression and nonlinear regression were used to analyze the relationships between maternal SVL and female reproductive traits (litter size, litter mass, and neonate sizes). We used ANOVA or ANCOVA (with maternal SVL as a covariant) to determine the influence of female age and parturition timing (advanced vs. normal parturition) on female reproductive traits. Tukey's post-hoc multiple-comparisons were used to distinguish the means of significantly affected traits among age groups. A stepwise cox regression analysis was used to detect the effect of female age and parturition timing on offspring survival. All hypotheses were tested for statistical significance at the level of *p* < 0.05.
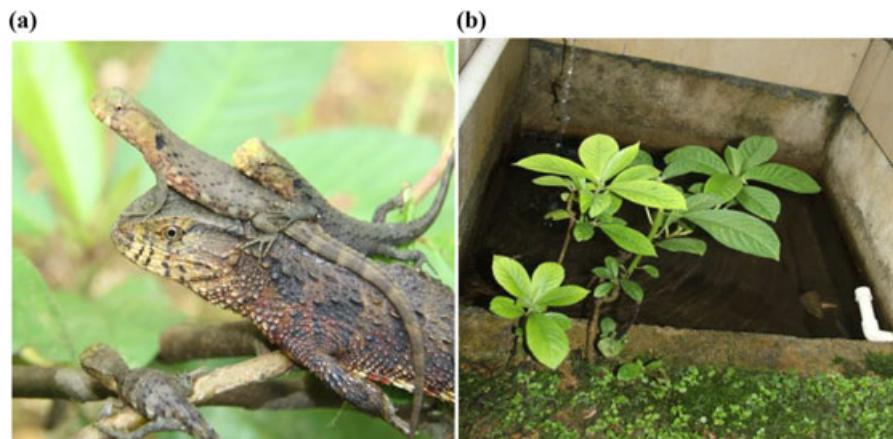

FIGURE 1 Captive female and neonate crocodile lizards, *Shinisaurus crocodilurus* (a) and their outdoor enclosures (b) in Daguishan National Nature Reserve for the crocodile lizard, Hezhou city, Guangxi Province of China
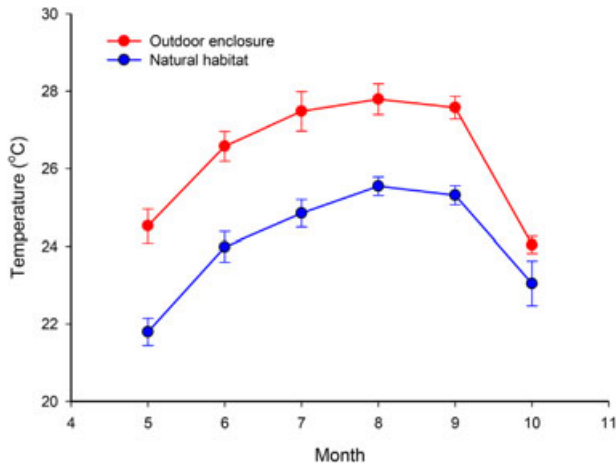
FIGURE 2 Ambient temperatures in outdoor enclosures and in the natural habitat of crocodile lizards, *Shinisaurus crocodilurus* in Daguishan National Nature Reserve from May to October 2017

3 | RESULTS

Ambient temperatures from May to October in outdoor enclosures were significantly higher than those in the natural habitat ($F_{1,96}$ = 81.3, $p < 0.0001$) (Figure 2). In captivity, some females matured at the age of 2 years, with the SVL of the smallest reproductive females at 121 mm. Females produced one litter per year, containing 3–11 (average 6.4) neonates with a mean SVL of 54.82 mm and a mean BM of 3.7 g. Larger females produced more neonates (R^2 = 0.225, $F_{1,27}$ = 7.830, $p = 0.009$) and a greater litter mass (R^2 = 0.292, $F_{1,27}$ = 11.114, $p = 0.002$) (Figures 3a and 3b). The relationship between maternal SVL and living litter size ($F_{1,27}$ = 0.453, $p = 0.506$) or living litter mass ($F_{1,27}$ = 1.358, $p = 0.254$) was nonlinear; living litter size and mass increased with the increase of maternal SVL prior to reaching 160 mm and decreased thereafter (Figures 3c and 3d). Given the positive relationship between maternal age and SVL (SVL = 3.573
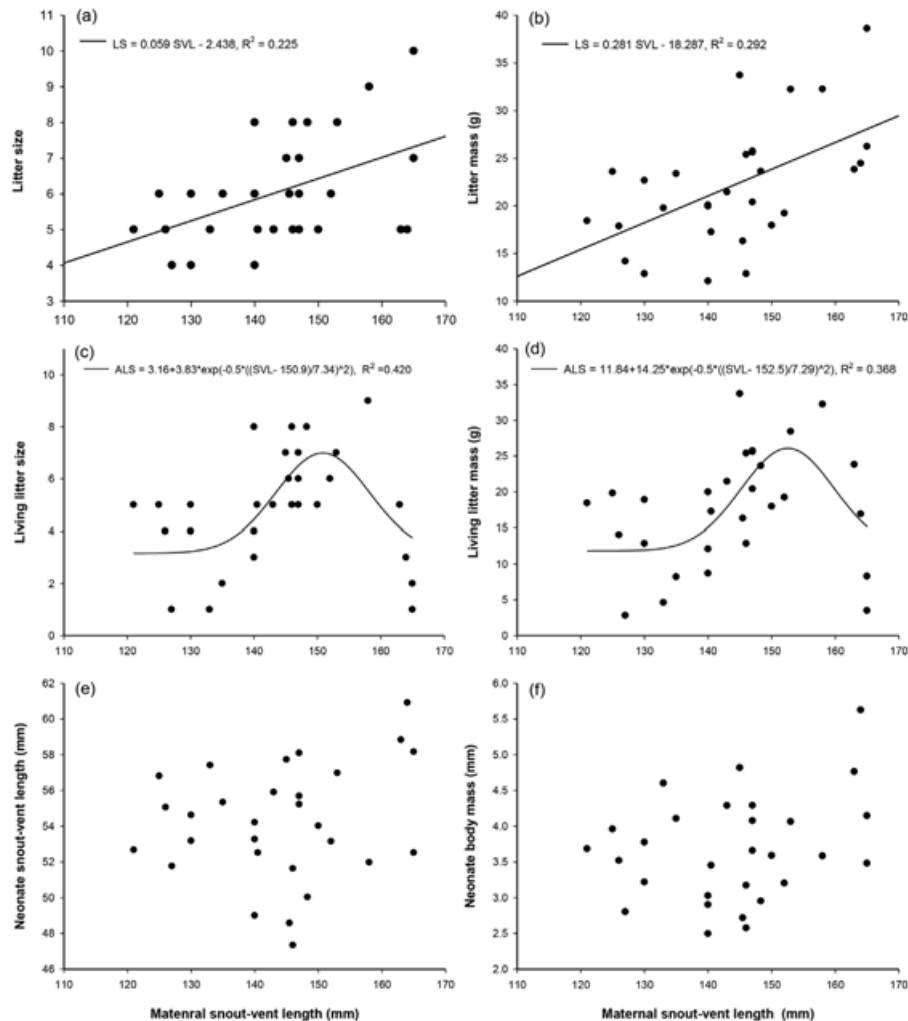

FIGURE 3 Relationships between maternal snout-vent length (SVL) and reproductive traits, including (a) litter size, (b) litter mass, (c) live litter size, (d) live litter mass, (e) neonate SVL, and (f) neonate body mass in the crocodile lizard, *Shinisaurus crocodilurus*. The relationship between maternal SVL and litter size and mass was estimated using linear regression, while the relationship between maternal SVL and living litter size and mass was estimated using nonlinear regression with a Gaussian equation
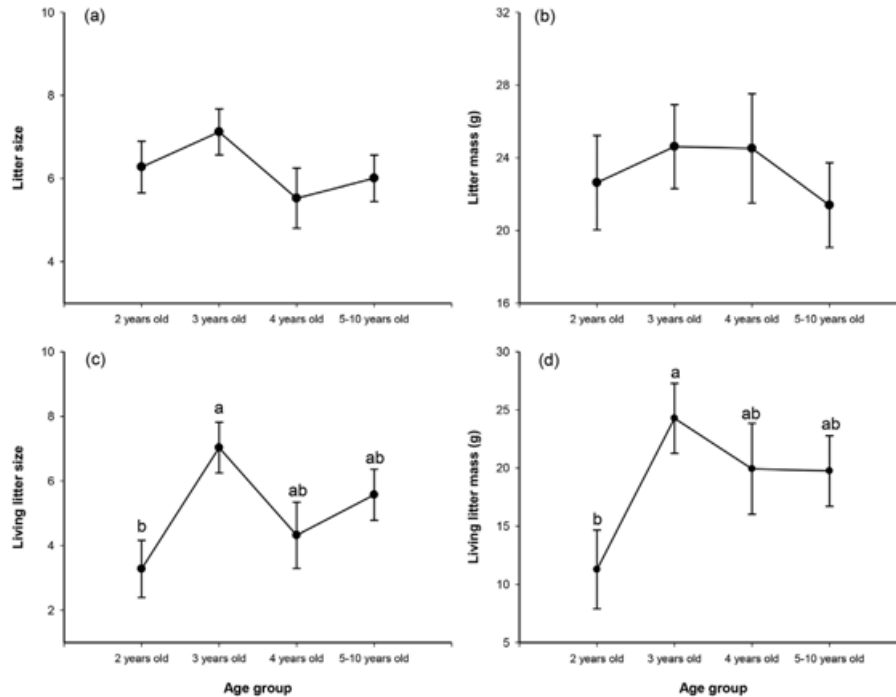
FIGURE 4 Reproductive output in different age groups of the crocodile lizard, *Shinisaurus crocodilurus*, including (a) litter size, (b) litter mass, (c) living litter size, and (d) living litter mass. Values are expressed as mean ± SE. The sample size was 12, 6, 4, and 7 for 2, 3, 4, and 5–10-year-old females, respectively

year + 130.20, R^2 = 0.459, $F_{1,27}$ = 22.872, p < 0.0001), a drop in living litter size and mass among large females indicated a decreased reproductive output in aged females. Neither neonatal SVL ($F_{1,27}$ = 1.253, p = 0.273) nor BM ($F_{1,27}$ = 2.438, p = 0.130) was correlated with maternal SVL (Figures 3e and 3f). When maternal SVL was held constant, neonatal BM was negatively correlated with litter size (r = 0.91, t = 10.92, df = 29, p < 0.0001).

After statistically removing the influence of maternal SVL, we found that litter size ($F_{3,24}$ = 1.234, p = 0.319), and litter mass ($F_{3,24}$ = 0.458, p = 0.714) did not differ among different age groups (Figures 4a and 4b). In contrast, living litter size ($F_{3,24}$ = 3.885, p = 0.021) differed significantly across age groups, while living litter mass trended toward significance ($F_{3,24}$ = 2.674, p = 0.070). Overall, the young 2-year-old females had significantly smaller living litter size and litter mass (Figures 4c and 4d). The SVL ($F_{3,24}$ = 1.087, p = 0.374), BM ($F_{3,24}$ = 1.945, p = 0.149) of neonates, and offspring survival rate through 3 years (χ^2 = 1.848, p = 0.174) were similar among different age groups.

In captivity, 33.3% (18/54) of female crocodile lizards gave birth in autumn and winter from October to December, while the remainder gave birth in the next spring from March to May, similar to natural populations (Figure 5). Although female reproductive output and neonate morphology did not differ between the early- and normal-parturition groups in terms of litter size, litter mass, alive litter size, alive litter mass, neonatal SVL, or BM (Table 1), neonates from normal-parturition females survived longer than those from early-parturition females (χ^2 = 4.484, p = 0.034) (Figure 6).

4 | DISCUSSION

A captive program enables us to quantify the reproductive traits of the crocodile lizard more easily than studying a wild population. We found that female reproductive output increased with body size and age.
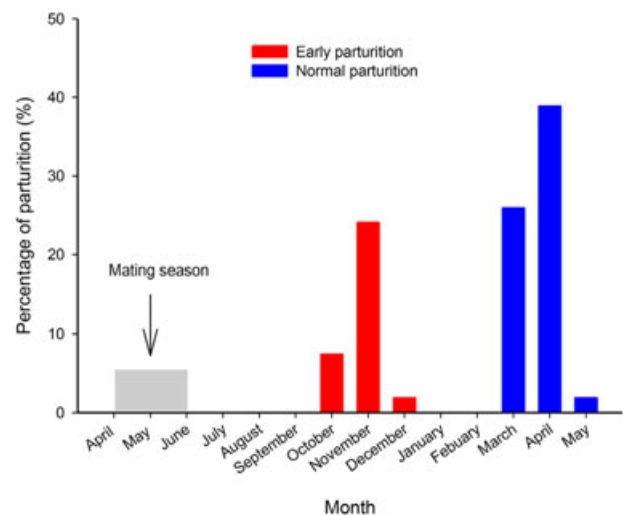

FIGURE 5 Distribution of parturition timing in the crocodile lizard, *Shinisaurus crocodilurus*, showing the mating season (April, May, and June), early parturition in the autumn and winter (October, November, and December), and normal parturition in the next spring (March, April, and May)

TABLE 1 Body size and reproductive traits of early- and normal-parturition females in the crocodile lizard (*Shinisaurus crocodilurus*)

Maternal and neonatal traits	Early parturition		Normal parturition		Statistical significance
	N	Mean ± SE	N	Mean ± SE	
Maternal snout-vent length/mm	11	140.00 ± 3.04	18	146.24 ± 3.11	$F_{1,27} = 1.808$, $p = 0.190$
Maternal postpartum body mass/g	14	91.11 ± 3.47	23	97.20 ± 5.18	$F_{1,35} = 0.716$, $p = 0.403$
Litter size	18	6.17 ± 0.44	36	6.50 ± 0.29	$F_{1,52} = 0.419$, $p = 0.520$
Litter mass/g	18	22.03 ± 1.38	36	24.62 ± 1.33	$F_{1,52} = 1.511$, $p = 0.225$
Alive litter size	18	5.33 ± 0.49	36	5.53 ± 0.43	$F_{1,52} = 0.077$, $p = 0.782$
Alive litter mass/g	18	18.87 ± 1.47	36	22.94 ± 1.78	$F_{1,52} = 0.578$, $p = 0.450$
Neonate snout-vent length/mm	18	54.82 ± 0.56	36	54.81 ± 0.79	$F_{1,52} = 0.0001$, $p = 0.993$
Neonate body mass/g	18	3.61 ± 0.18	36	3.81 ± 0.12	$F_{1,52} = 0.909$, $p = 0.345$
RCM1	14	0.23 ± 0.02	23	0.27 ± 0.03	$F_{1,35} = 1.342$, $p = 0.254$
RCM2	14	0.19 ± 0.01	23	0.21 ± 0.02	$F_{1,35} = 1.128$, $p = 0.296$

Maternal snout-vent length and body mass were only recorded for a subset of females that gave birth to neonates. Early parturition: females that give birth in the autumn and winter (October, November, and December); Normal parturition: females that give birth in the following spring (March, April, and May). RCM: Relative clutch mass.

N: Sample size; RCM1 = litter mass/maternal postpartum body mass; RCM2 = litter mass/(maternal postpartum body mass + litter mass).

However, both young and old females produced fewer living neonates than did middle-aged females. Unexpectedly, some females had earlier parturition, likely in response to the higher ambient temperatures in captivity. Offspring from early-parturition females died earlier than those from the normal-parturition females. These results not only provide new insight into the reproductive life history of a rare lizard species, but are also helpful in designing future conservation measures.

As in many other lizards (Du, Ji, & Shine, 2005; Du, Robbins, Warner, Langkilde, & Shine, 2014; Warne & Charnov, 2008; Winck & Rocha, 2012), larger female crocodile lizards produce more offspring than smaller ones, but neonate size is independent of maternal body size. These results have several implications. First, maternal body size is the major determinant of reproductive output when pregnant females have no environmental constraints, such as no food limitation in captivity. Second, female crocodile lizards boost reproductive output mainly through producing more, rather than larger, offspring. Third, female crocodile lizards likely prioritize offspring size over litter size when allocating limited resources among offspring, presumably because optimal offspring size may give the female a simple rule to maximize reproductive success (Ji, Du, Lin, & Luo, 2007; Sinervo, 1999; Sinervo & Licht, 1991; Smith & Fretwell, 1974).

Interestingly, maternal reproductive output varied across age groups. Living litters of young females had significantly less mass and contained fewer individuals than 3-year-old females and older. Old females (>5 years) had slightly lower reproductive output and produced significantly fewer living offspring than did 3- or 4-year-old females (Figures 3 and 4). In the wild, crocodile lizards reach maturity around 3–4 years (Zhao et al., 1998), a duration that can be shortened to 13 months in captivity (van Schingen, Schepp, Pham, Nguyen, & Ziegler, 2015; Ziegler, Quyet, Thanh, Hendrix, & Boehme, 2008). Thus, captive females can reach sexual maturity in 2 years, owing to an adequate supply of food and a benign environment in captivity. The early maturity of captive females appears to increase reproductive frequency and lifetime reproductive output, although their low reproductive success implies that 2-year-old females contribute relatively little to population size. These links are difficult to empirically demonstrate, however, due to trade-offs between current and future reproduction (Stearns, 1992). Early maturity and reproduction may reduce somatic maintenance and growth, in turn decreasing longevity and late-life reproduction (Maklakov et al., 2017; Reed et al., 2008). Therefore, measuring lifetime reproductive output is critical for understanding the benefits and costs of early maturity in captive females. These data also provided a basis for deciding whether 2-year-old females should be included in breeding programs.
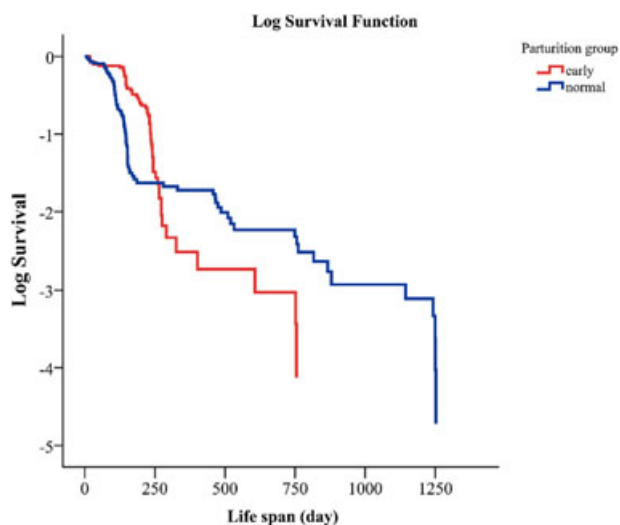
FIGURE 6 Survival rates of offspring *Shinisaurus crocodilurus* following early parturition (autumn and winter) and normal parturition (spring) females

Parturition in autumn and winter (from October to December) during captivity is unexpected because wild crocodile lizards give birth in spring following mating (from April to May) (Zhao et al., 1998). In contrast, one female from the Vietnamese population collected in mid-September had small eggs and folded oviducts, suggesting that the female already gave birth (Ziegler et al., 2008). These observations suggest that a warmer habitat (south Vietnam) results in autumn parturition, while a cooler habitat (northern China) results in parturition during spring of next year. Alternatively, the small eggs and folded oviducts may not necessarily be a sign of a postpartum state, given that some females skipped reproduction in certain years. Better evidence supporting the actual breeding time would be neonate emergence in the wild populations, an angle that deserves further examination in the future. Regardless of the uncertainty and complexity of reproductive timing in wild populations, the warm conditions and the associated early parturition of captive females suggest that high temperature is an important reproductive stimulus. Analogously, female snow skinks (*Niveoscincus microlepidotus*) from Australia normally mate in summer and give birth the following spring in the field, but shift to earlier parturition prior to hibernation when they are provided more basking opportunities in the captivity (Olsson and Shine, 1998). In addition, both field observations and experimental manipulations demonstrate that warm climate may advance the timing of reproduction in many other animals, from invertebrates to mammals (Parmesan, 2006, 2007). This is because increasing temperatures shorten the gestation period through accelerating embryonic developmental processes in both viviparous and oviparous species (Lu, Wang, Tang, & Du, 2013; Ma et al., 2014; Tang et al., 2012; Wang et al., 2016; Wang, Lu, Ma, & Ji, 2013). Nonetheless, early parturition could also be the result of influence from other biotic and abiotic factors (e.g., food availability and genetic variability) that differed in captivity (Du, 2006; Quinn, Unwin, & Kinnison, 2000).

Although female reproductive output and neonatal body size did not differ between the early- and normal-parturition females, offspring from the former group died earlier than those from the latter (Figure 6). Moreover, neonates from the early-parturition females are more likely to experience unpredictable surroundings in the wild (e.g., winter) that may pose great threats to them. Neonates of ectothermic species with summer parturition have time to store energy and seek shelter, thus increasing their chances of survival through the winter (Olsson & Shine, 1997; Rodríguez-Díaz, González, Ji, & Braña, 2010; Warner & Shine, 2007). In contrast, crocodile-lizard neonates born in autumn immediately experience a harsh winter, and thus likely face high mortality. Field studies on the survival of snow skink offspring provide supportive evidences for this notion; the survival rate of offspring born in autumn is substantially lower than that of offspring born in spring (Olsson and Shine, 1998). Climate-change-induced mismatch between animals and their environments (e.g., food availability and camouflage mismatch) results in high fitness costs and disrupts interspecific connectedness in current ecosystems (Marketa, Scott, & Joshua, 2016; Parmesan, 2006, 2007; Root et al., 2003). For example, offspring born earlier may miss benefits from the synchronization of resource peaks and breeding events. Food mismatch is likely to affect early-born offspring—especially among range-restricted species—thus hampering

neonatal growth rate and even survival rates (McKinnon, Picotin, Bolduc, Juillet, & Bêty, 2012). Early parturition in crocodile lizards adds an additional fitness cost from the mismatch between offspring emergence and a benign environment suitable for their growth and survival. Therefore, in addition to habitat loss and unsustainable use (Brooks et al., 2002; Pimm & Askins, 1995), anthropogenic global warming has far-reaching influences on ectotherm species distribution and life history traits (Dillon, Wang, & Huey, 2010; Li et al., 2013; Memmott, Craze, Waser, & Price, 2007; Parmesan, 2006).

Overall, our findings have important implications for the captive breeding and conservation of *S. crocodilurus*. More research is necessary to determine if 2-year-old females should be included in the breeding program, and whether such an inclusion benefits the sustainment of healthy populations. More importantly, our study raises concerns about the early shift of female parturition in response to climate change, as the altered timing may significantly hamper offspring survival and population regeneration. Given the extreme thermal sensitivity of parturition timing in *S. crocodilurus*, ongoing climate change might impose a severe threat on the sustainability of wild populations and deserves special attention in the conservation practices of this endangered species.

CONFLICT OF INTERESTS

The authors declare that there is no conflict of interests regarding the publication of this article.

ORCID

Qiyu Li (iD) http://orcid.org/0000-0002-7635-2489

REFERENCES

Ahl, E. (1930). Amphibia and reptilia. *Oppenh & Pincussen Tabulae Biologicae*, *1930*, 598–715.

Andrew, B., Georgina, M. M., & Leader-Williams, N. (1996). Designing the ark: Setting priorities for captive breeding. *Conservation Biology*, *10*, 719–727. https://doi.org/10.1046/j.1523-1739.1996.10030719.x.

Brooks, T. M., Mittermeier, R. A., Mittermeier, C. G., Fonseca, G. A. B., Rylands, A. B., Konstant, W. R., . . . Hilton-Taylor, C. (2002). Habitat loss and extinction in the hotspots of biodiversity. *Conservation Biology*, *16*, 909–923.

Charlesworth, D., & Charlesworth, B. (1987). Inbreeding depression and its evolutionary consequences. *Annual Review of Ecology and Systematics*, *18*, 237–268. https://doi.org/10.1146/annurev.ecolsys.18.1.237.

Dillon, M. E., Wang, G., & Huey, R. B. (2010). Global metabolic impacts of recent climate warming. *Nature*, *467*, 704–706. https://doi.org/10.1038/nature09407.

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., & Shine, R. (2005). Does body-volume constrain reproductive output in lizards? *Biology Letters*, *1*, 98–100.

Du, W. G., Ji, X., Zhang, Y. P., Xu, X. F., & Shine, R. (2005). Identifying sources of variation in reproductive and life-history traits among five populations of a Chinese lizard (*Takydromus septentrionalis*, Lacertiade). *Biological Journal of the Linnean Society*, *85*, 443–453.

Du, W. G., Robbins, T. R., Warner, D. A., Langkilde, T., & Shine, R. (2014). Latitudinal and seasonal variation in reproductive effort of the eastern fence lizard (*Sceloporus undulatus*). *Integrative Zoology*, *9*, 360–371. https://doi.org/10.1111/ 1749-4877. 12072.

Forsman, A., & Shine, R. (1995). Parallel geographic variation in body shape and reproductive life history within the Australian scincid lizard *Lampropholis delicata*. *Functional Ecology*, *9*, 818–828.

Griffiths, R. A., & Pavajeau, L. (2008). Captive breeding, reintroduction, and the conservation of amphibians. *Conservation Biology*, *22*, 852–861. https://doi.org/10.1111/j. 1523-1739. 2008.00967.x.

Hua, L., Gong, S., Zhong, X., Tao, J., Chen, Y., & Deng, J. (2017). The effects of water depth and substrate conditions on changes in body weight and health status of captive Big-headed Turtles (*Platysternon megacephalum*) during hibernation. *Pakistan Journal of Zoology*, *49*, 2243–2248. https://doi.org/10.17582/journal.pjz/2017.49.6.2243.2248.

Huang, C. M., Yu, H., Wu, Z. J., Li, Y. B., Wei, F. W., & Gong, M. H. (2008). Population and conservation srategies strategies for the Chinese crocodile lizard (*Shinisaurus crocodilurus*) in China. *Animal Biodiversity and Conservation*, *31*, 63–70.

Huang, H., Luo, D., Guo, C., Tang, Z., Wu, Z., & Chen, J. (2015). Genetic analysis of multiple paternity in an endangered ovoviviparous lizard *Shinisaurus crocodilurus*. *Asian Herpetological Research*, *6*, 150–155.

Huang, H., Wang, H., Li, L., Wu, Z., & Chen, J. (2014). Genetic diversity and population demography of the Chinese crocodile lizard (*Shinisaurus crocodilurus*) in China. *PLoS ONE*, *9*, e91570. https://doi.org/10.1371/journal.pone.0091570.

Ji, X., Du, W. G., Lin, Z. H., & Luo, L. G. (2007). Measuring temporal variation in reproductive output reveals optimal resource allocation to reproduction in the northern grass lizard, *Takydromus septentrionalis*. *Biological Journal of the Linnean Society*, *91*, 315–324.

Ji, X., & Wang, Z. W. (2005). Geographic variation in reproductive traits and trade-offs between size and number of eggs of the Chinese cobra (*Naja atra*). *Biological Journal of the Linnean Society*, *85*, 27–40.

Kati, V., Dufrêne, M., Legakis, A., Grill, A., & Lebrun, P. (2004). Conservation management for Orthoptera in the Dadia reserve, Greece. *Biological Conservation*, *115*, 33–44. https://doi.org/10.1016/s0006-3207(03)00091-0.

Kleiman, D. G., (1980). The sociobiology of captive propagation in mammals. In M. E. Soule, & B. A. Wilcox, (Eds.), *Conservation biology*. (pp. 243–262). Sunderland, MA: Sinauer Associates, Inc.

Li, X., Tian, H., Wang, Y., Li, R., Song, Z., Zhang, F., . . . Li, D. (2013). Vulnerability of 208 endemic or endangered species in China to the effects of climate change. *Regional Environmental Change*, *13*, 843–852. https://doi.org/10.1007/s10113-012-0344-z.

Lu, H., Wang, Y., Tang, W., & Du, W. (2013). Experimental evaluation of reproductive response to climate warming in an oviparous skink. *Integrative Zoology*, *8*, 175–183. https://doi.org/10.1111/1749-4877.12025.

Ma, L., Sun, B. J., Li, S. R., Sha, W., & Du, W. G. (2014). Maternal thermal environment induces plastic responses in the reproductive life history of oviparous lizards. *Physiological and Biochemical Zoology*, *87*, 677–683. https://doi.org/10.1086/678050.

Maklakov, A. A., Carlsson, H., Denbaum, P., Lind, M. I., Mautz, B., Hinas, A., & Immler, S. (2017). Antagonistically pleiotropic allele increases lifespan and late-life reproduction at the cost of early-life reproduction and individual fitness. *Proceedings of the Royal Society B: Biological Sciences*, *284*(1856), https://doi.org/10.1098/rspb.2017.0376.

Marketa, Z., Scott, M. L., & Joshua, N. J. (2016). High fitness costs of climate change-induced camouflage mismatch. *Ecology Letters*, *19*, 299–307. https://doi.org/10.1111/ele.12568.

Martin, M. S., & Shepherdson, D. J. (2012). Role of familiarity and preference in reproductive success in sx situ breeding programs. *Conservation Biology*, *26*, 649–656. https://doi.org/10.1111/j.

McKinnon, L., Picotin, M., Bolduc, E., Juillet, C., & Bêty, J. (2012). Timing of breeding, peak food availability, and effects of mismatch on chick growth in birds nesting in the High Arctic. *Canadian Journal of Zoology*, *90*, 961–971. https://doi.org/ 10.1139/z2012-064.

Memmott, J., Craze, P. G., Waser, N. M., & Price, M. V. (2007). Global warming and the disruption of plant-pollinator interactions. *Ecology Letters*, *10*, 710–717. https://doi.org/ 10.1111/j. 1461-0248. 2007. 01061.x.

Nuss, K., & Warneke, M. (2010). Life span, reproductive output, and reproductive opportunity in captive Goeldi's monkeys (*Callimico goeldii*). *Zoo Biology*, *29*, 1–15. https://doi.org/10.1002/zoo.20239.

Olsson, M., & Shine, R. (1997). The seasonal timing of oviposition in sand lizards (*Lacerta agilis*): why early clutches are better. *Journal of Evolutionary Biology*, *10*, 369–381.

Olsson, M., & Shine, R. (1998). Timing of parturiton as a maternal care tactic in an alpine lizard species. *Evolution*, *52*, 1861–1864. https://doi.org/10.1111/j. 1558-5646. 1998.tb02265.x.

Parmesan, C. (2006). Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution, and Systematics*, *37*, 637–669. https://doi.org/ 10.1146/annurev.ecolsys.37.091305.110100.

Parmesan, C. (2007). Influences of species, latitudes and methodologies on estimates of phenological response to global warming. *Global Change Biology*, *13*, 1860–1872. https://doi.org/10.1111/j. 1365-2486. 2007.01404.x.

Pimm, S. L., & Askins, R. A. (1995). Forest losses predict bird extinctions in eastern North America. *Proceedings of the National Academy of Sciences*, *92*, 9343–9347. https://doi.org/10.1073/pnas.92.20.9343.

Quinn, T. P., Unwin, M. J., & Kinnison, M. T. (2000). Evolution of temporal isolation in the wild: Genetic divergence in timing of migration and breeding by introduced chinook salmon populations. *Evolution*, *54*, 1372–1385.

Quyet, L. K., & Ziegler, T. (2003). First record of the Chinese Crocodile Lizard from outside of China: Report on a population of *Shinisaurus crocodilurus* Ahl, 1930 from north-eastern vietnam. *Hamadryad*, *27*, 193–199.

Reed, T. E., Kruuk, L. E. B., Wanless, S., Frederiksen, M., Cunningham, E. J. A., & Harris, M. P. (2008). Reproductive senescence in a long-lived seabird: Rates of decline in late-life performance are associated with varying costs of early reproduction. *The American Naturalist*, *171*, E89–E101. https://doi.org/10.1086/524957.

Ricklefs, R. E. (1998). Evolutionary theories of aging: Confirmation of a fundamental prediction, with implications for the genetic basis and evolution of life span. *American Naturalist*, *152*, 24–44. https://doi.org/10.1086/286147.

Ricklefs, R. E. (2000). Intrinsic aging-related mortality in birds. *Journal of Avian Biology*, *31*, 103–111. https://doi.org/10.1034/j.1600-048X 2000. 210201.x.

Ricklefs, R. E., & Scheuerlein, A. (2001). Comparison of aging-related mortality among birds and mammals. *Experimental Gerontology*, *36*, 845–857. https://doi.org/10.1016/s0531-5565(00)00245-x.

Robert, A. (2009). Captive breeding genetics and reintroduction success. *Biological Conservation*, *142*, 2915–2922. https://doi.org/10.1016/j.biocon.2009.07.016.

Rodríguez-Díaz, T., González, F., Ji, X., & Braña, F. (2010). Effects of incubation temperature on hatchling phenotypes in an oviparous lizard with prolonged egg retention: Are the two main hypotheses on the evolution of viviparity compatible? *Zoology*, *113*, 33–38. https://doi.org/10.1016/j.zool.2009.05.001.

Root, T. L., Price, J. T., Hall, K. R., Schneider, S. H., Rosenzweigk, C., & Pounds, J. A. (2003). Fingerprints of global warming on wild animals and plants. *Nature*, *421*, 57–60. https://doi.org/10.1038/nature01309.

Schmidt, D. J., Espinoza, T., Connell, M., & Hughes, J. M. (2018). Conservation genetics of the Mary River turtle (*Elusor macrurus*) in natural and captive populations. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *28*, 115–123. https://doi.org/10.1002/aqc.2851.

Schulte-Hostedde, A. I., Zinner, B., Millar, J. S., & Hickling, G. J. (2005). Restitution of mass-size residuals: Validating body condition indices. *Ecology*, *86*, 155–163. https://doi.org/10.1890/04-0232.

Shine, R. (2005). Life-history evolution in reptiles. *Annual Review of Ecology Evolution and Systematics*, *36*, 23–46. https://doi.org/10.1146/annurev.ecolsys.36.102003.152631.

Sinervo, B. (1999). Mechanistic analysis of natural selection and a refinement of Lack's and Williams's principles. *American Naturalist*, *154*, S26–S42.

Sinervo, B., & Licht, P. (1991). Proximate constraints on the evolution of egg size, number, and total clutch mass in lizards. *Science*, *252*, 1300–1302.

Slade, B., Parrott, M. L., Paproth, A., Magrath, M. J., Gillespie, G. R., & Jessop, T. S. (2014). Assortative mating among animals of captive and wild origin following experimental conservation releases. *Biology Letters*, *10*, 20140656. https://doi.org/ 10.1098/rsbl.2014.0656.

Smith, C. C., & Fretwell, S. D. (1974). The optimal balance between size and number of offspring. *American Naturalist*, *108*, 499–506.

Smucny, D. A., Abbott, D. H., Mansfield, K. G., Schultz-Darken, N. J., Yamamoto, M. E., Alencar, A. I., & Tardif, S. D. (2004). Reproductive output, maternal age, and survivorship in captive common marmoset females (*Callithrix jacchus*). *American Journal of Primatology*, *64*, 107–121. https://doi.org/10.1002/ajp.20065.

Snyder, N. F. R., Derrickson, S. R., Beissinger, S. R., Wiley, J. W., Smith, T. B., Toone, W. D., & Miller, B. (1996). Limitations of captive breeding in endangered species recovery. *Conservation Biology*, *10*, 338–348. https://doi.org/10.1046/j. 1523-1739. 1996.10020338.x.

Stearns, S. C. (1992). *The Evolution of Life Histories*. Oxford: Oxford University Press.

Tang, X. L., Yue, F., Yan, X. F., Zhang, D. J., Xin, Y., Wang, C., & Chen, Q. (2012). Effects of gestation temperature on offspring sex and maternal reproduction in a viviparous lizard (*Eremias multiocellata*) living at high altitude. *Journal of Thermal Biology*, *37*, 438–444. https://doi.org/10.1016/j.jtherbio.2012.03.002.

van Schingen, M., Cuong The, P., Hang An, T., Bernardes, M., Hecht, V., Truong Quang, N., . . . Ziegler, T. (2014). Current status of the Crocodile Lizard *Shinisaurus crocodilurus* Ahl, 1930 in Vietnam with implications for conservation measures. *Revue Suisse De Zoologie*, *121*, 425–439.

van Schingen, M., Duc Le, M., Thi Ngo, H., The Pham, C., Quy Ha, Q., Quang Nguyen, T., & Ziegler, T. (2016). Is there more than one crocodile lizard? An integrative taxonomic approach reveals vietnamese and chinese shinisaurus crocodilurus represent separate conservation and taxonomic units. *Der Zoologische Garten*, *85*, 240–260. https://doi.org/10.1016/j.zoolgart.2016.06.001.

van Schingen, M., Ihlow, F., Truong Quang, N., Ziegler, T., Bonkowski, M., Wu, Z., & Roedder, D. (2014). Potential distribution and effectiveness of the protected area network for the crocodile lizard, *Shinisaurus crocodilurus* (Reptilia: Squamata: Sauria). *Salamandra*, *50*, 71–76.

van Schingen, M., Schepp, U., Pham, C., Nguyen, T., & Ziegler, T. (2015). Last chance to see? A review of the threats to and use of the crocodile lizard. *Traffic Bulletin*, *27*, 19–26.

Wang, Y., Zeng, Z. G., Li, S. R., Bi, J. H., & Du, W. G. (2016). Low precipitation aggravates the impact of extreme high temperatures on lizard reproduction. *Oecologia*, *182*, 961–971. https://doi.org/10.1007/s00442-016-3727-x.

Wang, Z., Lu, H.-L., Ma, L., & Ji, X. (2013). Viviparity in high-altitude Phrynocephalus lizards is adaptive because embryos cannot fully develop without maternal thermoregulation. *Oecologia*, *174*, 639–649. https://doi.org/10.1007/s00442-013-2811-8.

Wang, Z., Wu, Z., Chen, L., Yu, S., Yu, H., Huang, C., & Jie, J. (2009). Effects of pregnancy and ages on temperature selection and resting metabolic rates ing Chinese crocodile lizard, *Shinisaurus crocodilurus*. *Journal of Guangxi Normal University: Natural Science Edition*, *27*, 80–84.

Wang, Z., Wu, Z., Yu, H., Huang, C., & Zhong, Y. (2008). Thermoregulatory and thermal dependence of resting metabolic rates in the Chinese crocodile lizard *Shinisaurus crocodilurus* in the Luokeng Nature Reserve, Guangdong. *Acta Zoologica Sinica*, *54*, 964–971.

Warne, R. W., & Charnov, E. L. (2008). Reproductive allometry and the size-number trade-off for lizards. *American Naturalist*, *172*, E80–E98. https://doi.org/ 10.1086/589880.

Warner, D. A., & Shine, R. (2007). Fitness of juvenile lizards depends on seasonal timing of hatching, not offspring body size. *Oecologia*, *154*, 65–73. https://doi.org/10.1007/s00442-007-0809-9.

Winck, G. R., & Rocha, C. F. D. (2012). Reproductive trends of Brazilian lizards (Reptilia, Squamata): the relationship between clutch size and body size in females. *North-Western Journal of Zoology*, *8*, 57–62.

Wu, Z., Dai, D., Nin, J., Huang, C., & Yu, H. (2012). Seasonal differences in habitat selection of the Crocodile lizard (*Shinisaurus crocodilurus*) in Luokeng Nature Reserve, Guangdong. *Acta Ecologicla Sinica*, *32*, 4691–4699.

Yu, S., Wu, Z., Wang, Z., Chen, L., Huang, C., & Yu, H. (2009). Courtship and mating behavior of Shinisaurus crocodilurus in Luokeng nature reserve, Guangdong. *Chinese Journal of Zoology*, *44*, 38–44.

Zhang, G. Q., Swaisgood, R. R., & Zhang, H. M. (2004). Evaluation of behavioral factors influencing reproductive success and failure in captive giant pandas. *Zoo Biology*, *23*, 15–31. https://doi.org/10.1002/zoo.10118.

Zhang, Y. X. (2002). *Biology of Shinisaurus crocodilurus*. Guilin: Guangxi Normal University Press.

Zhang, Y. X., Zeng, S. F., & Zhou, K. Y. (2002). Status and conservation of Shinisaurus crocodilurus. *Herpetologica Sinica*, *9*, 186–189.

Zhao, E. M., Jiang, Y. M., Huang, Q. Y., Zhao, K. T., Liu, Y. Z., Liu, M. Y., . . . Zhang, Y. X. (1998). *Fauna Sinica (Reptilia 2): Squamata (Lacertilia)*. Beijing: Science Press. (in Chinese).

Ziegler, T., Quyet, L. K., Thanh, V. N., Hendrix, R., & Boehme, W. (2008). A comparative study of crocodile lizards (*Shinisaurus crocodilurus* Ahl, 1930) from Vietnam and China. *Raffles Bulletin of Zoology*, *56*, 181–187.