

Expression of phenotypic plasticity in hatchlings of the lizard *Calotes versicolor* (Squamata: Agamidae): influence of nest moisture

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Abstract

Expression of phenotypic plasticity in hatchlings of the lizard *Calotes versicolor* (Squamata: Agamidae): influence of nest moisture. *Calotes versicolor* breed from late May to early October. The breeding activity begins with the onset of the southwest monsoon. The eggs laid in early breeding season experience more wet conditions than those of the late breeding season. We studied the influence of nest moisture levels on the phenotypic traits of hatchlings by burying the eggs in 5-cm-deep sand nests with ~50% (wet nest) or ~20% (relatively dry nest) moisture to simulate nesting conditions of early and late breeding seasons. A group of eggs were subjected to standard laboratory incubation procedure in which eggs are half-buried in the moist sand and the other half exposed to air. Hatching time and hatchling body size varied with the treatment. The eggs from dry nests hatched later and hatchlings were the biggest but possessed least amount of residual yolk compared to those of "wet nest" and also "lab incubated" groups. In these hatchlings head and limb sizes were significantly larger than that of the other two groups. The findings show: (1) a developmental plasticity in the lizard, (2) that under low moist conditions larger body size is preferred, and (3) that the trade-off between somatic growth of embryos and future energy reserves (residual yolk) of hatchlings is influenced by the soil moisture in *C. versicolor*.

Keywords: developmental plasticity, hatchlings, laboratory incubation, nest moisture, phenotype, residual yolk.

Resumo

Expressão da plasticidade fenotípica em filhotes do lagarto *Calotes versicolor* (Squamata: Agamidae): influência da umidade do ninho. *Calotes versicolor* se reproduz do final de maio ao início de outubro. A atividade de reprodução começa logo após a monção sul-oeste. Os ovos depositados no início da estação reprodutiva experimentam condições mais úmidas do que aqueles do final da estação. Nós estudamos a influência do nível de umidade do ninho sobre as características fenotípicas dos filhotes recém-eclodidos enterrando os ovos em ninhos de areia de 5 cm de

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profundidade com ~50% (ninho úmido) ou ~20% (ninho relativamente seco) de umidade para simular as condições de nidificação do início e do final da estação reprodutiva. Um grupo de ovos foi submetido a um procedimento padronizado de incubação laboratorial em que os ovos são semi-enterrados na areia úmida enquanto a outra metade permanece exposta ao ar. O tempo de eclosão e o tamanho corporal dos filhotes recém-eclodidos variaram com o tratamento. Os ovos dos ninhos secos eclodiram mais tarde e os filhotes foram os maiores, mas possuíam menor quantidade de vitelo residual comparados com os grupos de "ninhos úmidos" e também de "incubação laboratorial". Nesses filhotes, os tamanhos da cabeça e dos membros foram significativamente maiores do que os dos outros dois grupos. Os resultados mostram: (1) uma plasticidade de desenvolvimento no lagarto, (2) que sob condições de baixa umidade um tamanho corporal maior é preferível e (3) que o compromisso entre o crescimento somático dos embriões e as reservas energéticas futuras (vitelo residual) dos filhotes é influenciado pela umidade do solo em *C. versicolor*.

Palavras-chave: fenótipo, filhotes, incubação laboratorial, plasticidade do desenvolvimento, umidade do ninho, vitelo residual.

Introduction

Reptile eggs with flexible shell are highly susceptible to desiccation in the absence of adequate soil moisture (Packard 1999). Therefore, the gravid females generally select oviposition sites with suitable soil moisture. In the absence of suitable nesting sites the females tend to retain eggs in oviducts for long periods (Shine and Guillet 1988, DeMarco 1993, Radder *et al.* 1998). The soil moisture condition available during incubation is reported to influence hatchling size, growth, locomotor speed, and desiccation tolerance, and survival in different species of reptiles (Packard 1991, Finkler 1999, Brown and Shine 2005). In addition, it is known to influence the amount of yolk that is utilized by the developing embryos of *Sceloporus undulatus* (Warner and Andrews 2002). The previous studies analyzed the effects of moisture on hatchling phenotype by incubating the eggs partially buried in the substratum at constant temperature and moisture (Muth 1980, Packard *et al.* 1987, Packard 1999, Lin *et al.* 2005, Finkler 2006). However, it is not clear whether phenotypic features of hatchlings obtained from standard laboratory incubation method and those emerging from natural nests are comparable. Warner and Shine (2009) compared phenotypic features of *Amphibolurus muricatus* hatchlings

obtained through laboratory incubation and natural nests, and opined that extrapolation of results from laboratory incubation to field conditions needs to be done with caution.

Many species of lizards that lay flexible shelled eggs, dig nest in the soil, oviposit the eggs and refill the nest with soil. The eggs are laid in this fashion in order to protect them from direct exposure to sun (desiccation) and predation (Pianka and Vitt 2003). The lizard *Calotes versicolor* (Daudin) has an extended breeding season coinciding with the southwest monsoon (May to October) and lays flexible shelled eggs by digging the nest hole up to 5–9 cm deep (Shanbhag 2003, Pandav *et al.* 2010). Thus, eggs laid in early and late breeding season experience different levels of nest moisture. Interestingly, the *C. versicolor* eggs laid in the late breeding season are larger than those of early breeding season (Shanbhag *et al.* 2000). Yet, incubation of early and late breeding season eggs by standard laboratory method at comparable temperature and moisture conditions yields hatchlings of comparable size. Interestingly, hatchlings from late clutches retain more residual yolk than those of early clutches (Radder *et al.* 2002a). However, influence of nest moisture per se, if any, on phenotypic traits of *C. versicolor* hatchlings is not known. Therefore, the present study was designed to elucidate the influence of low or

high moisture conditions typical of early and late breeding seasons on the hatching time and phenotypic features of *C. versicolor* hatchlings.

Materials and Methods

Seventy seven eggs from five gravid *C. versicolor* (SVL 99.95 ± 1.99 mm, body mass 34 ± 1.87 g; clutch size 21 ± 0.63 ; average egg mass 523 ± 31.5 mg; mean \pm SE) collected in June, 2010 were used for this study. We used a split-plot design with eggs from each clutch arbitrarily allocated as equally as possible to three groups. Further, eggs from each clutch allocated to a treatment group were incubated as separate sub-sets and were not mixed with those of other clutches. The experimental protocol is given below.

Group I: Five eggs from a clutch were incubated in a plastic box ($15 \times 12 \times 6$ cm) having a sand bed of 4 cm. They were placed 2 cm apart and were half buried in the sand as described earlier (Radder *et al.* 2002b). A total of 25 eggs from five females were subjected to this treatment in five separate boxes without lids. Water was added daily or on alternate day to each box depending upon the evaporation to avoid desiccation of eggs. The substrate water content of this group (lab incubated) varied between 30–35%.

Group II: The plastic containers ($12 \times 12 \times 18$ cm) filled with sand were used to incubate the eggs. Five or six eggs from a clutch were buried in sand at 5 cm depth simulating field nests ($N = 26$). Five such boxes were maintained without any lids. The sand moisture in the boxes was maintained at ~50% so as to simulate the natural nest conditions of early breeding season. This group represents "wet nest".

Group III: The eggs ($N = 26$) from this group were also buried at 5 cm depth in the sand bed inside plastic boxes without lids. The sand moisture was maintained at ~20% to resemble moisture conditions of late breeding season. Each box contained five or six eggs from a clutch. This group represents "relatively dry nest".

Moisture and temperatures (ambient and substrate) of the nests were recorded daily at 09:30, 14:00, and 18:00 h. Water was uniformly sprayed on the surface of the substrate to maintain required moisture levels that was monitored using a "Soil pH and Moisture Tester" (DM-15, Japan). The substrate temperature was recorded by placing a soil thermometer at the corner of the box in the soil at a depth to which the eggs are buried. The substrate/ambient temperature for half buried eggs (Group I) varied between 23–26°C (Mean = 24.52 ± 0.25 °C). The nests temperature of groups II and III varied between 20–22°C (Mean = 21 ± 0.19 °C).

At hatching, snout-vent length (SVL), tail length (TL), fore limb length (FLL), hind limb length (HLL); head length (HL) and head width (HW) of hatchlings were measured with a digital caliper. The FLL and HLL were measured from the place of attachment of the limb bone (humerus or femur) with the body to the tip of longest digit. The HL was measured from the neckline to the tip of the snout and HW was measured from right tympanum to left tympanum. Body mass and residual yolk mass were recorded with electronic balance to the nearest 0.001 g.

As there was no variation in the initial egg mass within sub-sets in each group, to avoid pseudoreplication, data on hatchlings of a clutch were pooled, and mean was used for analysis. Thus, the sample size for each group was considered as five (clutch origin) instead of hatchling number ($N = 72$). One sample Kolmogorov-Smirnov Z test was done to ascertain for normal distribution of data. All the data met with the assumption of normality. Analysis of variance (ANOVA) was used to determine the influence of moisture on hatching time, body mass, residual yolk and other morphometric traits of hatchlings among the groups. To avoid variation due to SVL/size effect, the residuals were generated by linear regression of each non-SVL morphometric traits [TL, FLL, HLL on SVL and for HL and HW on trunk length (SVL–HL)] and residuals were used in ANOVA analysis. Pairwise comparisons were made using post-hoc LSD tests.

Results

Incubation Duration and Hatching

The time taken for emergence of hatchlings differed significantly ($F_{2,13} = 56.59$, $P < 0.001$) among the three groups. The "lab incubated" eggs took 71.4 ± 0.6 days to hatch while those in "wet nest" and "relatively dry nest" took 74.2 ± 0.2 days and 78.8 ± 0.58 days, respectively. The eggs in the "wet nest" hatched at a significantly later time than those in the "lab incubated" but earlier than the "relatively dry nest". The eggs from "relatively dry nests" took significantly longer time to hatch compared to the other two groups. Hatching success was 100% in "lab incubated" and 96% in both "wet nest" and "relatively dry nest".

Hatchling Morphology

Hatchlings emerging from the "relatively dry nest" were significantly larger in SVL than those of the "lab incubated" and "wet nest" ($F_{2,13} = 26.48$, $p < 0.00$). The SVL of the hatchlings was comparable in "lab incubated" and "wet nest" groups (Figure 1A). Relative tail length of hatchlings did not differ significantly between the groups ($F_{2,13} = 0.442$, $p < 0.653$; Figure 1B). The relative limb dimensions differed significantly among the groups (Figures 1C, D). Both fore limb ($F_{2,13} = 16.09$, $p = 0.00$) and hind limb ($F_{2,13} = 33.73$, $p = 0.00$) lengths in the hatchlings emerging from the "wet nest" and "relatively dry nest" were larger than in the "lab incubated" group. The relative head length ($F_{2,13} = 12.41$, $p = 0.001$) and width ($F_{2,13} = 15.86$, $p < 0.00$) of hatchlings among the three groups also differed significantly. The head length and width of hatchlings of "relatively dry nest" were significantly greater than those of the other two groups. The head width of the hatchlings of "wet nest" was significantly greater than in the "lab incubated" group (Figures 1E, F).

The body mass of hatchlings was comparable between the three groups ($F_{2,13} = 0.293$, $p =$

0.751; Figure 1G), but post-hatching residual yolk mass differed significantly between them ($F_{2,13} = 300.03$, $p < 0.00$). Residual yolk was significantly low in hatchlings of "relatively dry nest" compared to the other two groups. However, it was comparable in "lab incubated" and "wet nest" groups (Figure 1H).

Discussion

In squamates and chelonians laying eggs with flexible shell, the moisture of the nest or substrate for incubation are known to influence developmental rate of embryos and hatching time (Packard 1991). The influence of moisture on hatching time varies among species. For instance, in *Pituophis melanoleucus* (Gutzke and Packard 1987) and *Chelydra serpentina* (Packard et al. 1987) high soil moisture conditions delay hatching (Packard 1991) while no clear pattern between substrate moisture and incubation duration is seen in desert Iguana, *Dipsosaurus dorsalis* (Muth 1980) and *Ophedryx aestivus* (Plummer and Snell 1988). Packard and Packard (1988) opined that hatching is induced when water potential of the yolk (or some other component) declines below the threshold level. Such a threshold is reached early in dry settings than in the wet settings leading to early hatching under low moist incubation conditions. Interestingly and in contrast to this view *C. versicolor* eggs in "relatively dry nest" hatched later than those in the "wet nests" though both nests experienced comparable incubation temperatures. Apparently, under comparable incubation temperature of the nests, low moisture conditions delay rather than hasten hatching in *C. versicolor*. The half buried eggs of "lab incubated" group hatched earliest because they experienced temperatures higher (by 3–4°C) than the other groups in which the eggs were buried 5 cm deep in the nest.

The previous laboratory studies on the influence of moisture on hatchling phenotype have yielded mixed results. In *Elaphe carinata* (Ji and Du 2001), *Bassiana duperreysi* (Flatt et

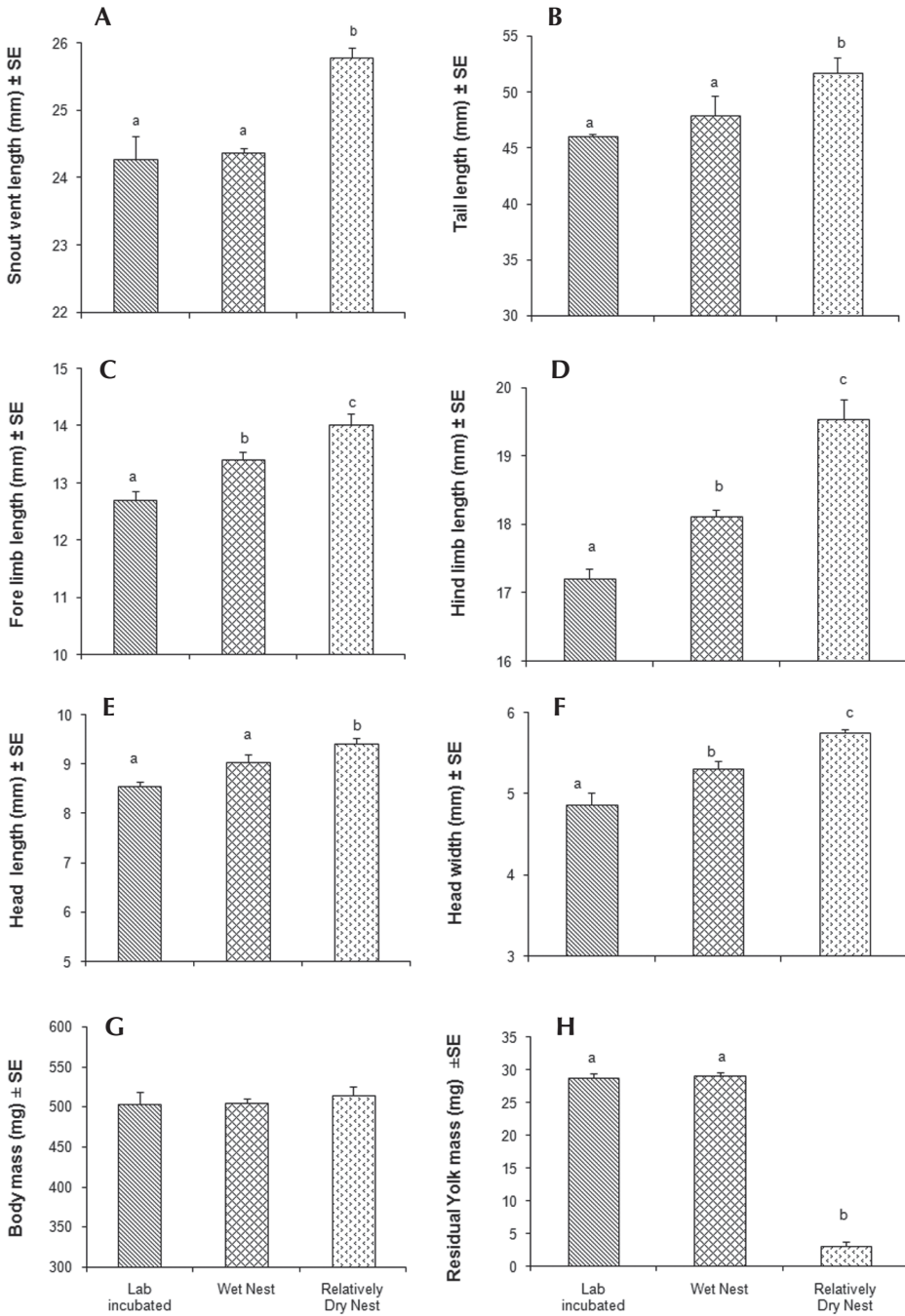


Figure 1. Mean SVL (A), tail length (B), forelimb length (C), hind-limb length (D), head length (E), and head width (F), body mass (G) and residual yolk mass (H) of *C. versicolor* hatchlings emerging from different incubation conditions. The values of lengths of the tail, fore- and hind-limbs, and head length and width are relative to SVL. Significant differences among groups are indicated by different letters above the bars.

al. 2001); *Oligosoma suteri* (Hare et al. 2002) and *Eumeces chinensis* (Du 2004), the hydric conditions used for incubation had no influence on phenotypic traits of the hatchlings. However, hatchlings of *Iguana iguana*, from both wet as well as dry incubation substrates were smaller in size than those at intermediate moisture condition (Werner 1988). But another study on *I. iguana* showed that the incubation of eggs under relatively dry incubation condition results in the production of smaller hatchlings (Phillips et al. 1990). The cause of discrepancy in the results of these two studies is not clear. Also, in *S. undulatus* dry settings produced smaller hatchlings than those from wet settings (Warner and Andrews 2002). Recent study by Robbins and Warner (2010) reported that the incubation moisture regimes have an influence on post-hatching growth in *S. undulatus* rather than on the size at hatching. The study suggested that high yolk reserves in the hatchlings from fluctuating moisture condition may have a role in promoting rapid post-hatching growth unlike that in their counterparts from constant moisture regime which possess small yolk reserves.

In the present study, *C. versicolor* hatchlings emerging from "relatively dry nest" were the largest in size with longer limbs compared to those of "wet nest" and "lab incubated" groups. The time taken to hatch in "relatively dry nest" was also the longest thereby providing longer period for growth and production of larger hatchlings. Further, hatchlings of "dry nest" appear to be superior to those of the other two groups based on their phenotypic traits. It is believed that in nature larger hatchlings of lizards have greater survival than the smaller ones (Ferguson and Fox 1984, Van Damme et al. 1992). Larger hatchlings with longer limbs run faster and thus better at escaping from the predators (Losos 1990, Sinervo and Losos 1991). It has been suggested that asocial animals disperse from their birth site (neonatal dispersal) mainly to avoid sociality and competition for resources (reference in Cote and Clobert 2007). If so, emergence of larger hatchlings of *C.*


versicolor in dry/late breeding season may improve their dispersal due to better sprint speed.

In oviparous lizards, a portion of yolk remains in the body at hatching and this subcutaneous residual yolk is utilized for the immediate post-hatching needs by hatchlings (Troyer 1987, Pandav et al. 2006). Several studies show that soil moisture of nests has an influence on residual yolk in reptiles (Phillips et al. 1990, Christian et al. 1991, Cagle et al. 1993, Shine and Brown 2002). For instance, the hatchlings of *Tropidonophis mairii*, *I. iguana*, *Cyclura nubila* and *Chrysemys picta* from drier nests were smaller in size with more residual yolk than those from wetter nests. In contrast, no such effect is reported in *Podarcis muralis* obtained from wet or dry conditions (Ji and Brana 1999). The differences in the findings in these studies are possibly due to the variations in experimental design or species specific sensitivity of eggs to nest moisture. In the present study, *C. versicolor* eggs in "relatively dry nest" hatched late and consequently most yolk was utilised by the growing embryos for somatic growth. Thus, these hatchlings possessed very little residual yolk at hatching. They were larger in size than those of "wet nest". The findings suggest that in *C. versicolor* hatching at larger size is preferred over retention of more residual yolk during dry/late breeding season. In an earlier study on *C. versicolor* it was suggested that retention of more residual yolk is preferred over body growth in late breeding season (Radder et al. 2002a). The authors opined that advantage of more residual yolk outweigh increasing body size at hatching. The greater amount of residual yolk in hatchlings emerging in the late breeding season was suggested to help in the immediate post hatching activities. It may be noted that in the study by Radder et al. (2002a) hatchlings were obtained using laboratory incubation procedure.

In summary, the present study shows that moisture levels and nesting condition have an influence on body size and internalization of residual yolk in *C. versicolor* hatchlings. Importantly, the energy trade-off between

residual yolk (storage) and body growth is influenced by moisture content of the nest. Under less moist conditions (often experienced during late breeding season) larger body size is favored over the retention of residual yolk. Thus, the hatchlings of *C. versicolor* show phenotypic plasticity in relation to incubation moisture.

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References

- Brown, G. P. and R. Shine. 2005. Do changing moisture levels during incubation influence phenotypic traits of hatchling snakes (*Tropidonophis mairii*, Colubridae)? *Physiological and Biochemical Zoology* 78: 524–530.
- Cagle, K. D., G. C. Packard, K. Muller, and M. J. Packard. 1993. Effects of the microclimate in natural nests on development of embryonic painted turtles, *Chrysemys picta*. *Functional Ecology* 7: 653–660.
- Christian, K. A., W. T. Lawrence, and H. L. Snell. 1991. Effect of soil moisture on yolk and fat distribution in hatchling lizards from natural nests. *Comparative Biochemistry and Physiology A*: 99: 13–19.
- Cote, J. and J. Clobert. 2007. Social personalities influence natal dispersal in a lizard. *Proceedings of Royal Society B* 274: 383–390.
- DeMarco, V. 1993. Estimation of egg retention time in sceloporine lizards. *Journal of Herpetology* 27: 453–458.
- Du, W. G. 2004. Water exchange of flexible-shelled eggs and its effect on hatchling traits in the Chinese skink, *Eumeces chinensis*. *Journal of Comparative Physiology* 174B: 489–493.
- Ferguson, G. W. and S. F. Fox. 1984. Annual variation of survival advantage of large juvenile side-blotched lizards, *Uta stansburiana*: its causes and evolutionary significance. *Evolution* 38: 342–349.
- Finkler, M. S. 1999. Influence of water availability during incubation on hatchling size, body composition, desiccation tolerance and terrestrial locomotor performance in the snapping turtle, *Chelydra serpentina*. *Physiological and Biochemical Zoology* 72: 714–722.
- Finkler, M. S. 2006. Does variation in soil water content induce variation in the size of hatchling snapping turtles (*Chelydra serpentina*)? *Copeia* 2006: 769–777.
- Flatt, T., R. Shine, P. A. Borges-Landaez, and S. J. Downes. 2001. Phenotypic variation in an oviparous montane lizard (*Bassiana duperreyi*): the effects of thermal and hydric incubation environments. *Biological Journal of the Linnean Society* 74: 339–350.
- Gutzke, W. H. N. and G. C. Packard. 1987. Influence of the hydric and thermal environments on eggs and hatchlings of bull snakes *Pituophis melanoleucus*. *Physiological Zoology* 60: 9–17.
- Hare, K. M., C. H. Daugherty, and A. Cree. 2002. Incubation regime affects juvenile morphology and hatching success, but not sex, of the oviparous lizard *Oligosoma suteri* (Lacertilia: Scincidae). *New Zealand Journal of Zoology* 29: 221–229.
- Ji, X. and F. Brana. 1999. The influence of thermal and hydric environments on embryonic use of energy and nutrients, and hatchling traits, in the wall lizards (*Podarcis muralis*). *Comparative Biochemistry and Physiology* 124A: 205–213.
- Ji, X. and W. G. Du. 2001. The effects of thermal and hydric environments on hatching success, embryonic use of energy and hatchling traits in a colubrid snake, *Elaphe carinata*. *Comparative Biochemistry and Physiology* 129A: 461–471.
- Lin, Z. H., X. Ji, L. G. Luo, and X. M. Ma. 2005. Incubation temperature affects hatching success, embryonic expenditure of energy and hatchling phenotypes of a prolonged egg-retaining snake, *Deinagkistrodon acutus* (Viperidae). *Journal of Thermal Biology* 30: 289–297.
- Losos, J. B. 1990. The evolution of form and function: morphology and locomotor performance in West Indian *Anolis* lizards. *Evolution* 44: 1189–1203.
- Muth, A. 1980. Physiological ecology of desert Iguana (*Dipsosaurus dorsalis*) eggs: temperature and water relations. *Ecology* 61: 1335–1343.
- Packard, G. C. 1991. Physiological and ecological importance of water to embryos of oviparous reptiles. Pp. 213–227 in D. C. Deeming and M. J. W. Ferguson (eds.), *Egg Incubation: its Effects on Embryonic Development in Birds and Reptiles*. New York. Cambridge University Press.

- Packard, G. C. 1999. Water relations of chelonian eggs and embryos: is wetter better? *American Zoologist* 39: 289–303.
- Packard, G. C. and M. J. Packard. 1988. The physiological ecology of reptilian eggs and embryos. Pp. 523–605 in C. Gans and R. B. Huey (ed.), *Biology of Reptilia, Vol. 16, Ecology B, Defense and life history*. New York. Allan R. Liss Inc.
- Packard, G. C., M. J. Packard, K. Miller, and T. J. Boardman. 1987. Influence of moisture, temperature, and substrate on snapping turtle eggs and embryos. *Ecology* 68: 983–993.
- Pandav, B. N., B. A. Shanbhag, and S. K. Saidapur. 2006. Functional significance of post hatching residual yolk in the lizard, *Calotes versicolor*. *Journal of Herpetology* 40: 385–387.
- Pandav, B. N., B. A. Shanbhag, and S. K. Saidapur. 2010. Growth patterns and reproductive strategies in the lizard *Calotes versicolor* raised in captivity. *Acta Herpetologica* 5: 131–142.
- Phillips, J. A., A. Garel, G. C. Packard, and M. J. Packard. 1990. Influence of temperature and moisture on eggs and embryos of green iguanas, *Iguana iguana*. *Herpetologica* 46: 238–245.
- Pianka, E. R. and L. J. Vitt. 2003. *Lizards. Windows to the Evolution of Diversity*. Berkeley and Los Angeles. University of California Press. 346 pp.
- Plummer, M. V. and H. L. Snell. 1988. Nest site selection and water relations of eggs in the snake, *Opheodrys aestivus*. *Copeia* 1988: 58–64.
- Radder, R. S., B. A. Shanbhag, and S. K. Saidapur. 1998. Prolonged oviductal egg retention arrests embryonic growth at stage 34 in captive *Calotes versicolor*. *Herpetological Review* 29: 217.
- Radder, R. S., B. A. Shanbhag, and S. K. Saidapur. 2002a. Pattern of yolk internalization by hatchlings is related to breeding timing in the garden lizard, *Calotes versicolor*. *Current Science* 82: 1484–1486.
- Radder, R. S., B. A. Shanbhag, and S. K. Saidapur. 2002b. Influence of incubation temperature and substrate on eggs and embryos of the garden lizard, *Calotes versicolor* (Daud.). *Amphibia-Reptilia* 23: 71–82.
- Robbins, T. R. and D. A. Warner. 2010. Fluctuations in the incubation moisture environment affect growth but not survival of hatchling lizards. *Biological Journal of the Linnean Society* 100: 89–102.
- Shanbhag, B. A. 2003. Reproductive strategies in the lizard, *Calotes versicolor*. *Current Science* 84: 646–652.
- Shanbhag, B. A., R. S. Radder, and S. K. Saidapur. 2000. Maternal size determines clutch mass whereas breeding timing influences clutch and egg sizes in tropical lizard, *Calotes versicolor* (Agamidae). *Copeia* 2000: 1062–1067.
- Shine, R. and G. P. Brown. 2002. Effects of seasonally varying hydric conditions on hatchling phenotypes of Keelback snakes (*Tropidonophis mairii*, Colubridae) from the Australian wet-dry tropics. *Biology Journal of the Linnean Society* 76: 339–347.
- Shine, R. and L. J. Jr. Guillette. 1988. The evolution of viviparity in reptiles: a physiological model and its ecological consequences. *Journal of Theoretical Biology* 132: 43–50.
- Sinervo, B. and J. B. Losos. 1991. Walking the tight rope: arboreal sprint performance among *Sceloporus occidentalis* lizard populations. *Ecology* 72: 1225–1233.
- Troyer, K. 1987. Post hatching yolk in a lizard: internalization and contribution to growth. *Journal of Herpetology* 21:102–106.
- Van Damme, R., D. Bauwens, F. Brana, and R. F. Verheyen. 1992. Incubation temperature differentially affects hatching time, egg survival, and hatchling performance in the lizard *Podarcis muralis*. *Herpetologica* 48: 220–228.
- Warner, D. A. and R. M. Andrews. 2002. Laboratory and field experiments identify sources of variation in phenotypes and survival of hatchling lizards. *Biological Journal of the Linnean Society* 76: 105–124.
- Warner, D. A. and R. Shine. 2009. Maternal and environmental effects on offspring phenotypes in an oviparous lizard: do field data corroborate laboratory data? *Oecologia* 161: 209–220.
- Werner, D. I. 1988. The effect of varying water potential on body weight, yolk and fat bodies in neonate green iguanas. *Copeia* 1988: 406–411.