

Maternal thermoregulation influences offspring viability in a viviparous lizard

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Abstract. Gravid females of the viviparous scincid lizard *Eulamprus heatwolei* were maintained in the laboratory, with some females allowed to bask for 8 h/day and others for only 2 h/day. Maternal basking regimes influenced the gestation period, and significantly affected the body shapes, activity levels and running speeds of the offspring born to these females. Neonates from females with lesser basking opportunities were relatively short and fat, were very active, and were relatively fast runners. Effects of the embryos' thermal regime on the young lizards' morphology and running speed were still detectable two months after birth. Thus, much of the morphological and behavioral variation among neonatal reptiles may arise from phenotypically plastic responses to the thermal environments experienced during embryonic development, rather than from heritable genetic differences among individuals. Hence, selection on maternal thermoregulatory behavior may be an important avenue for adaptive modifications to neonatal phenotypes in reptiles.

Key words: Life history – Phenotypic plasticity – Embryo – Reptiles – Scincidae

The role of phenotypic plasticity has received increasing attention in analyses of life-history evolution (Bull 1980; Stearns and Koella 1986). If important phenotypic traits are modified by direct environmental influences during early development, then selection for 'optimal' values of traits may only be possible through selection for parental choice of appropriate conditions for embryogenesis (Bull 1980; Vleck 1988). For example, hatchling morphology in some species of turtles depends on hydric conditions during egg incubation, so that maternal choice of nesting substrates may be a primary determinant of offspring traits (Packard 1991). Incubation temperatures in oviparous reptiles can also influence hatchling phenotypic characteristics, so that maternal thermoregulation in viviparous species might influence the size, shape, color,

gender, behavior and survival rates of the resulting offspring (e.g., Fox et al. 1961; Osgood 1978; Bull 1980; Beuchat 1988; Phillips et al. 1990; Packard 1991). However, the available data are relatively meagre. Most studies have dealt with oviparous rather than viviparous species, and few investigations have included measures of hatchling behavior or performance ability which may be directly relevant to organismal fitness in the field (but see Lang 1985 and Webb and Cooper-Preston 1989 for studies on captive crocodiles, and Burger 1989, 1990, 1991 for behavioral studies on hatchling snakes). To investigate these aspects, we experimentally manipulated thermoregulatory opportunities in gravid scincid lizards and monitored the size, shape, behavior and running speed of their offspring.

Materials and methods

The scincid genus *Eulamprus* contains a series of morphologically and ecologically similar congeneric species in montane forests of southeastern Australia (Cogger 1986). Although the thermal biology and reproductive cycles of this group have been well documented (Spellerberg 1972a–c; Pengilley 1972; Shine 1983), recent taxonomic and nomenclatural rearrangements mean that it is sometimes difficult to determine which species has been studied in earlier work. The highland water skink, *Eulamprus heatwolei*, is a medium-sized (to 100 mm snout-vent length, henceforth = SVL) viviparous scincid species. This taxon has been separated only recently from *Eulamprus tympanum*, and hence is referred to as '*E. tympanum*' in most previous studies, including our own (Shine 1980, 1983). These two species of water skinks appear to be very similar ecologically, and are sympatric over broad areas (Cogger 1986). Mating occurs in spring (October), and female *E. heatwolei* produce a litter of about three offspring in late summer (late January to early March; Pengilley 1972). Water skinks are highly heliothermic, with mean selected temperatures around 32° C, but the cool and cloudy weather of their montane habitat typically restricts basking to a few hours per day (Shine 1983; Schwarzkopf and Shine 1991). Gravid female lizards spend more of their time basking than do males or non-gravid females, both in *E. heatwolei* (Shine 1980) and *E. tympanum* (Schwarzkopf and Shine 1991), and also differ from other conspecifics in emerging to bask even under relatively cool conditions (Schwarzkopf and Shine 1991).

Eighteen gravid female *E. heatwolei* were collected on 14–16 November 1991 at Picadilly Circus (elevation 1246 m) in the Brindabella Ranges 40 km west of Canberra in the Australian Capital Territory. The females were early in gestation (probably less than 2 weeks post-ovulation) at this time, based on their swollen body

shapes and on previous dissection studies (Pengilly 1972; Shine 1983). The lizards were brought to the University of Sydney, where they were randomly assigned to four cages (each $90 \times 35 \times 40$ cm; either 4 or 5 lizards per cage). Each cage contained a water dish, leaf-litter and hiding places. The lizards were fed three times per week on commercial cat food, so that excess food was always available in each cage. Heating was provided by two incandescent globes suspended above the substrate in each cage. Previous studies (Schwarzkopf and Shine 1991) showed that lizards basking under these lights could rapidly (<15 min) attain temperatures in excess of 30°C , and that the lizards cooled to air temperatures ($=23 \pm 2^\circ\text{C}$) during times when the lights were switched off. The room was illuminated with natural photoperiod, but the heating bulbs were switched on for briefer periods: two h/day (1100–1300 h) in two of the tanks, and eight h/day (0800–1600 h) in the other two. Treatments (duration of heating) were assigned randomly to cages. Incidental observations suggested that most lizards basked whenever given the opportunity.

All gravid lizards were weighed, measured and individually marked (toe-clipped) at the beginning of the study. Cages were checked daily. After a female gave birth, she and her offspring were removed from the cage for weighing and measuring. The neonates were then kept individually in plastic containers ($22 \times 13 \times 7$ cm) with one end of each container placed over a heating element so as to maintain a thermal gradient from ambient ($=26 \pm 2^\circ\text{C}$) to 38°C for 8 h per day, falling to ambient temperatures overnight. Neonates thus had ample opportunity for behavioral thermoregulation.

At one week of age, each neonate was tested for running speed in a styrofoam runway 1 m long and 5 cm wide. The runway was kept in a room held at $25 \pm 1^\circ\text{C}$, and the lizards were filmed with an overhead video camera (at 25 frames/s) as they were chased down the runway with an artist's paintbrush. Each lizard was run three times per day with a 10-s rest between successive trials, and was tested on each of three successive days. The lizard's mean speed over 50 cm and over the fastest 20 cm was calculated for each trial, and overall means were then calculated from these data (based on the

total of nine trials per lizard). Activity patterns were then assessed in the neonates' individual containers, at an air temperature of 25°C but with an underfloor heating element under one end of the container such that each hatchling had the opportunity to control its own body temperature. Water was provided in each container. Each lizard was kept in one of these containers for 24 h while being filmed by a time-lapse video-camera (1 frame per s) from 0800 to 1600 h. The resulting videos were scored to provide an index of basking frequency every ten minutes. Overall activity levels were determined by scoring the total number of times the lizard crossed lines set 5.5 cm apart across the length of the container. All measurements of morphology, running speed and activity were repeated when the offspring were seven to nine weeks of age.

The data on offspring phenotypes in Table 1 are reported as mean values for offspring from each treatment. This presentation facilitates comparison, but treats data from each offspring as an independent value and thus may be misleading if differences among litters confound differences due to treatments. All analyses of offspring phenotypes in Table 1 were thus based on two-factor nested ANOVAs, with the factors being (i) treatment (8 h vs. 2 h/day basking) and (ii) identification number of the litter, nested within treatment. Significance levels for litter effects are also reported in Table 1. Statistical analyses revealed no significant differences between animals from the two replicate cages within each treatment, and hence the data from the two replicate cages were pooled for statistical comparisons.

Results

All of the gravid lizards settled well into captivity, ate the food provided, and survived until after parturition. No obvious agonistic behavior between cage-mates was observed, and lizards typically lay in contact with each other

Table 1. Effects of maternal thermoregulation (8 h/day vs. 2 h/day basking) on female water skinks (*Eulamprus heatwolei*) and their offspring at one week of age. The Table shows means \pm SD for each treatment, and the results of statistical tests of the null hypotheses that the relevant variables were not affected by (i) incubation treatment, and (ii) litter. Associated probability levels are also given. Statistical results show unpaired two-tailed t tests for maternal characteristics (shown in "Treatment Effects" columns, to save space), and F values from two-factor ANOVAs (factors are treatment, and litter number nested within treatment) for offspring characteristics. Frequency data are tested using χ^2 values, based on 2×2 contingency tables, corrected for continuity

Variable	Mean \pm SD 8 h/day	Mean \pm SD 2 h/day	Statistic for treatment effect	Probability for treatment effect	Statistic for litter effect	Probability for litter effect
Maternal SVL (mm)	90.9 \pm 4.2	88.7 \pm 4.9	$t_{17} = 1.07$	0.30	–	–
Maternal body mass (g)	12.08 \pm 2.12	12.00 \pm 1.69	$t_{17} = 0.08$	0.93	–	–
Gestation period as captives (days)	59.4 \pm 1.4	72.5 \pm 4.5	$t_{17} = 13.83$	0.0001*	–	–
Litter size	2.89 \pm 0.78	2.89 \pm 0.78	$t_{17} = 0$	1.00	–	–
% deformed offspring	16.7%	6.7%	$\chi^2 = 0.53$ (1 df)	0.47	$\chi^2 = 8.57$ (9 df)	0.48
Offspring mass (g)	0.92 \pm 0.08	0.97 \pm 0.11	$F_{1,11} = 1.82$	> 0.50	$F_{11,34} = 19.80$	0.001*
Offspring SVL (mm)	40.0 \pm 1.2	39.1 \pm 1.6	$F_{1,11} = 2.04$	0.046*	$F_{11,34} = 5.46$	0.001*
Offspring tail length (mm)	66.6 \pm 2.8	65.9 \pm 2.9	$F_{1,11} = 0.01$	> 0.80	$F_{11,34} = 2.36$	0.03*
Time to run 50 cm (s)	1.81 \pm 0.42	1.34 \pm 0.45	$F_{1,11} = 7.95$	0.001*	$F_{11,34} = 2.48$	0.02*
Time to run fastest 20 cm (s)	0.50 \pm 0.12	0.37 \pm 0.10	$F_{1,11} = 12.34$	0.001*	$F_{11,34} = 1.24$	0.30
Number of stops/m	3.1 \pm 1.1	2.1 \pm 1.2	$F_{1,11} = 2.16$	> 0.50	$F_{11,34} = 1.50$	0.18
% of time basking	47.6 \pm 28.6	50.5 \pm 24.8	$F_{1,11} = 0.46$	> 0.50	$F_{4,37} = 5.43$	0.002*
Activity score (lines crossed per hour)	22.2 \pm 17.9	27.5 \pm 20.1	see text	0.001*	$F_{4,37} = 3.11$	0.03*
% offspring surviving to two months of age	54.2%	60.0%	$\chi^2 = 0.02$	0.88	$\chi^2 = 0.14$	> 0.70

* = $P < 0.05$. The total sample sizes were as follows: 9 females and 24 offspring in the 8 h/day treatment; 9 females and 29 offspring in the 2 h/day treatment. 'SVL' = snout-vent length

while basking. Hence, social interactions probably had little or no effect on the lizards' access to the heat source, and thermoregulatory behavior was constrained only by the duration of heating provided in the cage. Lizards maintained at the higher heat availability treatment (8 h/day) gave birth an average of 59 days after capture, whereas the females allowed to bask for only two hours/day gave birth significantly later (mean of 14 days later after capture: Table 1).

The experimental treatments did not affect the mean litter sizes of the females, the body masses of their offspring, or the frequency of deformities among neonates (Table 1). However, the body shape of the neonatal lizards was affected. Offspring from mothers allowed to bask for 8 h/day were significantly longer-bodied, although their tails were of similar lengths (Table 1). Given the equivalence of body masses (above), this result suggests that offspring from females that basked for 8 h/day were thinner than were offspring from females permitted to bask for only 2 h/day. Analysis of covariance confirms this deduction: offspring from the two treatments differed considerably in body mass at the same snout-vent length (with SVL as the covariate: slopes $F_{1,49} = 1.96$, $P = 0.17$; intercepts $F_{1,50} = 23.94$, $P < 0.0001$: see Fig. 1).

The maternal thermoregulatory schedule also influenced the running speeds of their offspring. Increased exposure to a heat source during embryogenesis reduced the mean running speed of the neonates by one-third (i.e., increased the time taken to cover a fixed distance: see Table 1). The animal's thermal history during embryonic development also affected the number of times that a neonatal skink stopped during its one-metre run, with more prolonged maternal basking giving rise to offspring that stopped more often (Table 1). This reduced running speed and higher stopping frequency were not due to the increased body lengths of offspring from females allowed to bask for longer periods. Although neonatal body length was significantly correlated with both measures of running speed (speed over 50 cm, $n = 48$, $r = -0.28$, $P = 0.05$; over 20 cm, $n = 48$, $r = -0.32$, $P < 0.03$) and with the num-

ber of times a neonate stopped during its run ($n = 48$, $r = 0.48$, $P < 0.001$), analysis of covariance of these data showed that the difference between treatments persisted even when SVL was held constant (with SVL as the covariate: speed over 50 cm – slopes $F_{1,44} = 0.001$, $P = 0.97$; intercepts $F_{1,45} = 10.69$, $P < 0.002$; speed over 20 cm – slopes $F_{1,44} = 1.13$, $P = 0.29$; intercepts $F_{1,45} = 13.62$, $P < 0.001$; number of stops – slopes $F_{1,44} = 0.58$, $P = 0.45$; intercepts $F_{1,45} = 5.37$, $P < 0.03$: see Fig. 1). Similarly, the reduced running speed of offspring from the "prolonged maternal basking" treatment was not due to their tendency to stop more often during running trials. Analysis of covariance (with running speed as the dependent variable, and number of stops per trial as the covariate) showed that offspring from the two treatments differed in running speed even when the number of stops was held constant (for 50 cm, slopes $F_{1,73} = 5.00$, $P = 0.028$; for 20 cm, slopes $F_{1,73} = 0.39$, $P = 0.53$ but intercepts $F_{1,74} = 8.75$, $P = 0.004$).

The thermal regime experienced during embryonic development also affected the subsequent activity levels of the neonatal lizards, but not the proportion of time they spent basking in heated portions of their cages. The only significant influence on basking frequency was the age of the lizard: older skinks spent less time basking (correlation of age with percentage of time basking: $n = 71$, $r = -0.49$, $P < 0.0001$). The maternal thermoregulatory regime did not influence the basking frequency of neonates (Table 1). In contrast, overall activity levels (number of lines crossed per hour, from 0800 to 1600 h) were not significantly correlated with age ($n = 72$, $r = -0.18$, $P = 0.12$) or affected by time of day (one-factor ANOVA, with time period as the factor: $F_{7,248} = 0.98$, $P = 0.45$), but were strongly influenced by the maternal thermal regime. In each of the eight hourly periods monitored, the mean activity scores of neonates from females allowed to bask only 2 h/day were higher than those of neonates from females allowed to bask for 8 h/day (two-tailed binomial test, $P < 0.01$).

Many of the differences in morphology and running speed observed in the week-old neonates were still evident

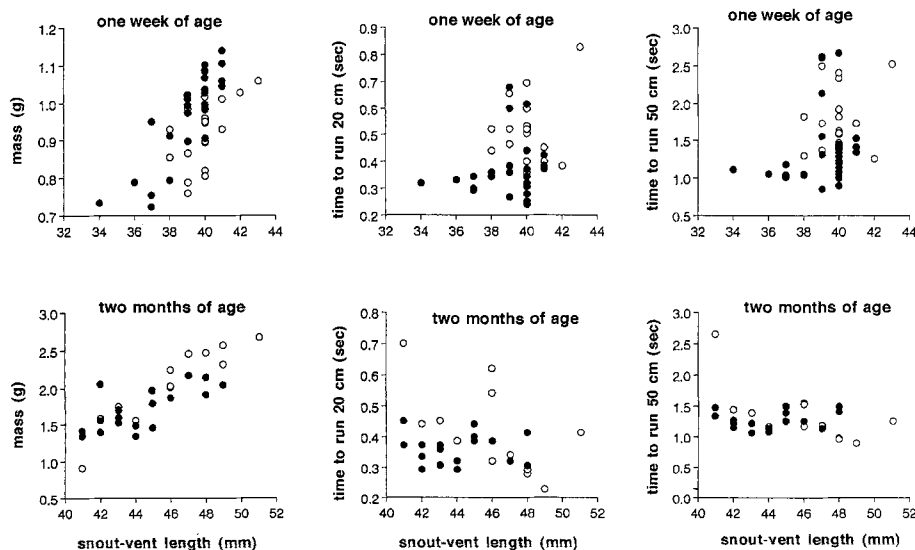


Fig. 1. Relationships between offspring snout-vent length (= SVL) and other aspects of offspring phenotype in *Eulamprus heatwolei*. Two left-hand panels show body mass relative to SVL, and other panels show running speed (middle panels = speed over 20 cm; right-hand panels = speed over 50 cm) relative to SVL. Circles show data from offspring born to mothers allowed to bask for up to 8 h per day during gestation, and dots show data from offspring born to mothers allowed to bask for only 2 h per day. See text for methodology and statistical results

when the measurements were repeated fifty days later, on two-month-old lizards. Although the two groups were similar in growth rates (daily rate of change in mass $-t = 0.64$, 28 df, $P = 0.53$; daily rate of change in SVL $-t = 1.63$, 28 df, $P = 0.12$) and survival rates (Table 1), the relationship between body length and mass differed between the offspring from the two experimental treatments (slopes $F_{1,27} = 7.32$, $P < 0.02$: see Fig. 1), as it had at one week of age. The difference in mean running speeds between treatments disappeared, with no significant effect of maternal thermoregulatory regime on the offspring's running speed over 50 cm ($t_{27} = 0.59$, $P = 0.56$), over 20 cm ($t_{27} = 1.36$, $P = 0.18$), or on the number of times the lizard stopped during its run ($t_{27} = 0.14$, $P = 0.89$). However, the relationship between body length and running speed continued to differ between lizards from the two groups. Analysis of covariance, with SVL as the covariate, detected significant effects of maternal thermoregulatory regime on the relationship between the offspring's SVL and its mean running speed (over 50 cm – slopes $F_{1,25} = 10.50$, $P < 0.004$; over 20 cm – slopes $F_{1,25} = 5.19$, $P < 0.04$; number of stops per run – slopes $F_{1,25} = 4.34$, $P < 0.05$: see Fig. 1). These significant results are due to a trend for larger neonates from the females that could bask for 8 h/day, to be heavier-bodied, run faster and stop less often than did their smaller litter-mates, whereas no such effect of body size was obvious in the offspring from females able to bask for only 2 h/day.

Finally, we carried out Model II analyses of variance to assess the level of variation in offspring phenotypes induced by the treatment (basking regime) relative to the variation that occurred among different litters within each treatment. Undoubtedly, this latter (among-litter) variation results from genetic factors as well as other non-genetic differences among mothers. Some fraction of this familial variance within treatments may also be due to differences among individual females in thermal regime, if some females basked more than others. We used treatment as one factor in these analyses, and litter (nested within treatment) as the other. Not surprisingly, there were consistent differences among litters in mean offspring sizes (Table 1). However, the maternal basking regime was responsible for a high proportion of the total variance in offspring characteristics such as mean running speed over 50 cm (27.8%) and 20 cm (38.6%), and for analyses using residual scores from the regressions of SVL to mass (26.2%), and SVL to running speed (over 50 cm – 24.9%; over 20 cm – 33.2%). Thus, our manipulation of maternal basking regime contributed a considerable proportion of the overall phenotypic variation that we measured in the neonatal lizards.

Discussion

The clear result from these experiments is that the basking opportunities available to a gravid lizard affect not only the duration of her gestation, but also the morphology, behavior and performance abilities of her offspring. An influence of maternal thermoregulation on the rate of embryogenesis, and hence on the duration of gestation, is not surprising. Limited data suggest that such an effect is

widespread among snakes and lizards (e.g., Blanchard and Blanchard 1941; Naulleau 1986; Beuchat 1986), and there is good experimental evidence for such an effect in the related *Eulamprus tympanum* (Schwarzkopf and Shine 1991). Data from the present study mirror many of the results obtained with *E. tympanum* for example, maternal thermal regimes did not affect litter size, offspring mass, or embryonic survival rate (Schwarzkopf and Shine 1991).

More interesting, however, is the demonstration that the experimental treatment affected the shape, behavior and performance of the neonatal lizards. This effect is presumably due to differences between the two treatments in the thermal regime experienced by embryos, because no other factor varied between the treatments. The experimental design of the present study may be criticised on the grounds that the difference in basking opportunities (2 h vs. 8 h/day) might be greater than the variance experienced by gravid lizards in the field, but a closer analysis fails to support this challenge. Despite the large difference in hours available for basking per day, parturition in the group of females with briefer access to the heat lamp was delayed by only about two weeks. Indeed, parturition dates almost overlapped: the 'prolonged basking' group gave birth from 13 to 17 January, and the 'brief basking' group from 20 January to 4 February. All of these dates fall within the normal range of parturition dates recorded in the field (= January to March, Pengilly 1972), and the difference between the groups in this respect is lower than the year-to-year variation in mean parturition dates recorded in this population (Pengilly 1972; Shine, unpubl.). There is considerable spatial as well as temporal variation in the duration of basking opportunities also, because the habitats occupied by *E. heatwolei* range from relatively exposed areas to heavily vegetated habitats where basking is possible for only a few hours per day (Schwarzkopf and Shine 1991).

The mechanism by which incubation temperatures affect neonatal characteristics in *E. heatwolei* is unknown, but could be either direct (i.e., working on the embryo) or indirect (mediated through the mother's response to lowered availability of basking opportunities). An indirect influence of incubation conditions on hatchling characteristics is difficult to reconcile with the fact that incubation temperatures similarly affect hatchling morphology and performance in many oviparous reptiles, including skinks (Burger 1989, 1990, 1991; Shine, in prep.). It thus seems likely that the embryo's thermal regime influences the phenotype of the resulting offspring by directly affecting morphogenetic processes. Incubation temperatures affect the degree to which yolk is converted to body tissue in some species of turtles (Gutzke 1984), snakes (Gutzke and Packard 1987), lizards (Phillips et al. 1990), crocodylians (Whitehead and Seymour 1990) and frogs (Seymour et al. 1991), such that embryos raised at low (or intermediate) temperatures hatch with a greater yolk-free mass but less residual yolk. Such a mechanism might explain our observation of a difference in body length and shape in neonatal *E. heatwolei* exposed to different thermal regimes during embryonic development, but is unlikely to explain all of the variation in neonatal phenotype – especially since effects on body shape were still detectable in two-month-old lizards (and see Van Damme et al. 1992).

Whatever its specific physiological basis, the dependence of neonatal morphology and behavior on thermal conditions during embryogenesis is widespread, having been reported in a diverse array of invertebrates (e.g., Ghouri and McFarlane 1958; Meats 1984; Roff 1986), fishes (Gray 1928), frogs (Smith-Gill and Berven 1979), snakes (Burger 1989, 1990, 1991), lizards (Phillips et al. 1990, Van Damme et al. 1992), turtles (Miller et al. 1987) and crocodylians (Lang 1985; Webb and Cooper-Preston 1989). A high proportion of the overall morphological and behavioral variance among hatchling and neonatal reptiles within a population may thus reflect phenotypic plasticity rather than genetic factors (Vleck 1988; Packard 1991). Interpretations of life-history strategies or studies of natural selection cannot afford to ignore this source of variation.

If much of the variance among neonates reflects phenotypically plastic responses to incubation conditions, how can natural selection operate to optimise neonatal phenotypes? In such a situation, selection may operate on parental selection of incubation conditions, rather than working directly on alleles 'for' offspring size, shape, and behavior (Packard 1991; Schmitt et al. 1992). This hypothesis is supported by the widespread tendency of female reptiles to modify their thermal preferences when they are gravid (e.g., Shine 1980; Werner 1990; Schwarzkopf and Shine 1991; Van Damme et al. 1992). Such modified thermoregulation by gravid reptiles may enhance maternal fitness not only by changing rates of embryogenesis (and thus, the duration of gestation – e.g., Shine 1980; Schwarzkopf and Shine 1991) but may also directly modify offspring phenotypes. More basking may not always be better. For example, a fourfold increase in basking opportunities in *Eulamprus heatwolei* produced only a 12% decrease in gestation period (Table 1) and resulted in neonates being less active, and in being slower runners (Table 1). Direct influences of incubation conditions on the viability of hatchling reptiles may offer an ideal system for analysis of the role of phenotypic plasticity in micro-evolutionary phenomena, and for the ways in which selection on parental behavior feeds back into offspring fitness.

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References

- Beuchat CA (1986) Reproductive influences on the thermoregulatory behavior of a live-bearing lizard. *Copeia* 1986: 971–979
- Beuchat CA (1988) Temperature effects during gestation in a viviparous lizard. *J Therm Biol* 13: 135–142
- Blanchard FN, Blanchard FC (1941) Factors determining time of birth in the garter snake *Thamnophis sirtalis sirtalis* (Linnaeus). *Pap Mich Acad Sci Arts Lett* 26: 161–176
- Bull JJ (1980) Sex determination in reptiles. *Quart Rev Biol* 55: 4–21
- Burger J (1989) Incubation temperature has long-term effects on behavior of young pine snakes (*Pituophis melanoleucus*). *Behav Ecol Sociobiol* 24: 201–207
- Burger J (1990) Effects of incubation temperature on behavior of young black racers (*Coluber constrictor*) and kingsnakes (*Lampropeltis getulus*). *J Herpetol* 24: 158–163
- Burger J (1991) Effects of incubation temperature on behavior of hatchling pine snakes: implications for reptilian distribution. *Behav Ecol Sociobiol* 28: 297–303
- Cogger HG (1986) *Reptiles and Amphibians of Australia*, 3rd edition. Reed Books, Sydney
- Fox WC, Gordon C, Fox MH (1961) Morphological effects of low temperatures during the embryonic development of the garter snake, *Thamnophis elegans*. *Zoologica* 46: 57–71
- Ghouri ASK, McFarlane JE (1958) Occurrence of a macropterous form of *Grylloides sigillatus* (Walker) (Orthoptera: Gryllidae) in laboratory cultures. *Can J Zool* 36: 837–838
- Gray J (1928) The growth of fish. III. The effect of temperature on the development of the eggs of *Salmo fario*. *Brit J Exp Biol* 6: 125–130
- Gutzke WHN (1984) The influence of environmental factors on eggs and hatchlings of painted turtles (*Chrysemys picta*). PhD Dissertation, Colorado State University, Fort Collins, Co.
- Gutzke WHN, Packard GC (1987) Influence of the hydric and thermal environments on eggs and hatchlings of bull snakes *Pituophis melanoleucus*. *Physiol Zool* 60: 9–17
- Lang JW (1985) Incubation temperature affects thermal selection of hatchling crocodiles. *Am Zool* 25: 18A
- Meats A (1984) Thermal constraints to successful development of the Queensland fruit fly in regimes of constant and fluctuating temperature. *Entomol Exp Appl* 36: 55–59
- Miller K, Packard GC, Packard MJ (1987) Hydric conditions during incubation influence locomotor performance of hatchling snapping turtles. *J Exp Biol* 127: 401–412
- Naulleau G (1986) Effects of temperature on 'gestation' in *Vipera aspis* and *V. berus* (Reptilia: Serpentes). In: Röcek Z (eds), *Studies in herpetology*. Charles Univ, Prague, pp 489–494
- Osgood DW (1978) Effects of temperature on the development of meristic characters in *Natrix fasciata*. *Copeia* 1978: 33–47
- Packard GC (1991) Physiological and ecological importance of water to embryos of oviparous reptiles. In: Deeming DC, Ferguson MWJ (eds), *Egg incubation: its effects on embryonic development in birds and reptiles*. Cambridge Univ Press, Cambridge, pp 213–228
- Pengilley R (1972) Systematic relationships and ecology of some lygosomine lizards from southeastern Australia. PhD Dissertation. Australian National University, Canberra, ACT, Australia
- Phillips JA, Garel A, Packard GC, Packard MJ (1990) Influence of moisture and temperature on eggs and embryos of green iguanas (*Iguana iguana*). *Herpetologica* 46: 238–245.
- Roff D (1986) The genetic basis of wing dimorphism in the sand cricket, *Gryllus firmus*, and its relevance to the evolution of wing dimorphism. *Heredity* 57: 221–231
- Schmitt J, Niles J, Wulff RD (1992) Norms of reaction of seed traits to maternal environments in *Plantago lanceolata*. *Am Nat* 139: 451–466
- Schwarzkopf L, Shine R (1991) Thermal biology of reproduction in viviparous skinks, *Eulamprus tympanum*: Why do gravid females bask more? *Oecologia* 88: 562–569
- Seymour RS, Geiser F, Bradford DF (1991) Metabolic cost of development in terrestrial frog eggs (*Pseudophryne bibronii*). *Physiol Zool* 64: 688–696
- Shine R (1980) "Costs" of reproduction in reptiles. *Oecologia* 46: 92–100
- Shine R (1983) Reptilian viviparity in cold climates: testing the assumptions of an evolutionary hypothesis. *Oecologia* 57: 397–405
- Smith-Gill SJ, Berven KA (1979) Predicting amphibian metamorphosis. *Am Nat* 113: 563–585
- Spellerberg IF (1972b) Thermal ecology of allopatric lizards (*Sphenomorphus*) in southeast Australia. I. The environment and lizard critical temperatures. *Oecologia* 9: 371–383
- Spellerberg IF (1972b) Thermal ecology of allopatric lizards (*Sphenomorphus*) in southeast Australia. II. Physiological aspects of thermoregulation. *Oecologia* 9: 385–398

- Spellerberg IF (1972c) Thermal ecology of allopatric lizards (*Sphenomorphus*) in southeast Australia. III. Behavioural aspects of thermoregulation. *Oecologia* 11: 1–16
- Stearns SC, Koella JC (1986) The evolution of phenotypic plasticity in life-history traits: predictions of reaction norms for age and size at maturity. *Evolution* 40: 893–914
- Van Damme R, Bauwens D, Brana F, Verheyen RF (1992) Incubation temperature differentially affects hatching time, egg survival and sprint speed in the lizard *Podarcis muralis*. *Herpetologica* 48: 220–228
- Vleck D (1988) Embryo water economy, egg size and hatchling viability in the lizard *Sceloporus virgatus*. *Am Zool* 28: 87A
- Webb GJW, Cooper-Preston H (1989) Effects of incubation temperature on crocodiles and the evolution of reptilian oviparity. *Am Zool* 29: 953–971
- Werner YL (1990) Do gravid females of oviparous gekkonid lizards maintain elevated body temperatures? *Hemidactylus frenatus* and *Lepidodactylus lugubris* in Oahu. *Amphib-Reptil* 11: 200–204
- Whitehead P, Seymour RS (1990) Patterns of metabolic rate in embryonic crocodylians *Crocodylus johnstoni* and *Crocodylus porosus*. *Physiol Zool* 63: 334–352