A NEW HYPOTHESIS FOR THE EVOLUTION OF VIVIPARITY IN REPTILES

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Abstract.—Viviparity has evolved many times within squamate reptiles, mostly in cool climates, but the selective advantages of uterine retention of eggs remain obscure. Previous analyses have assumed that intrauterine incubation enhances offspring survival because of early hatching or protection of the young in utero. I suggest instead that prolonged uterine retention directly enhances hatchling viability, because eggs incubated at maternal body temperatures produce "better" hatchlings than do eggs incubated at normal nest temperatures. To test this idea, I incubated eggs of two species of montane scincid lizards from southeastern Australia (Bassiana duperreyi and Nanoscincus maccoyi) under thermal regimes designed to simulate temperatures in nests and maternal oviducts. Hatchling phenotypes were substantially affected by incubation temperatures. The variables affected by incubation at maternal versus nest thermal regimes include the hatchling’s morphology (body size, relative tail length), running speed in a laboratory raceway, and behavior (activity levels, frequency of basking, antipredator tactics). The running speeds of hatchling B. duperreyi were also influenced by brief retention at “maternal” temperatures after the usual time of laying (a presumed intermediate stage for the evolution of viviparity) and by body temperatures of females prior to oviposition. Hence, a direct effect of uterine retention on offspring viability offers a plausible selective advantage for the evolution of viviparity in squamate reptiles and possibly in other vertebrates and invertebrates also. More generally, the expression of phenotypic plasticity may play an integral role in the adaptive modification of life-history phenomena.

Viviparity (production of fully formed offspring) has evolved from oviparity (egg laying) many times, with at least 100 separate origins of this trait within squamate reptiles (snakes and lizards) (Blackburn 1981; Shine 1985). Viviparity is more common among cool-climate reptiles than among species living in warmer climates (Sergeev 1940; Tinkle and Gibbons 1977; Shine and Berry 1978), and phylogenetic analyses suggest that squamate viviparity generally has evolved in cool climates (Shine 1985). In such areas, maternal body temperatures are likely to be considerably higher than soil temperatures, so that oviductally retained eggs develop at much higher temperatures in the oviduct (before oviposition) than in the soil (after oviposition) (see, e.g., Sergeev 1940). Higher incubation temperatures accelerate embryogenesis (Packard et al. 1977), and the resultant early hatching may enhance offspring survival by reducing mortality in the nest and by enabling hatchlings to emerge and seek shelter prior to the onset of lethally low

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soil temperatures in autumn (Packard et al. 1977; Tinkle and Gibbons 1977; Shine and Bull 1979).

Although this idea (popularly known as the “cold-climate hypothesis”) has enjoyed wide acceptance for more than 50 yr (Tinkle and Gibbons 1977), an alternative hypothesis may offer a simpler explanation for the adaptive significance of reptilian viviparity. In a wide variety of taxa, incubation conditions are known to profoundly influence the resulting offspring’s size (Gutzke and Packard 1987; Beuchat 1988; Whitehead and Seymour 1990; Seymour et al. 1991; Van Damme et al. 1992), shape (Fox 1948; Osgood 1978; Burger 1990), color (Vinegar 1974; Ewert 1979; Deeming and Ferguson 1989, 1991), gender (Bull 1980; Ferguson and Joanen 1982; Brooks et al. 1991), behavior (Burger 1989, 1990, 1991), and performance ability (Burger 1990, 1991; Van Damme et al. 1992). Field studies have revealed that some or all of these traits may influence an offspring’s chance of survival and hence its genetic fitness (see, e.g., Ferguson and Fox 1984; Vleck 1988; Brooks et al. 1991; Olsson 1992). I propose that the physical (especially, thermal) conditions of uterine incubation directly modify offspring phenotypes so that oviductally retained offspring are “fitter” than offspring that emerge from eggs incubated in nests. If retention of reptilian embryos at maternal body temperatures enhances hatching viability in this way, the main selective force for prolonged retention—and thus, eventually, viviparity—may lie in the phenotype of the offspring and not simply its survival rate to hatching or the time at which it is born. In order to test this hypothesis, one needs data on the effects of incubation at maternal versus nest temperatures on offspring phenotypes of an oviparous squamate species. Ideally, the animals studied should belong to a phylogenetic lineage that contains viviparous as well as oviparous species, so that the effects of different incubation temperatures on offspring phenotypes in the present-day oviparous taxon are likely to resemble those of the ancestral oviparous taxa in which viviparity evolved. Positive effects of “viviparous” temperatures on offspring phenotypes in an oviparous species do not necessarily mean that viviparity would be predicted to evolve in that species, because uterine retention of eggs may confer such high costs on the female as to outweigh the benefits to the offspring (see, e.g., Shine 1985).

MATERIAL AND METHODS

Two species of oviparous scincid lizards from southeastern Australia were studied. Bassiana duperreyi is a medium-sized (to 85-mm snout-vent length [SVL]) diurnal heliothermic species of montane grasslands, whereas the sympatric Nannoscincus maccoyi is a smaller (to 60-mm SVL) and more secretive species, usually found under logs on moist ground (Cogger 1986). Active B. duperreyi have mean selected temperatures around 32°C, whereas body temperatures of N. maccoyi are much lower and generally similar to soil temperatures (less than 20°C) (Shine 1983b). Females of both species lay their eggs under logs or rocks on moist soil in early summer (December) (Shine 1983b). The general natural history and reproductive biology of both species have been well documented (see, e.g., Pengilley 1972; Robertson 1981; Shine 1983b). Viviparity has arisen
several times within taxa closely related to *B. dupeffeyi* (Greer 1989; Hutchinson et al. 1990). Recent nomenclatural changes have affected both species: *B. dupeffeyi* is known as *Leiolopisma trilineata* in earlier work and *N. maccioyi* as *Anolis maccioyi*.

The data reported in this article were gathered over the summer of 1991–1992. Gravid females of both species were collected in November at a variety of sites within 10 km of Piccadilly Circus (elevation, 1,246 m) in the Brindabella Ranges 40 km west of Canberra in the Australian Capital Territory. Judging from the results of previous dissection studies (Pengilley 1972; Shine 1983b), the females were early in gestation (probably less than 2 wk postovulation) at this time. The lizards were brought to the University of Sydney, where they were placed into separate cages (each 22 cm × 13 cm × 7 cm). Each cage contained a water dish, and the lizards were fed on *Tribolium* larvae. The room was maintained at natural photoperiod. Heating was provided separately for each cage by means of an underfloor heating element that maintained a thermal gradient from ambient (25°–28°C) to 38°C within each cage for 8 h/d, falling to ambient temperatures overnight. The lizards thus had ample opportunity for behavioral thermoregulation.

All lizards were weighed, measured, and individually marked (toe clipped) at the beginning of the study. Cloacal temperatures of the ovigerous female *B. dupeffeyi* were recorded daily between 1200 and 1330 hours during the 5 d preceding oviposition. Cages were checked for eggs at least once per day. As soon as eggs were found, they were removed from the cage for weighing, and then each was incubated separately in a 64-mL glass jar containing moist vermiculite (−200-kPa water potential) and covered with plastic food wrap to prevent moisture loss. The amount of water needed to achieve this water potential (120% water by dry mass of vermiculite) was determined from a standard curve of water content (range, 20%–160% water by mass) versus water potential, as measured at 25°C with a Wescor HR-33T dew point microvoltmeter and a Wescor C-52 sample chamber. Two incubators were used. One incubator mimicked the thermal regimes measured in natural nests (daily cycles of gradual heating and cooling, ranging from 10°C to 25°C) (Shine 1983b), and the other mimicked maternal body temperature regimes of *B. dupeffeyi* (30°C from 0800 to 1800 hours, falling to 15°C by 1900 hours and staying at that level until the following morning, based on field measurements of gravid females) (Shine 1983b; R. Shine, unpublished data). Each clutch was divided into three treatments. Two eggs from each clutch were incubated at nest temperatures (simulating the natural condition), another two eggs were incubated at maternal body temperatures (simulating viviparity), and the remaining eggs were incubated for 20 d at maternal body temperatures and then transferred to nest temperatures for the duration of development (simulating prolonged uterine retention of eggs, a presumed necessary intermediate stage in the evolution of viviparity). Because many clutches contained less than six eggs, this allocation system meant that more eggs were allocated to the “viviparity” and “nest” simulations than to the intermediate (“uterine retention”) condition.

This experimental design did not ensure that all eggs developed under the same
hydric conditions (water potentials) throughout development, despite the fact that all eggs commenced incubation at identical water potentials. The vermiculite in the high-temperature treatment would tend to lose water more rapidly than the vermiculite in the low-temperature treatment (see, e.g., Packard 1991), so that high-temperature eggs may have developed in drier incubation conditions. Also, eggs developing at different temperatures will have different patterns of water exchange even when water potentials are identical (Packard 1991). Given the scarcity of information on hydric conditions in natural nests or oviducts of B. duperreyi, I adopted the simpler expedient of allowing incubation to proceed after establishing identical hydric conditions at the beginning of incubation in each treatment. The resulting differences in hydric conditions between eggs in the two thermal treatments may have contributed to the differences in hatching phenotypes observed in my experiment.

Incubators were checked daily and any hatchlings removed, weighed, measured, and placed in separate containers (the same kind and size as those used for adults) with access to food, water, and thermoregulatory opportunities. At 1 wk of age, each hatchling 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° ± 1°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 3 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).

After the running trials were completed, activity patterns of the young B. duperreyi were assessed by filming the week-old hatchlings in their individual containers with a time-lapse video camera (1 frame/s) from 0800 to 1600 hours. Ambient temperature in the room was maintained at 25° ± 1°C. The resulting videos were scored to provide an index of basking frequency every 10 min (i.e., time spent in the heated part of the cage). Frequency of movement was determined by scoring the total number of times the lizard crossed lines set 5.5 cm apart across the length of the container. Nannoscincus maccvoyi was not used in these activity trials because of their fossorial habits and because they desiccated rapidly even when the substrate was kept moist. All offspring (of both species) were released after these measurements were completed.

RESULTS

Mean cloacal temperatures measured on 11 female Bassiana duperreyi (n = 5 measurements per animal, one measurement per day) ranged from 30.3° to 34.5°C and differed consistently among animals (one-factor ANOVA with female identification number as the factor, $F = 2.32, df = 10, 64, P < .03$). For further analysis, these mean maternal temperatures were lumped into four categories (30°–31°, 32°–33°, 33.1°–34°, 34.1°–35°C). The data on incubation periods and hatching phenotypes of Bassiana were analyzed with a split-plot ANOVA, with the three factors being maternal temperature category prior to oviposition (df = 3); incuba-
tion temperature regime (df = 2); and identification number of the clutch, nested within the maternal temperature category prior to oviposition (df = 9). No information on maternal body temperatures prior to oviposition was available for *Nannoscincus*, so the data on incubation periods and hatching phenotypes of this species were analyzed by two-factor ANOVAs with incubation regime (fixed) and clutch identification number (random) as the factors.

**Influence of Maternal Thermoregulation Prior to Oviposition**

Maternal body temperatures of *B. duperreyi* prior to oviposition did not significantly influence subsequent incubation periods, rates of hatching success, or any of the morphological variables measured on the hatchlings, including their body masses, SVLs, or tail lengths (table 1). ANCOVA, using SVL as the covariate, showed that maternal temperature category also did not influence the hatchling’s tail length relative to SVL (homogeneity of slopes, $F = 0.19$, df = 3,55, $P = .90$; intercepts test, $F = 2.36$, df = 3,56, $P = .08$) or its mass relative to SVL (homogeneity of slopes, $F = 1.52$, df = 3,55, $P = .22$; intercepts test, $F = 0.76$, df = 3,56, $P = .52$). Similarly, the activity and thermoregulatory variables that I measured on the young lizards were not affected by maternal body temperatures (table 1). In the trials of running speed, however, maternal temperatures prior to oviposition influenced the average number of times the young lizards stopped during each run and the hatchling’s running speed over distances of both 20 and 50 cm (table 1). Thus, the body temperatures selected by gravid lizards in the week prior to oviposition affected the running speeds of their hatchlings 2 or 3 mo later, despite the relatively small variation in mean selected temperatures among females.

**Influence of Incubation Temperatures**

**Incubation periods.**—In both species, the thermal regime during incubation influenced the duration of embryogenesis (tables 1, 2). At equivalent temperatures, the smaller eggs of *Nannoscincus maccoyi* hatched in a shorter time than did the *Bassiana* eggs, but this difference was more pronounced at lower temperatures (40% interspecific difference in incubation periods at nest simulation) than at higher ones (5% difference at viviparity simulation).

**Survival rate.**—Eggs of *N. maccoyi* incubated in cooler conditions experienced significantly higher survival rates through to hatching (table 2) but no such effect was seen in *B. duperreyi* (table 1).

**Offspring size.**—Mean offspring mass did not vary significantly with incubation conditions in *B. duperreyi* but did in *N. maccoyi* (tables 1, 2). Hatching *N. maccoyi* from the viviparity simulation were shorter than their siblings from lower-temperature incubation conditions, whereas the heaviest hatchlings were those from the intermediate (uterine retention) treatment (table 2). The body lengths of hatching *B. duperreyi* were unaffected by incubation temperatures (table 1), although other work on this species, using constant-temperature incubation, found a significant effect (R. Shine, unpublished manuscript).

**Body condition.**—ANCOVA (comparing the relationship of SVL to body mass, using SVL as the covariate) showed that incubation conditions did not influence
### TABLE 1

**Effects of Incubation Temperature Regimes on Incubation Periods, Embryo Survival Rates, Morphology, Running Speed, and Behavior of Offspring in the Oviparous Scincid Lizard *Basiliscus duperrey*\u201d**

<table>
<thead>
<tr>
<th>Trait</th>
<th>Mean Values for Viparity Treatment</th>
<th>Mean Values for Uterine Retention Treatment</th>
<th>Mean Values for Nest Treatment</th>
<th>Statistical Test: Effect of Maternal Thermal Category</th>
<th>Statistical Test: Effect of Incubation Temperatures</th>
<th>Statistical Test: Differences among Clutches</th>
</tr>
</thead>
<tbody>
<tr>
<td>Incubation period (d)</td>
<td>53.24 ± 2.77</td>
<td>77.40 ± 3.67</td>
<td>97.44 ± 3.41</td>
<td>F = 9.12, df = 3, P &lt; .050</td>
<td>F = 1.720, df = 2, P &lt; .001</td>
<td>F = 4.84, df = 9, P &lt; .001</td>
</tr>
<tr>
<td>Survival rate to hatching (%)</td>
<td>55.6 ± 6.16</td>
<td>59.2 ± 6.16</td>
<td>58.4 ± 6.46</td>
<td>χ² = 4.69, df = 2, P = .001</td>
<td>χ² = 4.69, df = 2, P = .001</td>
<td>χ² = 4.69, df = 2, P = .001</td>
</tr>
<tr>
<td>Mass at hatching (g)</td>
<td>29.2 ± 2.74</td>
<td>27.4 ± 2.74</td>
<td>28.4 ± 2.74</td>
<td>F = 2.24, df = 2, P &lt; .12</td>
<td>F = 2.24, df = 2, P &lt; .12</td>
<td>F = 2.24, df = 2, P &lt; .12</td>
</tr>
<tr>
<td>SVL at hatching (mm)</td>
<td>26.2 ± .74</td>
<td>26.6 ± .74</td>
<td>26.8 ± .74</td>
<td>F = 1.39, df = 3, P = .31</td>
<td>F = 2.23, df = 2, P = .11</td>
<td>F = 2.23, df = 2, P = .11</td>
</tr>
<tr>
<td>Tail length at hatching (mm)</td>
<td>31.5 ± 1.86</td>
<td>29.16 ± 2.04</td>
<td>28.6 ± 2.34</td>
<td>F = 2.15, df = 3, P = .16</td>
<td>F = 13.39, df = 2, P &lt; .001</td>
<td>F = 13.39, df = 2, P &lt; .001</td>
</tr>
<tr>
<td>Running speed (m/s)</td>
<td>Over 50 cm</td>
<td>52.8 ± .05</td>
<td>54.4 ± .05</td>
<td>F = 7.45, df = 3, P &lt; .009</td>
<td>F = 3.16, df = 2, P = .054</td>
<td>F = 95, df = 3, P = .09</td>
</tr>
<tr>
<td>Over fastest 30 cm</td>
<td>1.24 ± .25</td>
<td>1.51 ± .15</td>
<td>2.09 ± .15</td>
<td>F = 3.94, df = 3, P &lt; .02</td>
<td>F = 12.17, df = 2, P = .001</td>
<td>F = 1.08, df = 3, P = .40</td>
</tr>
<tr>
<td>Mean no. of stops/50 cm</td>
<td>2.89 ± 1.39</td>
<td>3.41 ± 1.85</td>
<td>3.13 ± 1.75</td>
<td>F = 8.62, df = 3, P &lt; .006</td>
<td>F = 4.46, df = 2, P = .64</td>
<td>F = .89, df = 3, P = .34</td>
</tr>
<tr>
<td>Raised tail wag display (%)</td>
<td>3.0 ± 3.04</td>
<td>4.3 ± 3.5</td>
<td>2.3 ± 3.0</td>
<td>χ² = 5.09, df = 3, P = .17</td>
<td>χ² = 6.33, df = 2, P &lt; .05</td>
<td>χ² = 6.33, df = 2, P &lt; .05</td>
</tr>
<tr>
<td>Time spent basking (%)</td>
<td>27.48 ± 29.71</td>
<td>51.10 ± 37.23</td>
<td>58.23 ± 39.47</td>
<td>F = 2.21, df = 3, P = .054</td>
<td>F = 5.14, df = 2, P = .011</td>
<td>F = 1.03, df = 3, P = .43</td>
</tr>
<tr>
<td>Total activity score</td>
<td>157.06 ± 155.66</td>
<td>166.72 ± 150.97</td>
<td>203.20 ± 206.81</td>
<td>F = 4.01, df = 3, P = .054</td>
<td>F = 6.49, df = 2, P = .11</td>
<td>F = 6.49, df = 2, P = .11</td>
</tr>
</tbody>
</table>

**Note.**—The incubation conditions are simulated maternal body temperatures (viviparity), simulated uterine retention of eggs (uterine retention), and simulated nest temperatures (nest). See text for details. Table shows least-squares mean value ± SD for the three incubation conditions; no interaction terms were significant. Sample sizes for ANOVAs are shown in parentheses. SVL, Snout-vent length; raised tail wag, defensive behavior pattern (see text). The last three columns show the results of statistical tests of the null hypothesis that the variable in question is not affected by the thermal regime experienced by the embryo. Most variables were tested using split-plot ANOVAs, with the factors being maternal temperature category prior to oviposition, incubation thermal regime, and clutch number nested within maternal temperature category. Contingency table tests were used where parametric analyses were inappropriate.
### TABLE 2

**Effects of Three Different Incubation Temperature Regimes on Incubation Periods, Survival Rates, Morphology, and Running Speed of Offspring in the Oviparous Scincid Lizard *Nanoscincus maccott**

<table>
<thead>
<tr>
<th>Trait</th>
<th>Mean Values for Viviparity Treatment</th>
<th>Mean Values for Uterine Retention Treatment</th>
<th>Mean Values for Nest Treatment</th>
<th>Statistical Test: Effect of Incubation Temperatures</th>
<th>Statistical Test: Differences among Clutches</th>
</tr>
</thead>
<tbody>
<tr>
<td>Incubation period (d)</td>
<td>50.88 ± 2.32 (17)</td>
<td>60.17 ± 4.02 (6)</td>
<td>69.54 ± 2.76 (26)</td>
<td>$F = 1.490, df = 2,13, P &lt; .0001$</td>
<td>$F = 1.31, df = 16,13, P = .29$</td>
</tr>
<tr>
<td>Survival rate to hatching (%)</td>
<td>65 (17/26)</td>
<td>75 (6/8)</td>
<td>96 (26/27)</td>
<td>$x^2 = 8.17, df = 2, P &lt; .02$</td>
<td>$x^2 = 1.57, df = 15, P = 1.00$</td>
</tr>
<tr>
<td>Mass at hatching (g)</td>
<td>.16 ± .02 (17)</td>
<td>.17 ± .01 (6)</td>
<td>.16 ± .02 (26)</td>
<td>$F = 5.85, df = 2,13, P &lt; .016$</td>
<td>$F = 15.02, df = 16,13, P &lt; .001$</td>
</tr>
<tr>
<td>SVL at hatching (mm)</td>
<td>23.94 ± .75 (17)</td>
<td>24.50 ± .84 (6)</td>
<td>24.69 ± 1.01 (26)</td>
<td>$F = 6.07, df = 2,13, P &lt; .015$</td>
<td>$F = 1.67, df = 16,13, P = .15$</td>
</tr>
<tr>
<td>Tail length (mm)</td>
<td>22.35 ± 2.00 (17)</td>
<td>23.67 ± 1.03 (6)</td>
<td>24.35 ± 1.85 (26)</td>
<td>$F = 5.63, df = 2,13, P &lt; .018$</td>
<td>$F = 4.21, df = 16,13, P &lt; .003$</td>
</tr>
<tr>
<td>Running speed (m/s):</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Over 50 cm</td>
<td>.13 ± .02 (12)</td>
<td>.13 ± .06 (6)</td>
<td>.11 ± .05 (23)</td>
<td>$F = 3.99, df = 2,8, P = .063$</td>
<td>$F = .76, df = 16,8, P = .71$</td>
</tr>
<tr>
<td>Over fastest 20 cm</td>
<td>.32 ± .05 (12)</td>
<td>.40 ± .14 (5)</td>
<td>.64 ± .27 (23)</td>
<td>$F = 4.12, df = 2,8, P = .059$</td>
<td>$F = .90, df = 16,8, P = .59$</td>
</tr>
</tbody>
</table>

Note.—Statistical results are based on contingency tables (hatching success) or on two-factor ANOVA with one fixed factor (incubation thermal regime) and one random factor (clutch number). The incubation conditions are the same as those for table 1. SVL, Snout-vent length. Table shows mean value ± SD; sample sizes appear in parentheses. Format as for table 1.
The thermal regime of egg incubation affects the speed that the resultant hatchling Bassiana duperreyi can run over a distance of 20 cm (left) and the proportion of time that the hatchling spends basking (i.e., in a heated portion of its cage) (right). Mean values ± SE are shown. Hatchlings from eggs incubated at high temperatures (viviparous, simulating maternal body temperatures) ran faster and basked less of the time than did hatchlings from eggs incubated at lower temperatures (nest, simulating soil temperatures). Hatchlings from eggs kept only briefly at high temperatures then transferred to lower temperatures (simulating uterine retention) were also fast runners and were intermediate between hatchlings from viviparous and nest treatments in the proportion of time they spent basking. See text for statistical analyses of these data.

Tail length.—This trait varied significantly with incubation conditions in both species (see tables 1, 2). ANCOVA gave very similar results: the relationship between tail length and SVL varied in B. duperreyi incubated at different temperatures (ANCOVA with SVL as covariate: homogeneity of slopes, $F = 0.65, df = 2.86, P = .53$; intercepts test, $F = 9.00, df = 2.88, P < .001$), and the analogous differences in N. maccoppi were close to statistical significance (heterogeneity of slopes, $F = 2.71, df = 2.43, P = .08$; intercepts test, $F = 3.09, df = 2.45, P = .056$).

Running speed.—Nannoscincus maccoppi ran slowly, with frequent stops. Their running speeds were not significantly affected by the conditions under which the eggs had been incubated, although the results were close to statistical significance (table 2). Bassiana duperreyi ran more quickly, especially over relatively short distances, and incubation temperatures strongly affected running speeds over a distance of 20 cm (table 1; fig. 1). The effect of incubation temperatures on Bassiana running speeds over 50 cm was also close to statistical significance (table 1).

Antipredator behavior.—When chased along the runway, some B. duperreyi showed a distinctive behavior whereby they suddenly stopped, whirled around so as to face the oncoming paintbrush, and elevated their tails to a vertical posi-
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The thermal regime of egg incubation affects the daily activity pattern of the resultant hatchling skink (Bassiana duperreyi). Hatchlings from eggs incubated at high temperatures (viviparous, simulating maternal body temperatures) were active earlier in the day than were hatchlings from eggs incubated at lower temperatures (nest, simulating soil temperatures). Hatchlings from eggs kept only briefly at high temperatures, then transferred to lower temperatures (simulating uterine retention), were intermediate in activity patterns. See text for statistical analyses of these data.

Basking behavior.—The proportion of time that hatchling B. duperreyi spent basking was influenced by incubation temperatures (table 1; fig. 1). Lower incubation temperatures generally resulted in hatchlings that basked more frequently (table 1; fig. 1).

Activity patterns.—Data on B. duperreyi show that incubation thermal regimes significantly influenced the subsequent activity levels of hatchlings (fig. 2). Although incubation temperatures did not affect total activity levels in hatchlings (table 1), more detailed analysis shows that incubation conditions affected the daily timing of activity (fig. 2). Cooler incubation temperatures produced hatchlings that were active later in the day (a two-factor ANOVA, with incubation condition and hour of day as the factors, showed a significant interaction between these two variables in their effects on activity levels: $F = 2.13$, $df = 14, 672, P < .001$; fig. 2).
Interactions between Maternal Temperatures and Incubation Temperatures

The data above show that offspring phenotypes in *B. duperreyi* are influenced by the thermal regime throughout embryogenesis—both before oviposition (via differences in the mean selected body temperatures of the ovigerous females) and after oviposition (via the different incubation regimes used in this study). It is thus of interest to ask whether there is any interaction between pre- and postovipositional thermal effects on offspring phenotypes. That is, is developmental plasticity in the phenotype of the offspring a consequence of simple additive effects of the influences of thermal regimes at different stages of embryogenesis, or is there some interactive effect such that the influence of a particular thermal regime on hatchling phenotype is affected by thermal regimes earlier or later in embryonic development? Such an effect should be revealed by a significant interaction term between maternal temperature category and incubation thermal regime in the split-plot ANOVAs (above). These interaction terms are not significant for most of the phenotypic variables studied (body mass, $F = 1.21$, df = 6, 37, $P = .32$; SVL, $F = 2.01$, df = 6, 37, $P = .09$; tail length, $F = 1.05$, df = 6, 37, $P = .41$; total activity score, $F = 0.77$, df = 6, 37, $P = .60$; basking frequency, $F = 1.30$, df = 6, 37, $P = .28$; mean running speed over 50 cm, $F = 1.06$, df = 6, 37, $P = .41$; mean number of stops per run, $F = 1.25$, df = 6, 37, $P = .30$). However, an almost-significant interaction between the phenotypic effects of pre- and postovipositional thermal regimes was evident for the fastest running speed over a distance of 20 cm (interaction, $F = 2.31$, df = 6, 37, $P = .054$). Thus, the temperatures to which an embryo is exposed early in development may have little effect on the ways in which its eventual phenotype is affected by thermal influences later in embryogenesis.

Genetic versus Environmental Influences on Hatchling Phenotypes

If the mean body temperature selected by a preovipositional female is interpreted as a function of her genotype, the influence of maternal thermoregulation on offspring characteristics (see earlier analyses) would be taken as evidence of genetic effects on offspring phenotype. However, it remains possible that maternal selected temperatures are influenced by proximate environmental factors rather than genetic differences among females. Are there additional influences of maternal genotype on *B. duperreyi*, independent of the thermal effects analyzed above? Such effects should be apparent from the split-plot ANOVAs, since they included the female’s identification number (nested within the categories of mean selected maternal temperatures) as one of the independent variables. These ANOVAs revealed a significant among-female (and hence, possibly genetic) contribution to the observed variation in incubation periods, hatching success rates, and hatchling morphology (body mass, SVL, and tail length) but not for behavioral or performance measures (total activity, proportion basking, running speed over 50 and 20 cm, and number of stops per run; see table 1). Thus, taking maternal identity (including genotype) into account did not explain significantly more variation in hatchling behavior or running speeds than could be explained simply by the effects of thermal regimes during incubation.
Although I do not have data on body temperatures of gravid *N. maccoyi*, possible interclutch differences are of interest in this species also. The analysis shows a similar result to that for *B. duperreyi*: clutches differ in some aspects of mean hatching sizes (mass, tail length) but not in the performance characteristics of the resulting hatchlings (table 2). A significant interaction between incubation temperatures and clutch identification number (incorporating genotypic differences) was apparent for running speed over 50 cm ($F = 5.07$, df = 13,8, $P < .014$) but not for any of the other variables listed in table 2. This interaction term suggests that females differ in the extent to which running speeds of their offspring are affected by incubation temperatures.

**DISCUSSION**

My data support and extend the results of earlier studies on other types of reptiles and show that the thermal regime experienced by an embryo profoundly influences the phenotype of the resulting hatchling (see, e.g., Lang 1985; Webb and Cooper-Preston 1989; Deeming and Ferguson 1991; Packard 1991). This influence extends to behavior (activity levels, propensity to bask) as well as performance (running speeds) and morphology (body size and shape). Other work on *Bassiana duperreyi* has shown that the effects of incubation temperatures on hatching phenotypes persist for at least 2 mo (R. Shine, unpublished manuscript), and earlier studies have shown a similarly high repeatability of individual differences in body size and performance over the first few months of life (van Berkum et al. 1989). My data also show that hatching behavioral phenotypes are affected by the temperatures experienced prior to oviposition, as well as the thermal regime in the nest, but provide surprisingly little indication of genetic effects on hatching performance. Offspring tend to resemble their siblings morphologically, but at least part of this similarity is due to their common thermal experience during embryogenesis.

The sensitivity of major phenotypic features of hatchling reptiles to incubation temperatures has important implications not only for the relative success of oviparous and viviparous reptiles in cold climates but also in many other contexts. The implications for captive husbandry (in both commercial and conservation contexts) are obvious, but general ecological and evolutionary questions are also affected (see also Via and Lande 1985; Sultan 1987). The sensitivity of offspring phenotypes to relatively small differences in mean selected body temperatures of ovigerous females suggests that there should be intense natural selection on gravid female reptiles to maintain appropriate body temperatures for optimal embryonic development (Beuchat 1986, 1988; Beuchat and Ellner 1987). Adaptive modifications to offspring phenotypes may be achieved primarily through changes in maternal behavior (e.g., thermoregulation, nest site selection) rather than by shifts in the frequencies of alternative alleles “for” particular traits in offspring (Packard 1991). More generally, it may be difficult for natural selection to produce optimal mean values for traits, even under strong and consistent selection, if relatively little of the phenotypic variance among offspring is due to genetic factors (Fisher 1958; Bull 1987; Kirkpatrick and Lande 1989; Stratton 1989). Reptiles
thus may offer ideal model systems with which to disentangle the complex interplay between genetic and environmental determinants of organismal fitness.

The evolution of reptilian viviparity offers a clear example of the ways in which phenotypically plastic responses to incubation conditions have the potential to exert strong influences on life-history evolution. My results support the hypothesis that prolonged uterine retention (and thus, eventually, viviparity) may directly influence hatching viability in reptiles living in cool climates. Whether the observed changes in morphology, behavior, and performance of the hatchlings confer a selective advantage or disadvantage to uterine retention remains unknown, but previous studies have shown that these characteristics can affect the probability of survival of hatching reptiles (see, e.g., Ferguson et al. 1982; Olsson 1992). Indeed, I chose the variables to measure on my hatchlings on this basis. The wide variation in hatching phenotypes induced by incubation temperatures is thus unlikely to be neutral with respect to the fitness of offspring, and field studies of this question will be of great interest. The situation is likely to be complex, and generalities may be elusive. For example, several effects of incubation temperatures on hatching phenotypes differed significantly between the two scincid species used in the present study (tables 1, 2).

The widespread occurrence of prolonged uterine retention of developing embryos in oviparous squamates has proven difficult to explain in terms of selective advantage (Shine 1983a), but two lines of evidence from the present study may clarify this question. First, hatching phenotypes were sensitive to maternal thermoregulation prior to oviposition. Second, even brief retention at maternal body temperatures was sufficient to influence the size, behavior, and performance abilities of the resulting hatchlings (e.g., figs. 1, 2). Thus, effects of this kind offer a plausible selective advantage for the evolution of prolonged uterine retention of eggs in many oviparous squamates, as well as the exaggeration of this trend (the evolution of viviparity) in some lineages. Unlike the cold-climate hypothesis (which posits the evolution of viviparity only under conditions in which nest temperatures fall to lethally low levels in autumn, and the period available for embryogenesis at nest temperatures is close to the absolute period needed) (Shine 1985), the phenotypic plasticity hypothesis predicts that prolonged uterine retention might enhance offspring fitness in any environment in which maternal temperatures differ from nest temperatures. No threshold effect is needed.

Incubation temperature is not the only aspect of incubation conditions that might influence hatching viability through the expression of phenotypic plasticity. Uterine retention of eggs may often also influence their hydric environment, especially in arid areas. Because the hydric environment may influence hatching size, shape, and sprint speed (Gutzke and Packard 1987; Beuchat 1988; Whitehead and Seymour 1990; Seymour et al. 1991), uterine retention might influence hatching viability via changes in humidity as well as temperature. Analogous direct effects of incubation conditions on hatching viability may be widespread, in invertebrates (Ghouri and McFarlane 1958; Nijhout 1980; Meats 1984; Roff 1986) as well as vertebrates (Taning 1952; Harkey and Semlitsch 1988; Deeming and Ferguson 1991), and thus may have been of general importance in the evolution of viviparity in many groups of animals.
These results also address the wider issue of the interaction between life-history adaptation and phenotypic plasticity. The importance of such plasticity as a source of variance in life-history traits is widely appreciated (see, e.g., Bull 1987; Sultan 1987; Kirkpatrick and Lande 1989), but much remains to be learned about the ways in which norms of reaction produce the phenotypic variance acted on by selection. My results suggest that much of the variance in phenotypes (and by implication, fitnesses) of hatchling lizards results from the expression of phenotypic plasticity in response to a physical variable (incubation thermal regime) that is potentially modifiable by genetically coded characters (e.g., prolongation of uterine retention of eggs). Thus, the interplay between phenotypic plasticity and natural selection lies at the heart of adaptive modifications to the life history, and explanations of life-history evolution need to integrate both proximate and ultimate causes of variance in organismal fitness.

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LITERATURE CITED


REPTILIAN VIVIPARITY


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