

## Consequences of Extended Egg Retention in the Eastern Fence Lizard (*Sceloporus undulatus*)

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**ABSTRACT.**—Egg retention beyond the normal time of oviposition occurs frequently in oviparous squamate reptiles and is thought to be a response to unfavorable nesting conditions. During studies of the Eastern Fence Lizard (*Sceloporus undulatus*), we obtained data on the effects of extended egg retention on embryonic development, hatchling phenotypes, and posthatching survival under natural field conditions. Females that retained eggs beyond the normal time of oviposition produced heavier eggs with embryos more advanced (by one stage unit) at the time of oviposition than females that did not retain eggs for extended periods. Egg retention did not affect any hatchling phenotype (i.e., body size, thermal preference, running speed, desiccation rate, growth rate) but had a significant positive effect on posthatching survival in the field. However, the mechanism by which extended egg retention affects posthatching survival remains unclear. Our results have implications for the evolution of viviparity, but carefully designed experiments are needed to further understand the causes and consequences of extended egg retention.

The retention of eggs in the oviduct beyond the normal time of oviposition is common in squamate reptiles and may occur in response to dry environmental conditions (Jones et al., 1991; Andrews and Rose, 1994; Radder et al., 1998). For example, if nest sites are too dry, females may delay nesting and either retain eggs until conditions become favorable or oviposit (without nesting) when egg retention is no longer physiologically possible (Mathies and Andrews, 1996; Warner and Andrews, 2002a).

The developmental consequences of extended egg retention vary among species. For instance, extended egg retention results in developmental arrest for embryos of *Urosaurus ornatus* and *Sceloporus undulatus*, but embryogenesis continues in utero to a stage that is near the time of hatching in *Sceloporus scalaris* (Andrews and Mathies, 2000). For species in which development is arrested, embryogenesis is resumed after eggs are laid. Moreover, during the time embryos are retained in utero, the maternal embryonic environment can affect the hydration and size of hatchlings (Andrews and Mathies, 2000). Extended egg retention may thus affect offspring phenotype or fitness, but the long-term consequences of extended egg retention are unknown.

We evaluated effects of extended egg retention on embryonic development, hatchling phenotypes, and posthatching survival of the Eastern Fence Lizard (*Sceloporus undulatus*), a species that oviposits when embryos are at stages 28–30 on the Dufaure and Hubert (1961) scale. The

results presented in this paper were obtained while conducting studies on the nesting behavior of *S. undulatus* (Warner and Andrews, 2002a) and on the associations between phenotypes and survival of hatchling *S. undulatus* in the field (Warner, 2001; Warner and Andrews, 2002b).

### MATERIALS AND METHODS

Gravid *S. undulatus* ( $N = 23$ ) were collected between 15 May and 19 June 1999 in Jefferson National Forest (Montgomery County) near Blacksburg, Virginia. Females were brought to facilities at Virginia Polytechnic Institute and State University where they were housed in a 1.5 × 1.5-m enclosure. This enclosure was specifically designed to study nesting behavior of *S. undulatus* (Warner and Andrews, 2002a). The enclosure provided areas for basking and nine plastic containers (46 × 24 × 20 cm), filled with a mixture of vermiculite and peat moss (1:1 ratio), provided nesting substrate. All lizards readily had access to the nine nesting containers which were placed adjacent to one another in a 3 × 3 array. Thus, the total area available for nesting was 138 × 72 cm. The enclosure was illuminated by heat lamps and two 1.3-m Vitalites®. Females were placed in the enclosure as they were captured and removed from the enclosure after they oviposited. Thus, no more than 10 females were housed in the enclosure at a given time. Females were fed crickets and wax worm larvae dusted with a vitamin-mineral mix, and watered daily. See Warner and Andrews (2002a) for a complete description of the enclosure.

Seventeen females constructed nests and exhibited nest construction behavior similar to that of females in the wild (Warner and Andrews, 2002a). Six females oviposited on the

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surface of the substrate (without nesting). Eggs were either removed from nests or removed from the enclosure (eggs from females that did not nest), and one egg from each of the 23 clutches used in this study was sampled to determine the stage of the embryo at oviposition (staged according to Dufaure and Hubert, 1961). One embryo provides a reliable representation of an entire clutch because embryonic stage at oviposition does not vary within clutches (DeMarco, 1992). We could not determine the embryonic stage of one clutch from a female that nested because we did not find the embryo in the egg sampled. Immediately after oviposition, all remaining eggs were weighed and placed individually in glass jars (65 ml) containing vermiculite and covered with clear plastic wrap sealed with a rubberband. Jars were placed in an environmental chamber set at a constant 28°C and rotated to different positions within the chamber to minimize possible effects of temperature gradients within the chamber (Warner and Andrews, 2002b).

After hatching, we marked each hatchling individually by unique toe-clips and measured several phenotypic traits of each individual. For each individual, we measured snout-vent length (SVL), tail length (TL), and mass, and body shape was calculated as  $\text{mass}^{0.3}/\text{SVL}$ .

We also measured thermal preference, locomotor performance, desiccation rate, and growth rate for each hatchling in the laboratory. Thermal preference was measured by placing lizards within a thermal gradient (at 1–2 days of age). The thermal gradient contained nine thermal couples spaced at 10-cm intervals that measured air temperatures along the length (80 cm) of the gradient. Air temperatures varied linearly from 26–40°C along the gradient. The air temperature at the position of the lizard within the gradient reflected the lizard's body temperature. The position of the lizard within the gradient was recorded every 10 min for an hour and air temperatures within the gradient were recorded at the beginning, middle, and end of the hour. Lizard position was then converted to body temperature by regression analysis. Selected body temperature was calculated as the mean of the six temperature measurements over the 1-h observation period. See Qualls and Andrews (1999) and Warner and Andrews (2002b) for complete descriptions of protocols.

Locomotor performance was measured by chasing hatchlings along a 1-m electronically timed racetrack (at 3–4 days of age). The racetrack consisted of five infrared photocells (spaced at 25-cm intervals) connected to an electronic stopwatch. Hatchlings were placed at the beginning of the racetrack and gently prodded with a paintbrush if they did not run or

stopped. Locomotor performance over 1 m was measured three times for each individual and was assessed as the fastest speed (m/s) over 25 cm and 1 m. All running trials were conducted inside a walk-in environmental chamber set at 30°C. See Warner and Andrews (2002b) for a complete description of protocols.

Desiccation rate was measured by placing lizards in a desiccator set at 0% relative humidity and at a constant 30°C (at 6–7 days of age). Body mass was recorded before hatchlings were placed in the desiccator and again after 2 h. Desiccation rate was assessed as short-term evaporative water loss (change in body mass/h). Growth in both SVL and mass was calculated as a size specific growth rate: the difference between an individual's natural log-transformed SVL or mass at the time of release and hatching divided by the number of days between measurements.

Each hatchling was subsequently released (at an average age of nine days) between 24 July and 8 September 1999. The release site was located in Jefferson National Forest near Blacksburg, Virginia and included a 1500-m<sup>2</sup> forest clearing, a smaller clearing (500 m<sup>2</sup>), and an abandoned dirt road extending 80 m from the site. The open areas contained large woody debris and scattered small shrubs, which provided habitat for *S. undulatus*. The entire site was surrounded by dense forest, which provided a natural boundary because hatchling *S. undulatus* do not disperse through the forest (see Warner and Andrews, 2002b).

We searched the site for hatchlings about twice weekly from 31 July to 5 December 1999 and weekly from 5 March to 6 July 2000. The perimeter of the field site was searched thoroughly and few (6% of those released) hatchlings were found in the surrounding forest. Thus, dispersal did not appear to bias our recapture success, and disappearances from the site were likely caused by death. Furthermore, our recapture rates were nearly identical to recapture rates of *S. undulatus* hatchlings released in an enclosed area where dispersal was not possible (Niewiarowski and Roosenburg, 1993). Of 220 hatchlings released, 130 were recaptured (by hand) at least once after release. After recapture, hatchlings were identified by their toe clip, weighed, measured (SVL and TL) and then released where they were captured. Thus, this mark-recapture study allowed us to measure survival under natural field conditions. Detailed descriptions of the above protocols are presented by Warner and Andrews (2002b).

To determine the effect of prolonged egg retention on hatchling phenotypes and survival, we compared clutches from females that nested ( $N = 17$ ) with clutches from females that did

TABLE 1. Comparisons of maternal characteristics, egg characteristics, and hatchling phenotypes between females that nested and females that did not nest. Significant *P*-values are in **bold** type. Statistical tests were performed with ANOVA except where noted.

	Females that nested	Females that did not nest	Statistical test
	Mean $\pm$ 1 SE	Mean $\pm$ 1 SE	
Days females were in captivity	16.8 $\pm$ 2.0	29.0 $\pm$ 4.6	$F_{1,21} = 8.0, P = \mathbf{0.010}$
Embryonic stage at oviposition	28.9 $\pm$ 0.2	30.0 $\pm$ 0.1	$F_{1,20} = 13.4, P = \mathbf{0.002}$
Clutch size	8.4 $\pm$ 0.5	7.3 $\pm$ 0.6	$F_{1,21} = 1.1, P = 0.309$
Clutch mass (g)	4.5 $\pm$ 0.1	4.5 $\pm$ 0.3	$F_{1,21} = 0.0, P = 0.981$
Relative clutch mass (g) <sup>1</sup>	4.5 $\pm$ 0.1	4.4 $\pm$ 0.3	$F_{1,20} = 2.0, P = 0.158$
Egg mass at oviposition (g) <sup>1</sup>	0.384 $\pm$ 0.0	0.416 $\pm$ 0.0	$F_{1,20} = 5.0, P = \mathbf{0.035}$
Incubation period (days) <sup>2</sup>	50.3 $\pm$ 0.3	50.5 $\pm$ 0.5	$F_{1,19} = 1.1, P = 0.362$
Hatching success (%)	84.6 $\pm$ 3.4	82.3 $\pm$ 5.8	$F_{1,21} = 0.1, P = 0.731$
Date of hatching (Julian day)	218.4 $\pm$ 11.2	229.1 $\pm$ 8.5	$F_{1,21} = 4.6, P = \mathbf{0.045}$
Hatchling SVL (mm) <sup>3</sup>	23.7 $\pm$ 0.1	23.5 $\pm$ 0.3	$F_{1,20} = 0.2, P = 0.654$
Hatchling mass (g) <sup>3</sup>	0.511 $\pm$ 0.0	0.478 $\pm$ 0.0	$F_{1,20} = 3.8, P = 0.066$
Tail length (mm) <sup>4</sup>	27.5 $\pm$ 0.4	27.2 $\pm$ 0.8	$F_{1,19} = 0.1, P = 0.788$
Body shape (mass <sup>0.3</sup> /SVL)	0.034 $\pm$ 0.0	0.034 $\pm$ 0.0	$F_{1,21} = 1.4, P = 0.252$
Thermal preference (°C)	33.8 $\pm$ 0.3	34.3 $\pm$ 0.7	$F_{1,21} = 0.5, P = 0.473$
Running speed over 25 cm (m/s) <sup>4</sup>	0.589 $\pm$ 0.0	0.579 $\pm$ 0.1	$F_{1,20} = 0.0, P = 0.917$
Running speed over 1 m (m/s) <sup>4</sup>	0.228 $\pm$ 0.0	0.231 $\pm$ 0.0	$F_{1,20} = 0.0, P = 0.942$
Desiccation rate ( $\Delta$ g/h) <sup>5</sup>	0.003 $\pm$ 0.0	0.002 $\pm$ 0.0	$F_{1,20} = 0.7, P = 0.428$
Growth in SVL (log $\Delta$ mm/day)	0.009 $\pm$ 0.0	0.009 $\pm$ 0.0	$F_{1,21} = 0.0, P = 0.867$
Growth in mass (log $\Delta$ g/day)	0.015 $\pm$ 0.0	0.021 $\pm$ 0.0	$F_{1,21} = 1.3, P = 0.272$
Date of release (Julian day)	226.5 $\pm$ 2.8	238.8 $\pm$ 3.9	$F_{1,21} = 5.4, P = \mathbf{0.031}$

Superscripts denote traits analyzed with ANCOVA using the following covariates: <sup>1</sup> female mass after oviposition, <sup>2</sup> embryonic stage, <sup>3</sup> egg mass at oviposition, <sup>4</sup> snout-vent length at hatching, <sup>5</sup> body mass at hatching. Least-squares means are reported.

not nest but oviposited on the surface of the substrate ( $N = 6$ ). We made these comparisons assuming that the females that oviposited on the substrate surface had retained their eggs beyond the normal time of oviposition (see Results). This assumption was based on the observation that *Sceloporus* lizards retain eggs beyond the normal time of oviposition and oviposit on the substrate surface if suitable nesting conditions do not become available (Jones et al., 1991; Andrews and Rose, 1994; Mathies and Andrews, 1996). The six females that oviposited on the surface may have perceived nesting conditions as unsuitable.

Analyses of variance (ANOVA) and covariance (ANCOVA) were used to evaluate the effect of egg retention on embryonic development, hatchling phenotypes, and survival in the field. Female body mass was used as a covariate when analyzing the effect of egg retention on egg mass and clutch mass. Embryonic stage at oviposition was used as a covariate when analyzing incubation period. Egg mass was used as a covariate when analyzing hatchling body size (SVL and mass). Hatchling SVL and body mass were used as covariates when analyzing hatchling running speed and desiccation rate, respectively. All analyses of hatchling phenotypes were based on clutch means for each trait.

Hatchling survival was analyzed at three time

periods: survival at six and 12 weeks after release and again the following March 2000. If hatchlings were not recaptured, they were assumed dead (see above). Because egg retention by females that did not nest caused a delay in hatching date and subsequent delay in release of hatchlings (see Results), we performed an additional analysis to separate effects of release date and egg retention on hatchling survival. The release date of hatchlings from females that nested was distributed over a broad time range and, thus, allowed us to divide their clutches into early (19 July to 8 August) and late (18 August to 7 September) release time periods. Survival was then compared (ANOVA) at six weeks, 12 weeks, and March between clutches with hatchlings released early and clutches with hatchlings released late. Survival analyses were based on the percentage of individuals recaptured for each clutch.

## RESULTS

Egg retention time, embryonic stage, and egg mass at oviposition differed significantly between females that nested and those that did not nest (Table 1). Females that did not nest were in captivity for an average of 12 days longer than females that nested. Moreover, females that did not nest oviposited when embryos were one stage more advanced than females that

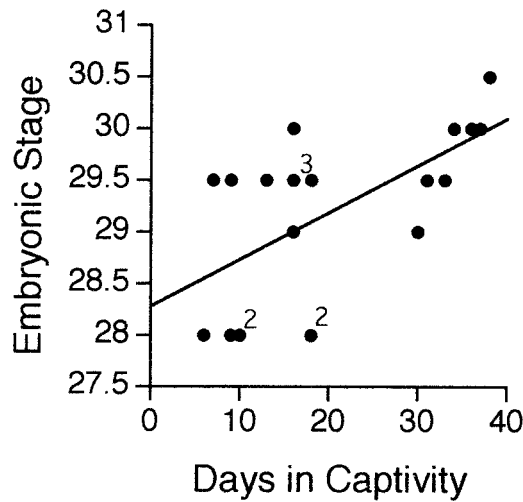


FIG. 1. Relationship between the number of days females were in captivity and the stage of their embryos at oviposition ( $N = 22$ ,  $r^2 = 0.360$ ,  $P = 0.003$ ). The numbers of datapoints that overlap are indicated on the graph.

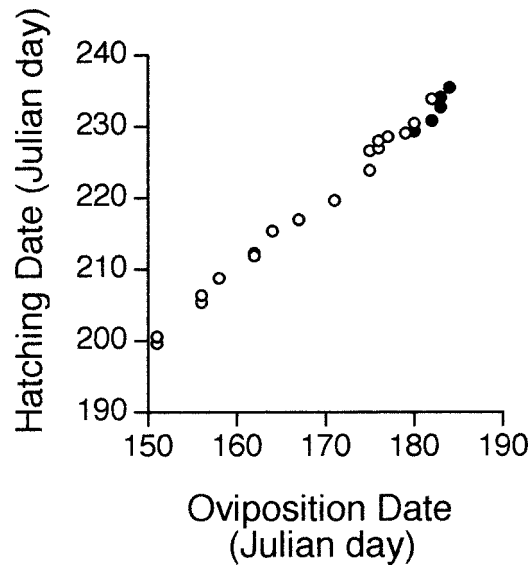


FIG. 2. Relationship between mean oviposition date and mean hatching date for clutches from females that nested (open circles) and females that did not nest (solid circles;  $r^2 = 0.992$ ,  $P < 0.001$ ).

nested. The number of days females were held in captivity was positively related to embryonic stage at oviposition ( $r^2 = 0.360$ ,  $P = 0.003$ ; Fig. 1). Females that did not nest produced heavier eggs at the time of oviposition than females that nested. However, clutch size, clutch mass, incubation period, and hatching success did not differ between females that nested and those that did not nest (Table 1). Delayed oviposition by females that retained eggs resulted in a shift in hatching dates by an average of 11 days (Table 1, Fig. 2). These observations clearly show that females that did not nest retained eggs beyond their normal time of oviposition.

Egg retention had no effect on hatchling body size (mass or SVL; Table 1), despite the significant effect on egg size, even when body size was not corrected for egg size (mass:  $F_{1,21} = 0.3$ ,  $P = 0.586$ ; SVL:  $F_{1,21} = 0.1$ ,  $P = 0.791$ ). Moreover, egg retention had no effect on any other morphological (tail length and body shape) or performance traits (thermal preference, running speed, desiccation rate, and growth) of the hatchlings (Table 1). However, females that retained their eggs produced clutches with greater posthatching survival in the field than females that nested normally (Fig. 3). This pattern of survival was highly significant at 12 weeks after release and in the following March 2000.

Hatchling release date did not influence posthatching survival in the field. In analyses using only clutches from females that nested, hatchlings released at the early and late time periods did not differ in survival at six weeks after release ( $F_{1,12} = 0.0$ ,  $P = 0.980$ ), 12 weeks after re-

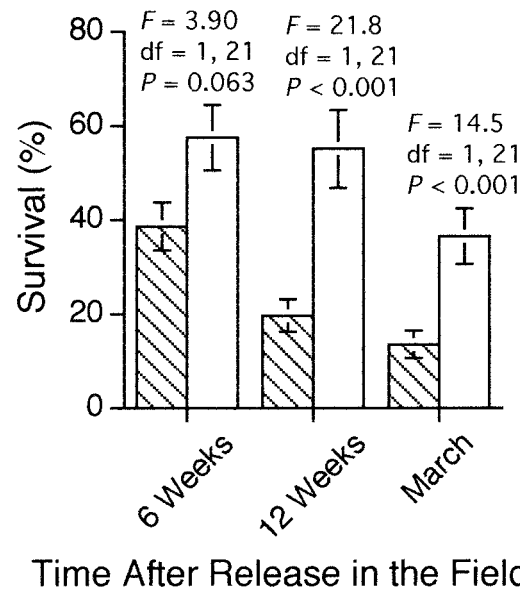


FIG. 3. Comparison of mean posthatching survival of clutches from females that nested (hatched bars) and females that retained eggs for prolonged periods (open bars). Mean survival is from release to six weeks, from release to 12 weeks, and from release to the following March 2000. Bars represent 1 SE.

lease ( $F_{1,12} = 0.6$ ,  $P = 0.471$ ) and at the following March 2000 ( $F_{1,12} = 2.3$ ,  $P = 0.154$ ).

#### DISCUSSION

Differences in oviposition dates between females that nested and females that oviposited on the substrate were caused by egg retention beyond the normal time of oviposition by the females that did not nest. Females that did not nest were in captivity 12 days longer (prior to oviposition) than females that nested. Moreover, females that oviposited on the substrate did so when embryos were at a slightly more advanced embryonic stage than embryos from females that nested. This result parallels that of another study on *S. undulatus* in which females exposed to unsuitable nesting conditions retained their eggs an average of 10 days beyond the normal time of oviposition (Andrews and Mathies, 2000). During that 10-day period, control embryos (from females that nested) reached stage 32, whereas retained embryos reached stage 30; the rate of embryonic development is retarded during egg retention (Andrews and Mathies, 2000). Egg retention would thus not be obvious from the stage of embryos alone in our study or theirs.

Females that retained eggs produced eggs that were 9% heavier than those produced by females that nested. The relatively large egg mass of females that retained eggs did not result in relatively large hatchlings, suggesting the increased egg mass was caused by water uptake during the 12-day period of prolonged egg retention. Reptile eggs must take up water after oviposition for successful development, and oviposited eggs of *S. undulatus* double or triple in mass before hatching (Warner and Andrews, 2002b). Water uptake in utero, however, may be restricted because of physical constraints within the female's oviducts (Mathies and Andrews, 1996). Indeed, egg expansion within the oviduct may eventually cause the female to oviposit even if no suitable nesting sites are available.

Egg retention did not affect the morphology or performance of hatchlings, but it did increase their survival after release in the field. The mechanism by which egg retention increased the survival of hatchlings, however, cannot be identified. We provide three possible explanations why egg retention increased the survival of hatchlings. First, release date could influence hatchling survival (Ferguson and Bohlen, 1978; Sinervo and Doughty, 1996; Madsen and Shine, 1998). In our study, the 11-day delay in hatching date (and subsequent delay in release dates) means that hatchlings from eggs that had been retained were released 12 days later than hatchlings from eggs that had not been retained. Re-

lease date, however, was not related to hatchling survival in the field, possibly because release dates of hatchlings that were from retained clutches and nested clutches were separated by a relatively short time period (only 12 days). Our results are in contrast to a previous study on the same population, which found that individuals that hatched late had higher survival than those that hatched early (Andrews et al., 2000). Release dates in that study, however, extended over a two-month period. The explanation of Andrews et al. (2000) was that individuals that hatched late were not exposed to predators for as long a period as those that hatched early.

Second, egg retention did not influence any hatchling phenotype that we measured and, therefore, did not indirectly influence survival through these phenotypes. Perhaps, however, egg retention influenced survival through its effect on other unmeasured phenotypes, whether morphological, physiological, or behavioral.

Third, the effect of egg retention on survival may be an artifact because of confounding effects of clutch and egg retention. Clutch has strong effects on posthatching survival in reptiles (Madsen and Shine, 1998; Warner and Andrews, 2002b). Thus, clutch (maternal) effects other than egg retention per se may explain the difference in survival between clutches that were retained in utero for an extended period and those that were laid at the normal time of oviposition.

Extended periods of egg retention have important implications for the evolution of viviparity. Viviparity is thought to have evolved through an increased capacity to retain eggs coupled with the maintenance of embryogenesis in utero (Andrews and Mathies, 2000). Our data suggest that extended egg retention could provide a survival advantage for offspring, but the mechanism by which extended egg retention affects survival remains unclear. An important point to consider, however, is that egg retention is beneficial for oviparous females only if females eventually encounter suitable nesting substrates. In nature, eggs laid on the surface would not survive, but given the variety of microenvironments in the field compared to those provided in the laboratory, females are likely to eventually encounter a suitable nesting site during a period of prolonged egg retention. Furthermore, the lack of nesting behavior by females in the laboratory probably rarely occurs in nature, if it does at all. Nevertheless, the positive affect of extended egg retention on survival may be an important step that favors the evolution of viviparity and could precede the ability to retain eggs in utero for prolonged periods. Ad-



ditional studies that are specifically designed to evaluate long-term effects of extended egg retention are needed. Furthermore, comparative studies of closely related taxa that vary in their capacity to retain eggs will help to identify causes and consequences of extended egg retention.

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