

Tom Mathies · Robin M. Andrews

Thermal and reproductive biology of high and low elevation populations of the lizard *Sceloporus scalaris*: implications for the evolution of viviparity

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Abstract Viviparity in squamate reptiles is presumed to evolve in cold climates by selection for increasingly longer periods of egg retention. Longer periods of egg retention may require modifications to other reproductive features associated with the evolution of viviparity, including a reduction in eggshell thickness and clutch size. Field studies on the thermal and reproductive biology of high (HE) and low (LE) elevation populations of the oviparous lizard, *Sceloporus scalaris*, support these expectations. Both day and night-time temperatures at the HE site were considerably cooler than at the LE site, and the activity period was 2 h shorter at the HE than at the LE site. The median body temperature of active HE females was 2°C lower than that of LE females. HE females initiated reproduction earlier in the spring than LE females, apparently in order to compensate for relatively low temperatures during gestation. HE females retained eggs for about 20 days longer than LE females, which was reflected by differences in the degree of embryonic development at the time of oviposition (stages 35.5–37.0 versus stages 31.0–33.5, respectively). These results support the hypotheses that evolution of viviparity is a gradual process, and is favored in cold climates. Females in the HE population exhibited other traits consistent with presumed intermediate stages in the evolution of viviparity; mean eggshell thickness of HE eggs (19.3 µm) was significantly thinner than that of LE eggs (26.6 µm) and the size-adjusted clutch sizes of HE females (9.4) were smaller than those of LE females (11.2).

Key words Egg retention · Viviparity · *Sceloporus scalaris* · Thermoregulation · Life history evolution

Introduction

To date, the most comprehensive and widely accepted hypothesis for the evolution of viviparity in squamate reptiles is the cold-climate model (Tinkle and Gibbons 1977; Packard et al. 1977; Shine 1985). According to this model, viviparity has evolved at high elevations and latitudes because of the thermal benefits of egg retention. Embryonic development is temperature dependent: embryonic development is faster at high than low temperatures, at least up to some critical point (e.g. Sexton and Marion 1974; Muth 1980; Shine 1983a). Thus, because of relatively low ambient temperatures, developmental rates of embryos in nests at high latitudes or elevations will be slower than at low latitudes or elevations. Relatively cool nest temperatures should favor extended egg retention, and ultimately viviparity, because gravid females can maintain relatively high body temperatures by behavioral thermoregulation when they are active, thus enhancing the rate of embryonic development. Late hatching as a result of relatively low incubation temperature could put juveniles at a competitive disadvantage with conspecifics that hatched earlier. Moreover, incubation at low temperatures can kill embryos outright (Christian et al. 1986) and low temperatures are associated with high mortality and developmental abnormalities (Beuchat 1988). Thus, extended egg retention at high elevations would enhance reproductive success.

Interspecific comparisons provide support for the cold-climate model. In Europe, for example, oviparous species of lacertid lizards that occur at high elevations retain eggs to more advanced stages than do species at lower elevations (Braña et al. 1991). Even more compelling support for the cold-climate model is provided by intraspecific variation in reproductive mode. Species with both viviparous and oviparous populations include *Lacerta vivipara*, (Braña 1986; Huelin 1988) and *Lerista bougainvillii* (Greer 1989), with the viviparous populations occurring at higher elevations or latitudes than the oviparous populations.

T. Mathies (✉) · R.M. Andrews
Department of Biology,
Virginia Polytechnic Institute and State University,
Blacksburg, VA 24061, USA
Fax: 703-231-9307

A weakness in the cold-climate model is the limited evidence for intraspecific variation in egg retention along a temperature gradient. The prediction that oviparous populations in cool climates should retain their eggs longer than conspecifics at warmer climates is supported only by geographic variation in the length of egg retention by *Saiphos equalis* (Greer 1989).

Sceloporus scalaris, the subject of the present study, has a broad elevational range throughout its distribution from central Mexico to Arizona and New Mexico in the United States (Smith and Hall 1974). Previous studies on the reproductive biology of this oviparous species focused on montane populations in Arizona (Newlin 1976; Ballinger and Congdon 1981) and central Mexico (Ortega and Barbault 1986). *S. scalaris* has also been reported from remnant semidesert grasslands at low elevations (Dixon and Medica 1965; Stebbins 1966; Bock et al. 1990), although the reproductive biology of these populations was virtually unknown at the time this study was initiated (Smith et al. 1990). The thermal biology of this species has been studied only at high elevations in Arizona (Smith et al. 1993).

S. scalaris would appear to be an ideal candidate to look for geographic variation in egg retention and other reproductive features associated with the putative intermediate stages in the evolution of viviparity. First, high and low elevation populations of *S. scalaris* occur in close proximity to one another. Second, this species is a member of the *scalaris* group which includes both oviparous and viviparous species (Sites et al. 1992); the occurrence of oviparous and viviparous within the same species group suggests that modifications in physiological, morphological, and endocrinological traits necessary for the evolution of viviparity would not be constrained by phylogenetic inertia.

Our objectives were twofold:

1. To compare the thermal biology of female *S. scalaris* from montane and lowland populations. These observations should confirm that high elevation populations indeed experience cooler climates than low elevation populations.

2. To examine some of the putative reproductive characteristics associated with the evolution of viviparity. We predicted that females from high elevation populations should retain eggs longer, oviposit eggs with a greater degree of embryonic development, produce eggs with thinner eggshells (Guillette 1993), and have smaller clutch sizes than females from low elevation populations (Ballinger 1983).

Materials and methods

Study sites

The high elevation (HE) study area was located in the Chiricahua Mountains, Cochise County, Arizona (31° 55' 13"N by 109° 15' 6"W). The dominant vegetation of the area is Northern Mesic evergreen forest (Kearney and Peebles 1960). Observations were made at two sites in the vicinity of Rustler Park (2664 m) and at a

third site 14 km southwest of Rustler Park at the summit of Monte Vista Peak (2852 m). All sites were on exposed, southeast-facing slopes with moderate to abundant coverage of bunchgrasses bounded by evergreen forest. Because of their close proximity to one another and their similar vegetation, altitude, and slope, data for the three HE sites were pooled.

The low elevation (LE) study area was located at the National Audubon Society Appleton-Whittell Research Ranch Sanctuary (1463 m) and its immediate vicinity on the Sonoita Plain, Santa Cruz County, Arizona (31° 36' 19"N by 110° 30' 1"W). The dominant vegetation of this area is desert-grassland transition (Kearney and Peebles 1960). The primary area we worked was relatively flat and supported an abundant coverage of bunchgrasses interspersed by a few low woody plants.

Field sampling of body and environmental temperatures

Body temperatures of female *S. scalaris* were measured in 1992 during 10 days in June, 11 days in July, and on 1 day in August at the HE site, and on 11 days in June and 5 days in July at the LE sites. Sampling effort on each day generally spanned the entire period of lizard activity. Body temperatures reported are cloacal temperatures of reproductive females, that is, females with large follicles or oviductal eggs.

We captured lizards by hand or noose and immediately measured body temperature (T_b), shaded air temperature 1 cm above perch ($T_{a,1\text{cm}}$), and shaded air temperature 1 m above perch ($T_{a,1m}$) to the nearest 0.1°C with a Physitemp thermocouple thermometer. We measured T_b only for lizards caught in less than 45 s of pursuit.

Minimum body temperatures of females at night were inferred from soil temperatures approximately 3.5 cm below the soil surface at the bases of bunch grass. Temperatures were measured with thermocouple thermometers and stored in an Omega OM-550 data logger. Observations were made in 1993 during 5 nights between 22 and 28 June at the HE site and during five nights between 18 and 30 June at the LE site. Thermometers were moved to new locations each night.

Selected body temperatures and critical thermal maxima

We used laboratory reared HE and LE juveniles to determine selected body temperature (T_{sel}) (Pough and Gans 1982) and the critical thermal maximum (CTMax), the temperature at which lizards lose their righting response (Cowles and Bogert 1944; Lowe and Vance 1955). We obtained juveniles by incubating eggs to hatching. We collected freshly laid eggs in June and July 1992, and placed them in environmental chambers within a few days of oviposition. Incubation temperatures approximated those of *Sceloporus* nests at mid-elevations in the Chiricahua Mountains (mean temperature of 25.0°C, daily range from 19.0° to 34.0°C; see Andrews and Rose 1994). Clutches were incubated in a 0.7–0.8 to 1.0 mixture of distilled water and vermiculite corresponding to a water potential of –100 to –50 kPa (Andrews and Rose 1994). Hatchlings were weighed to 0.01 g within 12 h of eclosion. We reared hatchlings in small groups in plastic tubs containing sand and a clump of grass. Windows in the animal room and 40 W fluorescent Vita-lite bulbs provided ambient light and photoperiod. A 75 W flood lamp suspended at one end of each of the tubs provided a heat gradient for thermoregulation (6–7 h/day). Lizards were fed crickets, *Tenebrio* larvae, and wax worm larvae daily and cage vegetation was sprayed with water twice daily.

We measured T_{sel} and CTMax when lizards reached 29–36 mm snout-vent length (SVL) at approximately 120 days of age. T_{sel} was determined for 32 HE juveniles from 13 clutches and 35 LE juveniles from 15 clutches. T_{sel} was measured at midday after fasting lizards for 24 h. To measure T_{sel} , we removed lizards quickly from their rearing tubs with a noose, and immediately measured their cloacal temperatures with a Physitemp thermocouple thermometer. The range of potential body temperatures in the rearing tubs was determined by placing a dead juvenile *Sceloporus* d.

rectly under the incandescent lamp and at the opposite end of the tub. Equilibrium body temperatures in these two positions were 49.1° and 26.2°C, respectively. It was unlikely that T_{set} was influenced by the presence of other individuals; juvenile *S. scalaris* exhibited no aggression towards conspecifics and all individuals appeared to move freely throughout their rearing tubs.

CTMax was determined for 11 HE juveniles from eight clutches and 10 LE juveniles from six clutches. To do so, we inserted a thermocouple probe 0.5 cm into the cloaca of each lizard and taped it in place. The lizard was then placed in an insulated can over a pre-heated hot plate and its temperature recorded upon loss of its righting response.

Reproductive condition of females

Approximate dates for the initiation and duration of oviposition in the field were determined by the number of reproductive and non-gravid females captured and released on each visit to a site.

We collected females in 1992 from 26 June to 5 August (HE site) and from 6 June to 2 August (LE site). Females were weighed to the nearest 0.1 g and SVL was measured to 0.1 mm at the time of capture. Females were killed within 24 h of capture with Nembutal and dissected. The presence or absence of yolked ovarian follicles was noted and oviductal eggs were counted. Eggs were removed from one randomly selected oviduct, weighed individually to 1 mg, and the developmental stage of the embryo determined (Dufaure and Hubert 1961). Embryos that were intermediate between two stages were assigned an intermediate stage (e.g., 33.5). Embryonic stage was invariant within clutches (see also DeMarco 1992). The remaining oviduct was removed intact with its eggs and fixed in Bouins solution for 24 h and then stored in 70% EtOH. Eggs from these oviducts were later used to determine the thickness of eggshells (see below). The total mass of the clutch was estimated by multiplying the total number of eggs per clutch by mean egg mass. Relative clutch mass (RCM) at oviposition was calculated by dividing the total mass of the clutch by the postoviposition mass of the female. Calculating RCM in this manner avoids statistical problems that can arise from including clutch mass in both the numerator and denominator (Shine 1980; Shine 1990). RCM for HE females was determined for field-caught females (clutch removed surgically) that contained embryos at the same stages at which eggs were oviposited in the field (see Results: Embryonic stages at oviposition). RCM for LE females was determined for females that oviposited in enclosures (see following section).

Embryonic stages at oviposition

To determine the developmental stages of embryos at oviposition, we placed gravid females individually in outdoor wire screen enclosures (44 cm in diameter, 39 cm high) and observed them daily until they laid eggs. Enclosures were placed in the open and were provided with clumps of grass, exposed soil, shade, and a subsurface retreat. This arrangement allowed females a choice of nest sites. Females were fed crickets at least every other day to supplement natural prey. We expected that females in the enclosures would lay eggs at the same time that free-ranging females laid eggs and that oviposition would be associated with the onset of the summer rains (Ballinger and Congdon 1981; Rose 1981). Thirteen HE females were placed in enclosures at a HE study site during the 2nd week in July. Seventeen LE females were placed in enclosures during the 3rd week of June. Enclosures for LE females were located at the Southwestern Research Station (SWRS), Portal, Arizona, rather than at the LE site, to facilitate daily monitoring. SWRS is situated in a valley and is approximately 130 m higher in elevation than the LE site; thus, LE females within enclosures at SWRS probably experienced slightly cooler temperatures than normal.

Both HE and LE sites received the first heavy summer rain (ca. 5 mm) on 7 July 1992. However, only one HE female oviposited naturally within an enclosure (3 August). Therefore, when approx-

imately 80% of free-ranging females at the HE site had oviposited (1st week in August), we brought the remaining HE females in the enclosures into the lab and induced oviposition with an intraperitoneal injection of 0.05 cc oxytocin. LE females began nest construction and egg laying within enclosures on 10 July. However, oviposition in the enclosures occurred over a much longer time period (10 July–8 August) than was observed in the field (approximately 7–13 July). Therefore, only those LE females from enclosures that had oviposited by 14 July ($n = 5$) were used to determine developmental stage at oviposition.

Eggs were weighed to the nearest 1 mg and embryos from 1–3 eggs were staged as described above. Eggs obtained with oxytocin were weighed immediately and eggs oviposited within enclosures were, in most cases, weighed within 2 h of oviposition.

Eggshell thickness

Eggshell thickness was determined for one egg from each of 12 HE and 8 LE clutches. We determined that the Bouins solution did not affect the thickness of these eggshells. To ensure that all eggshells were fully formed, eggs that contained embryos at developmental stage 29 or greater were used. The section of eggshell at the embryonic pole directly adjacent to embryos was removed, pinned lightly to a flat surface covered by absorbent paper, and allowed to air dry for 24 h. To minimize distortion of the shell edge, eggshell sections were dipped briefly into liquid nitrogen and then snapped in half. The fractured edge was photographed at 260–1200 x with a scanning electron microscope. Shell thickness was measured to 0.1 μm by taking five evenly spaced, but randomly placed, measurements from the Polaroid prints of each specimen. Means of the five measurements were used to represent the thickness of each shell. Measurements included the calcareous and fibril layers (see Packard et al. 1982; Packard and DeMarco 1991) as these were too interdigitated to measure separately.

Statistical analyses

Nonparametric measures of central tendency (median) and dispersion (interquartile distance, $Q_3 - Q_1$) were used to summarize body and air temperatures because data for some variables were not normally distributed. Wilcoxon Rank Sum tests for two groups were used to compare body and air temperatures. A Wilcoxon Rank Sum test was used to compare embryonic stages at oviposition.

Body temperatures exhibited by lizards were typically low upon morning emergence and just before retreating in the evenings (Fig. 1A,B). Thus, to express central tendencies, data recorded early in the day and in the evening were excluded from the analyses. To do so, the data for each population were first partitioned into those observations taken before and after 1200 hours. Then, for each data set (two for each population, four total) all observations within 0.5 h time intervals were sequentially deleted starting at the extreme ends of each activity period until linear regressions of T_b on time of day were not significant ($P_s > 0.05$). This resulted in the exclusion of all observations for the HE population taken before 0800 hours and exclusion of all observations for the LE population taken before 0900 hours and after 1830 hours.

The relationship between environmental temperature and body temperature was evaluated with linear regressions of T_b on $T_{a,1cm}$ and T_b on $T_{a,1m}$. These analyses utilized all observations of body and air temperatures. Microhabitat selection and other biophysical factors besides environmental temperature influence T_b and, thus, regression statistics cannot be used to make inferences about thermoregulation per se (Huey 1982; Hertz et al. 1993). We use this methodology here merely to provide comparative measures of the relationship between T_b and environmental temperatures for populations that occupy structurally similar habitats (i.e. bunchgrass) at different elevations.

Means are presented plus or minus their standard errors. Analysis of covariance (ANCOVA) was used to test for differences between regression equations following a homogeneity of slopes test. All analyses involving eggs and hatchlings are based on

clutch means. A significance criterion of $P < 0.05$ is used throughout. Statistical analyses were conducted using SAS software (SAS Institute Inc 1985).

Results

Field body temperatures of reproductive females

Daytime air temperatures were lower at the HE than the LE sites as judged by median $T_{a,1m}$ values of 22.8°C and 31.0°C, respectively. Body temperatures of active females at the two sites reflected these differences in daytime air temperatures.

Females at the HE and LE sites were first observed at approximately 0730 hours (Fig. 1 A,B), and they remained active until about 1600 hours and 1800 hours, respectively. HE females exhibited lower body temperatures than LE females throughout the activity period. Body temperatures of most HE females did not reach 30°C until approximately 0800 hours whereas body temperatures of LE females were always 30°C or more when first observed. Median T_b values of HE and LE females were 32.2°C and 34.0°C, respectively (Wilcoxon Rank Sum test, $Z = 5.7$, $P < 0.001$; Table 1). HE females also exhibited greater dispersions (Q_{3-1}) in T_b , $T_{a,1m}$, and $T_{a,1cm}$ than LE females. HE females maintained body temperatures that were more elevated above air temperatures than LE females. Median differences between T_b and $T_{a,1m}$ ($T_b - T_{a,1m}$) as well as T_b and $T_{a,1cm}$ ($T_b - T_{a,1cm}$) were greater for HE females compared to LE females (Wilcoxon Rank Sum tests, $Z = 7.9$ and 5.5, respectively; $P < 0.001$ for both; Table 1).

Body temperatures during inactivity were lower at the HE than the LE site as inferred from the median minimum soil temperatures of 15.0°C ($Q_{3-1} = 2.9$, $n = 5$) and 20.4°C ($Q_{3-1} = 1.6$, $n = 5$), respectively.

Relationship between body and air temperature

The relationship between body and air temperatures was very similar for both the HE and LE populations (Fig. 2;

Table 1 Body temperatures (T_b), air temperatures 1 m above perch ($T_{a,1m}$), air temperatures 1 cm above perch ($T_{a,1cm}$), difference between body temperatures and air temperatures 1 m above perch ($T_b - T_{a,1m}$), difference between body temperatures and air temperatures 1 cm above perch ($T_b - T_{a,1cm}$), and slopes ($b \pm SE$) of

	T_b	$T_{a,1m}$	$T_{a,1cm}$	$T_b - T_{a,1m}$	$T_b - T_{a,1cm}$	b: T_b on $T_{a,1m}$	b: T_b on $T_{a,1cm}$
High elevation							
Median	32.2	22.8	27.4	9.6	4.2	0.4±0.10	0.5±0.07
Q_{3-1}	2.7	4.6	5.0	4.6	5.0	—	—
Min – max	20.3–36.2	14.9–30.4	16.9–36.4	1.6–19.0	–2.5–9.3	—	—
n	56	56	56	56	56	66	66
Low elevation							
Median	34.0	31.0	33.5	3.2	0.7	0.4±0.07	0.4±0.06
Q_{3-1}	2.0	2.2	2.9	2.7	2.5	—	—
Min – max	28.3–37.9	26.2–35.2	20.6–37.7	–1.2–7.6	–4.1–5.1	—	—
n	52	52	45	52	45	67	59

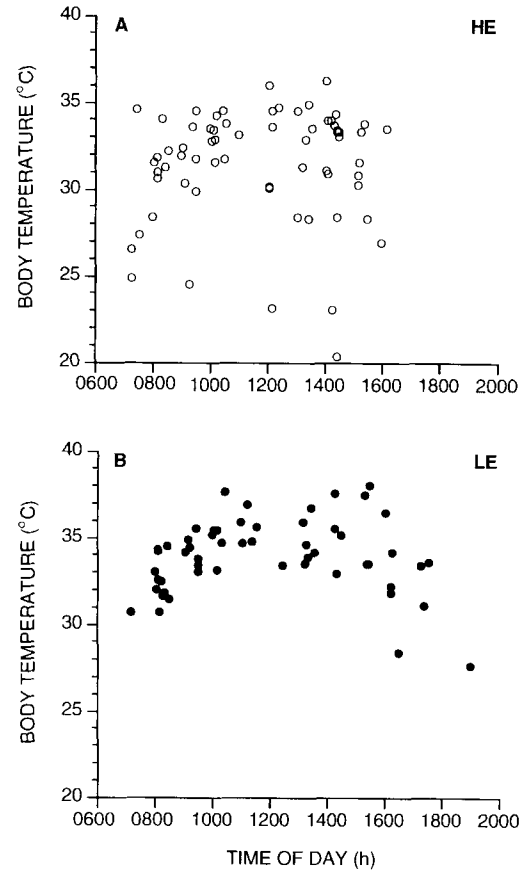


Fig. 1 Body temperatures of reproductive female *Sceloporus scalaris* at **A** high elevation (HE) and **B** low elevation (LE) sites throughout their daily activity periods

Table 1). Females at the two sites did not differ in either slope ($F_{1,133} = 0.0$, $P > 0.05$; $F_{1,125} = 2.7$, $P > 0.05$) or intercept ($F_{1,134} = 1.7$, $P > 0.05$; $F_{1,126} = 0.2$, $P > 0.05$) of the linear regressions of T_b on $T_{a,1m}$ and on $T_{a,1cm}$ respectively, although visual inspection of the plots shows that HE females were active at lower air temperatures than LE females and thus had lower body temperatures overall.

the regressions of body temperatures on air temperatures for reproductive females in high and low elevation populations of *Sceloporus scalaris*. Regression statistics utilize the entire data set; all other statistics utilize only those observations taken during the central portions of the daily activity periods (see text)

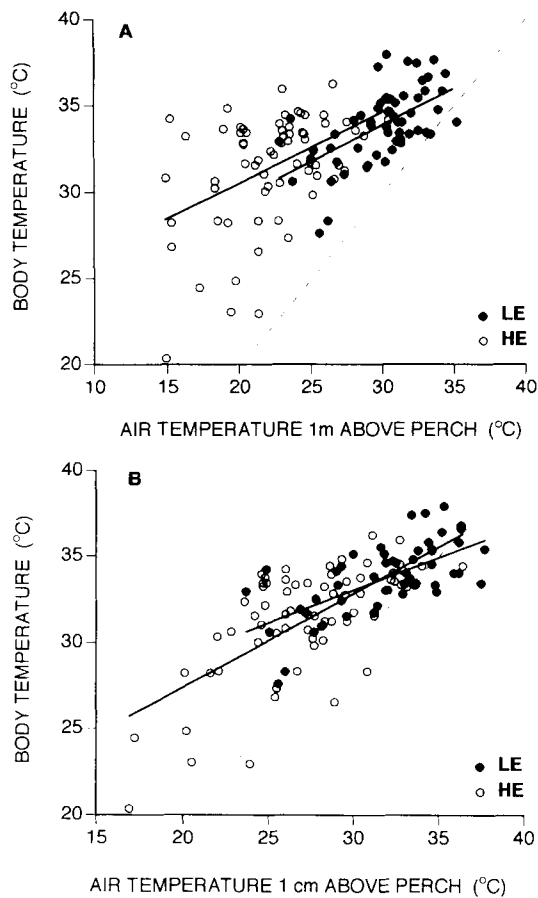
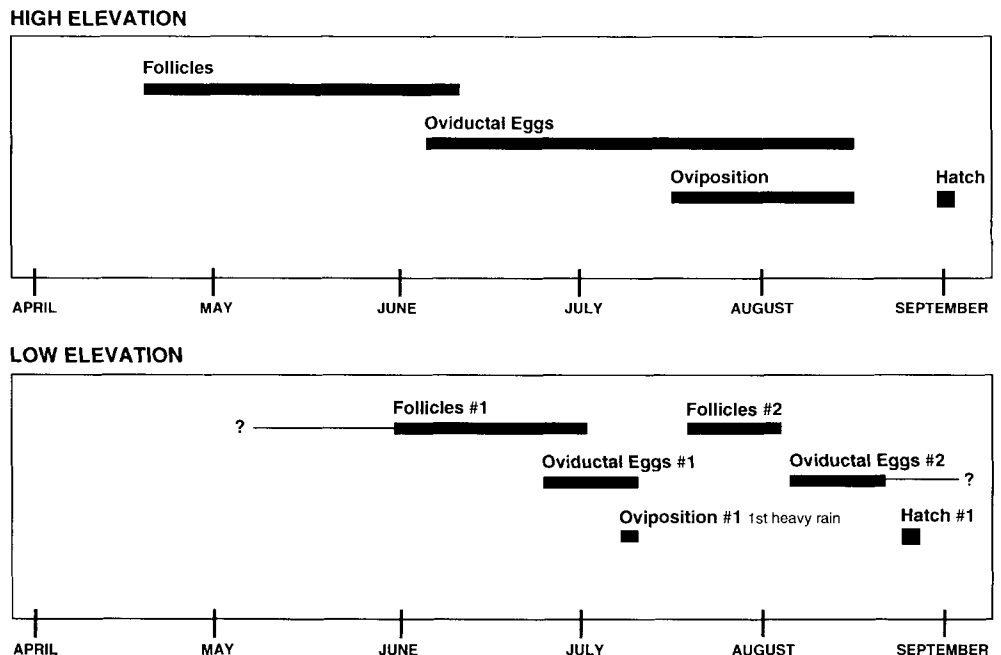


Fig. 2 Relationship between body temperature and **A** air temperature 1 m above perch and **B** air temperature 1 cm above perch for reproductive female *Sceloporus scalaris* at high (HE) and low (LE) elevation sites. Dashed lines represent equal body and air temperatures. Regression slopes and intercepts did not differ significantly in either data set (see text)

Fig. 3 Reproductive phenology of female *Sceloporus scalaris* at high and low elevation sites. Dates of hatching at high and low elevation sites are from Newlin (1976) and Smith et al. (1990), respectively



Selected body temperatures and critical thermal maxima

The median selected body temperatures for captive-raised HE and LE juveniles were 35.6°C ($Q_{3-1} = 0.5$, $n = 13$) and 35.8°C ($Q_{3-1} = 0.6$, $n = 15$), respectively, and T_{sc1} did not differ between populations (Wilcoxon Rank Sum test, $Z = 1.61$, $P > 0.05$). Median T_{sc1} of HE and LE juveniles was higher than the median field T_b of females in their respective parent populations (Wilcoxon Rank Sum tests, $Z = 3.3$ and 5.3 , respectively $P < 0.05$ for both). However, the difference in median T_{sc1} and median T_b was smaller for the LE population (1.8°C) than the HE population (3.4°C).

The median critical thermal maxima for HE and LE juveniles were 44.8°C ($Q_{3-1} = 0.75$, $n = 8$) and 44.6°C ($Q_{3-1} = 1.0$, $n = 6$), respectively, and did not differ between populations (Wilcoxon Rank Sum test, $Z = 0.39$, $P > 0.05$).

Female reproductive condition

All females at all sites were reproductive by early June; that is, all females contained either enlarged follicles or oviductal eggs (Fig. 3; Table 2).

The phenology of female reproduction differed between HE and LE populations in several respects. HE females began ovulating 2–3 weeks earlier than LE females. Vitellogenesis was presumably initiated earlier by HE females than LE females as well; Newlin (1976) suggested that vitellogenesis in HE populations begins in late April, but we have no data for the LE population. HE females retained their eggs considerably longer than LE females, approximately 40 days versus 20 days, respectively. Oviposition by HE females began about 2 weeks after the first heavy summer rain of 1992 (7 July)

Table 2 Reproductive condition of females and developmental stages of embryos in high and low elevation populations of *Sceloporus scalaris* from early June to early August 1992 (*n* number of females, *embryonic stage* oviductal eggs examined, *gravid* females with oviductal eggs or large follicles)

Date	Collected and autopsied				Collected and released	
	Reproductive condition (<i>n</i>)		Embryonic stage		Reproductive condition (<i>n</i>)	
	Enlarged follicles	Oviductal eggs	\bar{x}	Range	Gravid	Non-gravid
High elevation						
June 5–20	2	3	<30.0	–30.0 ^a	23	0
June 21–July 16	1	1	31.0	–	35	0
July 19–28	–	8	35.8	35.0–37.0	16	8
August 1–4	–	1	36.0	–	9	7
Low elevation						
June 9–11	3	–	–	–	13	0
June 26–July 3	1	5	<25.4	–30.0 ^a	12	0
July 9–15	–	2	31.2	30.0–32.5	18	15
July 30–31	1 ^b	1 ^b	28.5	–	5	0

^a Embryos too undeveloped to assign a stage

^b Second clutch

and continued into early August, while oviposition by LE females was synchronized by the onset of the rains; within a week of 7 July, 15 of 17 LE females observed were non-gravid.

At the HE site, females produced only one clutch. In contrast, at the LE site, at least some females produced a second clutch. Two females collected between 30 and 31 July contained oviductal eggs with very early stage embryos (stage 28 or less). Moreover, on 8 August, four females from the enclosures at SWRS (see following text) contained large yolked follicles in addition to their first clutch. Smith et al. (1990) observed gravid females as late as 20 August, but assumed (presumably in error) that these females were still carrying their first clutch.

Embryonic stages at oviposition

The median embryonic stages at oviposition for eggs obtained from HE and LE females maintained in enclosures were 36.0 (range = 35.5–37.0; *n* = 13) and 33.0 (range = 31.0–33.5; *n* = 5), respectively (Wilcoxon Rank Sum test, $Z = 3.38$, $P < 0.001$, Fig. 4). These data are in agreement with the data from free-ranging females. Clutches from HE females collected on 26 and 28 July, and 2 August (one each date), were at embryonic stages 37.0, 35.5, and 36.0, respectively. One LE female collected on 10 July contained embryos at stage 32.5, and the first clutch oviposited in the LE enclosures was at stage 33.0.

Female, egg, and hatchling size

Reproductive females at the HE site were smaller than reproductive females at the LE site. Mean SVLs and masses of HE females were 49.6 mm (range = 42–59 mm; *n* = 68) and 4.6 g (range = 3.0–7.1 g; *n* = 68) while mean SVLs and masses of LE females were 52.8 mm (range = 46–63 mm; *n* = 72) and 5.1 g (range = 3.3–8.6 g; *n* = 72), respectively (*t*-tests, P values < 0.05).

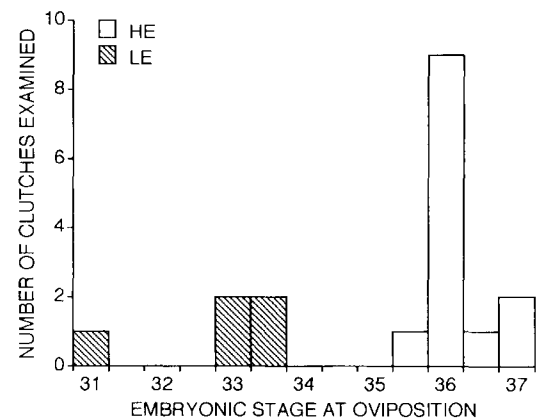


Fig. 4 Embryonic stage at oviposition for high (HE) and low (LE) elevation populations of *Sceloporus scalaris*. Embryos at the HE site were significantly more developed at oviposition than at the LE site (see text)

These comparisons included all reproductive females captured from early June through early August.

At the time of oviposition, eggs from HE females were larger than those from LE females. The mean egg masses at oviposition for HE and LE females were 0.37 g (± 0.008 , *n* = 13) and 0.29 g (± 0.012 , *n* = 5), respectively (*t*-test, $t = 5.64$, $P < 0.001$). The larger mean egg mass of HE eggs was reflected by a larger hatchling mass. Mean masses of HE and LE hatchlings were 0.33 g (± 0.009 , *n* = 13) and 0.28 g (± 0.004 , *n* = 13), respectively (*t*-test, $t = 5.35$, $P < 0.001$).

Clutch size and relative clutch mass

Clutch size was positively correlated with female size in both HE ($F_{1,14} = 22.0$, *n* = 16, $r^2 = 0.61$, $P < 0.001$) and LE ($F_{1,25} = 30.8$, *n* = 27, $r^2 = 0.55$, $P < 0.001$) populations (Fig. 5). The slopes of these regressions did not differ ($F_{1,39} < 0.1$, $P > 0.05$). However, HE females had smaller clutch sizes than LE females ($F_{1,40} = 11.3$, $P < 0.01$, ANCOVA, SVL used as the covariate). At the

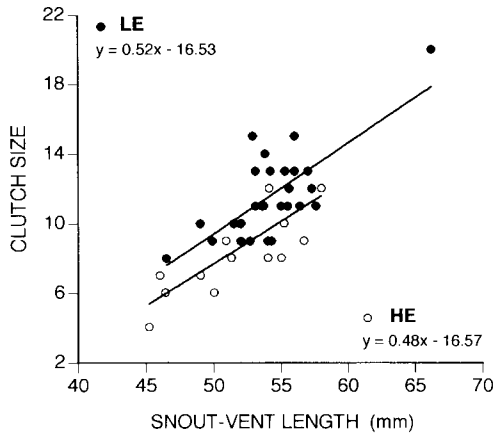


Fig. 5 Relationship between clutch size and female snout-vent length for high (HE) and low (LE) elevation populations of *Sceloporus scalaris*. Three data points for HE clutches are obscured. Clutch size of LE females was significantly larger than that of HE females (see text)

grand covariate mean (53.3 mm), the adjusted clutch sizes for HE and LE females were 9.4 (± 0.42) and 11.2 (± 0.32), respectively.

HE and LE females had similar RCMs at oviposition. Mean RCMs for HE and LE females were 0.86 (± 0.101 , $n = 7$) and 0.82 (± 0.059 , $n = 6$), respectively (t -test, $t = 0.40$, $P > 0.05$).

Eggshell thickness

Eggshells produced by HE females were thinner than those of LE females. Mean eggshell thicknesses of HE and LE eggs were 19.3 μm (± 1.36 , $n = 12$) and 26.6 μm (± 0.92 , $n = 8$), respectively (t -test, $t = 4.0$, $P < 0.001$). HE shells were thinner than LE eggshells because of a thinner fibril layer; the thickness of the calcareous layer appeared to be similar in both populations (Mathies 1994).

Discussion

Comparative thermal biology at HE and LE sites

The HE site was considerably cooler than the LE site with respective median $T_{a,1m}$ values of 23°C versus 31°C during the day when females were active, and median soil temperatures of 15°C versus 20°C at night, respectively. Females at the HE site were apparently able to partially compensate behaviorally for relatively low daytime temperatures. For example, median T_b of females at the HE site was only 2°C lower than at the LE site, and HE females tended to have body temperatures that were more elevated above air temperatures than LE females.

However, in the absence of a measure of the null distribution of T_b values at each site (see Hertz 1992; Hertz et al. 1993), these data cannot be used to infer active ther-

moregulation at either site. Overall, however, the relatively low ambient temperatures at the HE site were associated with a lower average body temperatures for HE females than LE females. HE females not only had lower T_b values than LE females while active, the daily period of activity at the HE site was about 2 h shorter than at the LE site as well. Moreover, during the period of inactivity, 15.5 h and 13.5 h for each diel cycle at the HE and LE sites, respectively, body temperatures of females at the sites would have been even more disparate, as inferred from the measurements of night-time soil temperatures. Thus, the cumulative amount of time spent at relatively high T_b values was less for HE females than LE females.

Observations on juvenile *Sceloporus scalaris* suggest that, given the same thermal opportunities, HE and LE females would have the same activity temperatures. Juveniles raised in the laboratory had virtually identical T_{sel} and CTMax. Because HE and LE juveniles were incubated and raised under the same conditions, their thermal behavior and physiology in the laboratory presumably reflects genetically determined responses. Thus, the higher T_{sel} of juveniles in the laboratory versus the T_b values of active females could reflect inability of females to raise their T_b values to preferred levels in the field. On the other hand, gravid females and juveniles may simply exhibit different thermal behaviors, or lizards raised in the laboratory may exhibit different behaviors than free-ranging lizards, or both.

Comparative reproductive biology at HE and LE sites

Environmental temperatures may directly affect life history characteristics (Adolph and Porter 1993). Because rates of embryonic development in lizards are temperature dependent (Muth 1980; Shine 1983a; Vial and Stewart 1985; Packard and Packard 1988), temperature directly affects the time that embryos require to reach stages appropriate for oviposition (i.e., duration of egg retention) as well as total developmental time. In our study, embryos were exposed to lower temperatures at the HE than the LE site. For example, temperatures of embryos during gestation would have averaged 2°C lower at high than low elevations during the day when females were active and as much as 5°C lower when females were inactive. After oviposition, incubation temperatures would have been lower at the HE site than the LE site as well, as temperatures of nests should closely reflect ambient air temperatures (Shine 1983a).

The prediction that females would retain their eggs longer at high than low elevations was upheld. HE females initiated reproduction approximately 2 weeks earlier, and completed oviposition about 1 month later, than LE females. Thus, HE females retained eggs considerably longer than LE females: 40 days (this study) to 50 days (Newlin 1976) versus 20 days, respectively. However, the extended period of egg retention exhibited by HE females was only partially due to relatively slow devel-

opmental rates of embryos. HE females retained eggs to more advanced stages of development than LE females, stages 35.5–37.0 versus 31.0–33.5, respectively, fulfilling our second prediction. Thus, the reproductive biology of LE females is typical of that of other temperate zone lizards at low elevations inasmuch as the duration of egg retention is relatively short, oviposition occurs when embryonic development reaches approximately stage 30 (Shine 1983b; DeMarco 1992, 1993), and females produce multiple clutches (Tinkle 1967), whereas the reproductive biology of HE females is typical of that of species that inhabit high elevations inasmuch as the duration of egg retention is relatively long, oviposition occurs when embryonic stage is relatively advanced, and females produce a single clutch per season (Braña et al. 1991). Moreover, our finding that egg retention varies along a thermal gradient provides strong support for the hypothesis that viviparity evolves in cold climates by increases in the duration of egg retention.

Also in accord with relatively low ambient temperatures, estimated total developmental times of embryos were longer at the HE site than at the LE site. Developmental time of HE clutches, based on 7 June as the date of first ovulation, and the observation of Newlin (1976) of the first appearance of hatchlings in early September, was at least 85 days. In contrast, the estimated developmental time of LE clutches (first clutch), based on 18 June as the date of ovulation, and the observation of Smith et al. (1990) of an approximate hatch date of 20 August, was about 60 days. The 1.4-fold increase in the total developmental time of embryos at the HE site compared to embryos at the LE site may be phenotypic: embryos from HE and LE sites had identical developmental rates when gestation temperatures were the same (T. Mathies, unpublished data). Thus, the relatively low temperatures experienced by embryos at the HE site resulted in a relatively lengthy period of development.

The relatively long period of egg retention and total developmental time of HE embryos limits the number of clutches HE females produce per year to one, whereas LE females can produce two. For *S. scalaris*, at least, the number of clutches produced per season may also be a phenotypic response to temperature. For example, the related species *Sceloporus aeneus* found at high elevations in Mexico normally has one clutch per year, but females reared in the laboratory at warm temperatures produce at least two (R.M. Andrews, unpublished data). Reduction in clutch frequency is typical of lizards that inhabit cool environments (Ballinger 1983; Licht 1984; Jones et al. 1987; James and Shine 1988), and is presumed to be a precondition for the evolution of viviparity (Shine 1985).

Our third prediction was that HE females would produce eggs with thinner shells than LE females. Reduction in eggshell thickness has been proposed as a critical modification for increasing rates of gas exchange between the developing embryo and the female (Packard et al. 1977; Guillette 1993). This may be especially important at high altitudes where the partial pressure of O₂ in arterial blood is lower than at low altitudes (Guillette et

al. 1980). Our observations were in accord with this prediction: eggshells from HE females were significantly thinner than eggshells from LE females, 19 µm versus 27 µm.

Our fourth prediction was that HE females would have smaller clutch sizes than LE females. Viviparity and longer durations of egg retention may require a reduction in clutch size because clutch mass and volume increase substantially during embryonic development due to water uptake by eggs (Goldberg 1971; Méndez de la Cruz et al. 1988; Vleck 1991). A large clutch mass could physically burden the female and thus increase her vulnerability to predators (Shine 1980; Van Damme et al. 1989; Sinervo et al. 1991). Viviparous species of *Sceloporus* have smaller clutch sizes than oviparous species of the same body size (Ballinger 1983). Populations of *S. scalaris* are consistent with this pattern: HE females produced approximately two fewer eggs per clutch than LE females of the same size (Fig. 5). However, RCM at oviposition did not differ between HE and LE populations. Similar RCMs were due, in part, to the larger eggs produced by HE than LE females (this study), but also to a higher egg water content associated with their more advanced stages of embryonic development at oviposition (T. Mathies, unpublished data).

The mechanistic bases underlying the interactions between clutch size and egg size of lizards are well understood (Sinervo 1990; Sinervo and Licht 1991), although the ecological bases that determine the direction of this trade-off are less clear. The shift in the per clutch reproductive effort by HE females to fewer but larger eggs has been noted for other members of the *scalaris* group: the viviparous *Sceloporus bicanthalis* has a smaller clutch size but larger hatchlings than its oviparous sibling species, *S. aeneus* (Guillette 1982), and *S. bicanthalis* occurs at higher elevations than *S. aeneus* (Thomas and Dixon 1976). In contrast, female *S. occidentalis* at a high elevation site have larger clutches and smaller eggs than females at a low elevation site (Sinervo 1990). Presumably, the direction of these trade-offs between offspring number and size reflect the particular environmental conditions at these montane sites or lineage-specific responses to these conditions, or both.

Comparative phenology of reproduction at HE and LE sites

Temperature typically serves as a proximate cue for initiating reproduction in temperate zone lizards where populations in warm environments (e.g., low altitudes or latitudes) generally initiate reproduction at an earlier date than populations in cooler environments (Licht 1984). This general pattern is reversed in HE and LE populations of *S. scalaris*. HE females initiate reproduction (vitellogenesis) earlier in the spring than LE females apparently in order to compensate for relatively low temperatures during gestation. Additional constraints on the tim

ing of reproduction are that soil moisture in southeastern Arizona is too low for successful incubation prior to the onset of the summer rains (Rose 1992), and following the onset of the summer rains, soil, and thus nest temperatures, drop as cloud cover reduces insolation. Thus, successful reproduction at the HE sites requires that a substantial portion of embryonic development occurs in utero so that embryos are at relatively advanced stages when the first rains occur. In 1992, however, HE females did not begin ovipositing until approximately 12 days after the onset of the rains. This suggests that the degree of embryonic development is the primary factor for initiating oviposition, at least in the HE population. Unseasonably cool temperatures during May 1992 may have delayed oviposition that year as oviposition and the first summer rains usually coincide (Ballinger and Congdon 1981).

Reproductive timing for LE females also must ensure that eggs are ready to be laid at the onset of the summer rains. Vitellogenesis and embryonic development in utero are relatively rapid because of relatively high body temperatures. Thus, relatively late initiation of reproduction ensures that LE females are not encumbered with a large clutch mass for longer than necessary before eggs can be laid. Reduced mobility of females might be particularly disadvantageous (Shine 1980; Sinervo et al. 1991) at the LE site because the diversity and density of potential predators for *S. scalaris* appear to be greater than at the HE site (T. Mathies, personal observation).

Evolution of extended egg retention

For lizards in the *scalaris* group, at least, viviparity may evolve relatively easily because most of the intermediate steps appear to result from either preexisting reaction norms or selection facilitated by phenotypic plasticity. The reduction in clutch frequency from multiple clutches at low elevations to a single clutch at high elevations is likely to be a direct consequence of the reaction norm between the rate of physiological processes (i.e., the rate of embryonic development) and temperature. However, the shift from multiple clutches to a single clutch per season is apparently not sufficient in itself to ensure successful reproduction at high elevations.

First, HE females retained eggs much longer and to much more advanced developmental stages than LE females. In addition, HE females initiated reproduction earlier than LE females. These observations suggest that successful reproduction at the HE site required additional adjustments to female reproductive biology. Moreover, the nature of these adjustments implies that these are adaptive evolutionary responses to the problems of reproduction in a cool climate. Extending egg retention to the degree exhibited by HE females should have been relatively easy to accomplish because egg retention by *S. scalaris* females is an extremely plastic trait: under laboratory conditions LE females retained embryos to as advanced stages as those of HE females without impairing

development (T. Mathies, unpublished data). This observation is consistent with the view that the ability of females to extend the duration of egg retention facultatively is a precursor to viviparity (Shine and Guillet 1988). Presumably, the time at which vitellogenesis is initiated is also intrinsically variable and would also respond rapidly to selection.

Second, eggshells produced by HE females were substantially thinner than those produced by LE females. Morphological studies suggest that eggshell thickness is a function of the number of shell glands in the oviduct (Guillette 1992), and that reduction in the number of shell glands requires selection (Guillette 1993). Thus for *S. scalaris*, reduction in the thickness of the eggshell appears to be the only "novel" trait associated with extended egg retention. Given the extensive phenotypic plasticity in the ability of LE females to retain eggs, invasion of high elevations by LE females would not be precluded by the thickness of their eggshells and reduction in eggshell thickness does not appear to be necessary during the initial stages in the evolution of viviparity.

In the preceding discussion we have assumed that low elevation populations of *S. scalaris* are ancestral to high elevation populations. Is this a valid assumption? At present, *S. scalaris* is largely confined to montane meadows throughout its range. However, Bock et al. (1990) point out that the historical range of *S. scalaris* on low elevation grasslands once far exceeded the area of montane distribution and suggest that montane populations are remnant populations. The once widespread distribution of *S. scalaris* at low elevations suggests that low elevation populations were ancestral to montane populations. That is not to say, however, that the sequence of events leading to extended egg retention described above is not reversible and that such reversals do not occur. Indeed, the capacity of *S. scalaris* to modify reproductive strategies to suit different thermal environments could account for the wide geographic and elevational distribution of this species.

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