

INCUBATION TEMPERATURE DIFFERENTIALLY AFFECTS HATCHING TIME, EGG SURVIVAL, AND HATCHLING PERFORMANCE IN THE LIZARD *PODARCIS MURALIS*

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ABSTRACT: Effects of incubation temperature on embryo survival, incubation duration, hatching size, post-hatching growth, and sprint speed were studied in the lizard *Podarcis muralis*. Embryos incubated at 32 C and 35 C hatched about 10 days before those of 28 C and over 5 wk before those of 24 C. Hatching success was high at 24 C and 28 C but much lower at higher temperatures (32 C and 35 C). Neonates incubated at low temperatures had larger snout-vent lengths and body masses (effects of egg mass removed), grew faster, and had higher sprint speeds (size effects removed) than hatchlings incubated at higher temperatures. Hence, incubation temperatures that accelerate embryo development (32-35 C) did not maximize embryo survival and hatchling characteristics. In this study, an incubation temperature of 28 C provided the best balance between developmental rate, hatching success, and posthatch performances.

Key words: Incubation temperature; Egg survival; Hatchling size; Growth rate; Sprint speed; *Podarcis muralis*

IN many reptiles, incubation temperature affects the duration of embryogenesis (e.g., Dmi'el, 1967; Gutzke and Packard, 1987; Miller, 1985; Mrosovsky and Yntema, 1980; Muth, 1980; Packard et al., 1987; Sexton and Marion, 1974) and the probability of embryo survival (e.g., Bustard, 1971; Fitch, 1964; Licht and Moberly, 1965; Rand, 1972; Sexton and Marion, 1974; Vinegar, 1973). Developmental temperature may also influence sex (reviewed in Packard and Packard, 1988), morphology (Bustard, 1969; Fox et al., 1961; Osgood, 1978), and body size at hatching (Beuchat, 1988; Ferguson and Joanen, 1982, 1983; Gutzke and Packard, 1987; Phillips et al., 1990; Vinegar, 1973; Whitehead et al., 1990).

In addition, recent studies reveal long term effects of incubation temperature on the physiology and behavior of hatchling reptiles. Posthatching survival and growth rates of crocodiles (*Crocodylus porosus*) are influenced by incubation temperature (Webb and Cooper-Preston, 1989). Lang (1985) suggested an effect of incubation

temperature on thermal selection behavior of young crocodiles (*Crocodylus siamensis*), and Burger (1989, 1990) demonstrated long-term effects on behavior and physiology of young pine snakes (*Pituophis melanoleucus*), black racers (*Coluber constrictor*), and kingsnakes (*Lampropeltis getulus*). In these snakes, hatchlings from eggs incubated at different temperatures differed in such important whole-animal functions as escape and striking behavior, maneuverability, and locomotion (Burger, 1989, 1990). The effects of incubation temperature may thus extend well beyond the incubation period.

We investigated the effects of incubation temperature on the embryos and hatchlings of the lacertid lizard *Podarcis muralis*. We examined incubation time, embryo survival, and hatchling size at four constant incubation temperatures. To assess long-term effects of the thermal environment experienced during incubation, hatchlings were reared under uniform conditions to the age of 2 mo. We measured their growth rate and locomotor

abilities (burst sprint speed), two attributes of hatchlings that are probably ecologically important. A major objective was to examine to what extent embryo development, embryo viability, and hatchling characteristics have divergent thermal requirements.

MATERIALS AND METHODS

Podarcis muralis is a rather small [adult snout-vent length (SVL) 48-67 mm], agile wall lizard that behaves like a typical heliotherm (Avery, 1978) and feeds on a large variety of invertebrates (Kabisch and Engelmann, 1969; Strijbosch et al., 1980). In many parts of its distributional range, which covers most of central and part of southern Europe, *P. muralis* is the most abundant member of the herpetofauna. It prefers dry, sunny, and stony habitats in the northern parts of its distribution but may also occupy more humid and shady places in the south (Cyren, 1934; Parent, 1978).

Females of *P. muralis* attain sexual maturity in their second year (Barbault and Mou, 1988; Rollinat, 1934; Street, 1979) and may produce between one (northern and montane populations) and three clutches (southern populations) per year. Clutch size varies between 2-10 eggs and increases with female SVL (Barbault and Mou, 1988; Rollinat, 1934; Sparreboom, 1981; Street, 1979). The stage of embryonic development at oviposition, according to the table of Dufaure and Hubert (1961), is 25-29, about midway through development (Braiia et al., 1991). Females preferentially bury their eggs in sandy or crumbly substrates, at the end of 10-20 cm deep tunnels (Angel, 1946; Fretey, 1975; Sparreboom, 1981). In nature, incubation duration varies between 6-11 wk (Angel, 1946; Mertens, 1947; Rollinat, 1934).

During early May 1990, 14 gravid *P. muralis* were collected near Oviedo, northeastern Spain and were transported to Belgium, where they were housed individually in terraria containing a sandy substrate, some mosses, and grass. Food (calcium-dusted crickets and mealworms) and water were provided ad libitum. A

150 w light bulb suspended 20 cm above the terrarium provided heat and light. Lizards were weighed and checked daily for skin folds (indicative for parturition). Egg laying started soon after the lizards arrived in the laboratory (14 May 1990) and ended about 1 mo later. Each female produced one clutch.

Immediately following parturition, the females and eggs were weighed (to the nearest 0.01 and 0.0001 g, respectively). Eggs were put individually in 200 ml jars filled with moistened vermiculite (1:1 water to vermiculite by mass). These jars were placed in incubation rooms (65 x 65 x 60 cm) at one of four experimental temperatures (24, 28, 32, and 35 C). A 100 w heat-bulb, mounted in the roof of these chambers, provided heat; temperature within the incubation rooms was controlled by a thermostat, connected to a thermistor placed in the center of the chamber. Incubation temperature was monitored continuously (DGT-LHM data logger) and varied <0.3 C throughout a daily cycle. Within each chamber, positions of the cups were shifted weekly to minimize effects of possible temperature gradients. Moisture conditions were not monitored, but we reduced evaporation from the cups by covering them with a plastic membrane. In addition, relative air humidity was kept near 100% by placing large dishes with water in the chambers; the water was replenished daily and never dried up entirely. Eggs from single clutches were distributed over the incubation temperatures. Eggs were scored for possible viability at oviposition; all eggs that were judged to exhibit reduced viability did not hatch, and were not taken into account for the analyses.

We checked the environmental chambers for hatchlings about four times a day. We weighed (0.01 g) and measured (SVL, to the nearest 0.1 mm) each hatchling and placed it in a plastic terrarium (50 x 20 x 20 cm) with a sandy substrate, some grasses, mosses, and several pieces of bark and schist for cover. A 150 w light bulb (8L:l6D) created a photothermal gradient, so that hatchlings could thermoregulate at their selected temperature. Substrate tem-

perature within the terraria varied between 45 C under the bulb, and room temperature (18-24 C) near the edge. During the clark phase, temperatures dropped to ambient (12-15C). Food (first instar crickets, dusted with commercial vitamin supplement and calcium) was provided in large quantities. Water (for drinking) was regularly sprayed on the vegetation and available ad libitum on small plastic dishes. Each terrarium contained two lizards. Pairs of hatchlings were first formed randomly and then reshuffled each week to match SVLs. None of the newborns exhibited obvious morphological abnormalities at birth, and all survived to the age of at least 2 mo. At that age, they could readily be sexed (color pattern, femoral pores).

We weighed and measured hatchlings at least once a week from hatching until the end of the normal activity season (15 October). During their first month, lizards grew linearly. The slopes of the regression lines of mass and SVL against time in this period were used to estimate individual post-hatch growth rates (all linear regressions yielded r^2 -values >0.95).

When juveniles were > 2 mo old, we determined their sprint speed by chasing them through a 2 m electronically timed racetrack (Van Damme et al., 1989, after an original idea of Huey et al., 1981). Prior to each trial, lizards were heated in an incubator to a body temperature of 35 C (which is near the optimum for sprint speed in this species: Bauwens, unpublished data). Each juvenile was given five trials (no more than two per day), and the fastest 0.5 m interval scored was used as an estimate of maximum sprint capacity. As we conducted all races within 1wk, juveniles differed in age (67-126 days) and SVL (34.4-46.7 mm).

Multiple regression analysis was used to estimate effects of three female traits (SVL, condition, and clutch size) on egg mass. Data entered in the regression were averages per clutch, weighed for clutch size. We estimated incubation temperature and family effects on hatchling attributes (SVL, mass, condition) by two-way ANOVA, with egg mass entered as a covariate, and assuming that our data met the required as-

sumptions of normality and homoscedasticity. Similarly, SVL was entered as a covariate when testing effects of incubation temperatures and family on sprint speed. In the analyses of hatching attributes, the juveniles at 32 and 35 C were lumped because of low sample sizes. G-tests were used to test for differences in embryonic survival and sex ratio. Because of small sample sizes, we have pooled data from male and female hatchlings. Therefore we are unable to evaluate possible sex-related differences in hatchling size, growth rate, and performance. All statistics were performed with SPSSPC+.

RESULTS

Egg mass varied considerably among clutches (ANOVA: $F = 35.3$, $df = 13, 62$, $P < 0.001$). To assess determinants of egg mass other than family effects, we used three female traits (Sinervo, 1990). (1) Female SVL was used as a measure of size. (2) Female condition was estimated using the residuals derived from the regression of $\log(\text{post partum mass})$ and $\log(\text{SVL})$, which was highly significant ($P < 0.001$). (3) In a similar way, residual clutch size was used as a measure of clutch size with female-size effects removed [residuals from the regression of $\log(\text{clutch size})$ and $\log(\text{SVL})$]. Multiple regression analysis revealed a significant contribution of all female traits considered. Female SVL [partial regression coefficient (pre) = 1.69, $t = 1.98$, $P = 0.076$] and female condition ($pre = 1.48$, $t = 2.84$, $P = 0.017$) were positively correlated to egg mass, whereas clutch size ($pre = -0.60$, $t = -1.82$, $P = 0.099$) was inversely related to egg mass. The combined effects of female SVL, condition, and clutch size explained 54% of the among dam variation ($F = 4.05$, $df = 3, 10$, $P = 0.04$).

Temperature profoundly affected embryo survival (G-test, $G = 16.3$, $df = 3$, $P = 0.001$). Hatching success was high at 24 and 28 C but much lower at higher temperatures (Table 1). Duration of incubation remained remarkably constant within, but varied considerably among, temperature treatments (ANOVA, $F = 1000$, $df = 3, 28$, $P < 0.0001$). Embryos

TABLE 1. Effects of incubation temperature on hatching success, incubation duration, sex-ratio, and post-hatch growth rate (first month) in the lizard *P. muralis*.

		Incubation temperature				<i>p</i>
		24	28	32	35	
Hatching success		11/15	10/15	6/17	2/16	0.001
Incubation duration (days)	%	73.3	66.7	35.3	12.5	<0.0001
	\bar{x}	73.6	35.8	26.7	25.5	
	SE	0.6	0.5	0.9	1.5	
Sex ratio (male :female)	<i>n</i>	11	10	6	2	0.001
		5:6	6:4	3:3	1:1	
Post-hatch growth rate (mm/day)	\bar{x}	0.353	0.282	0.244		0.001
	SE	0.017	0.018	0.014		
	<i>n</i>	11	10	8		

incubated at 32 and 35 C hatched about 10 days before those of 28 C and over 5 wk before those of 24 C (Table 1).

Incubation temperature did not influence sex ratio (G-test, $G = 0.18$, $df = 3$, $P > 0.9$; Table 1) and we pooled data for both sexes in subsequent analyses.

Both SVL and mass of the hatchlings were related to egg mass at oviposition (Figs. 1, 2). The condition of the hatchlings, estimated by the residuals of the regression of \log_0 (hatchling mass) on \log_0 (hatchling SVL), also exhibited a relation to egg mass. Incubation temperature proved to affect SVL and mass but not the condition of the neonates. Eggs incubated at 32 and 35 C produced juveniles that had lower residual SVL's (two-way ANOVA with family and temperature entered as

factors, and egg mass as covariate: $F = 24.89$, $df = 2, 3$, $P = 0.014$) and body masses (two-way ANOVA, same factors and covariate: $F = 7.07$, $df = 2, 3$, $P = 0.08$) than those maintained at 24 and 28 C. No significant family effects or family \times temperature interactions were found (all $p > 0.2$).

During their first month, SVL's of hatchlings increased linearly. Intercepts and slopes for different hatchlings were not correlated (Spearman rank correlation, $r_s = 0.09$, $n = 29$, $P = 0.70$), indicating no effect of SVL at hatching on subsequent growth rates. Growth rates of hatchlings differed among temperature treatments; lizards incubated at low temperatures grew faster than those incubated at high temperatures (two-way ANOVA with temperature and family entered as factors and clutch entered as a covariate: $F = 11.39$, $df = 2, 3$, $P = 0.02$; Table 1). No family

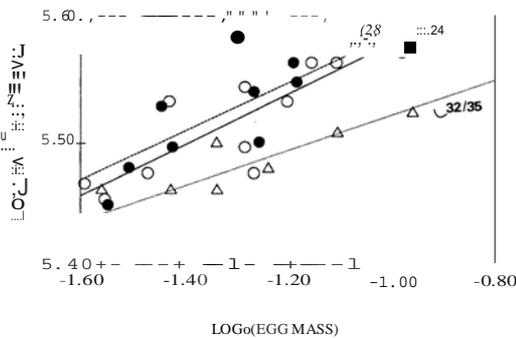


FIG. 1.-Snout-vent length of *Podarcis muralis* at hatching as a function of egg mass (both axes loge transformed). Eggs incubated at high temperatures (32 and 35 C, triangles) on average produce smaller juveniles than those incubated at 28 C (closed dots) or 24 C (open dots). The overall regression equation is $\log_0(\text{hatchling SVL}) = 5.75 + 0.18 \log_0(\text{egg mass})$: $r' = 0.55$, $P < 0.001$.

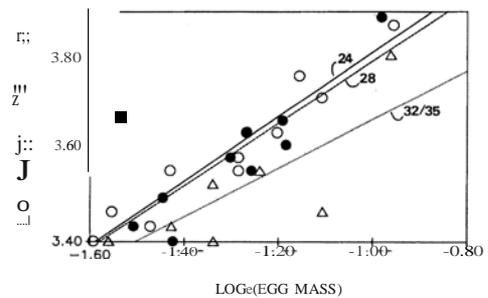


FIG. 2.-Hatchling mass as a function of egg mass (both axes log, transformed). Eggs incubated at 24 and 28 C produce heavier juveniles. Symbols as in Fig. 1. The overall regression equation is $\log_0(\text{hatchling mass}) = 4.27 + 0.54 \log_0(\text{egg mass})$: $r' = 0.63$, $P < 0.001$.

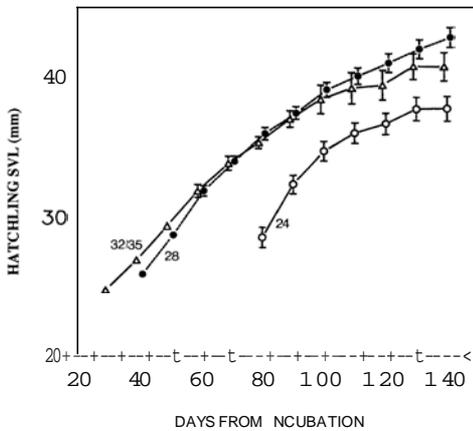


FIG. 3.-Body length of juvenile *Podarcis muralis* incubated at 35 and 32 C (triangles), 28 C (black dots), and 24 C (open dots) as a function of age since oviposition. Values shown are mean snout-vent lengths (uncorrected for egg mass) \pm 1 SE.

effects or family \times temperature interaction effects were observed (both $P > 0.1$).

Our results evidenced that incubation temperature affects the duration of the incubation period, and hence the timing of hatching, size at hatching, and juvenile growth rate (Fig. 3). How do these factors jointly affect juvenile size during the post-hatch growth period? By the end of the normal activity season (15 October), hatchlings from eggs incubated at 28 C (mean SVL = 43.4 mm, 1 SE = 8.7 mm, $n = 10$) had outgrown their companions from 32 and 35 C (mean SVL = 42.0 mm, 1 SE = 9.6 mm, $n = 8$), although the latter hatched 10 days earlier. At that moment, mean SVL of lizards incubated at 24 C (mean SVL = 39.2, 1 SE = 8.0 mm, $n = 11$) was still significantly smaller than that of their higher temperature counterparts.

Sprint speed increased with body size [$\log(\text{speed}) = -4.14 + 1.49 \log(\text{SVL})$, $P < 0.05$: Fig. 4). We therefore corrected for differences in SVL (originating from differences in age, size at birth, and/or growth rate) by entering SVL as a covariate in the ANOVA of sprint speed by incubation temperature. Lizards incubated at high temperatures were on average slower than those incubated at low temperatures (two-way ANOVA with family and temperature as factors and SVL entered as a covariate: $F = 10.90$, $df = 2, 2$, $P = 0.07$).

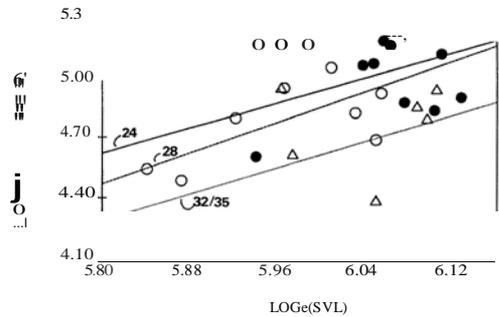


FIG. 4.-Sprint speed of juvenile *Podarcis muralis* as a function of snout-vent length (both axes log transformed). Lizards incubated at high temperatures (32 and 35 C, triangles) were slow relative to their counterparts incubated at 28 C (closed dots) and 24 C (open dots).

No family effects or family \times temperature effects were found (both $P > 0.2$).

DISCUSSION

Our data demonstrate both short- and long-term effects of incubation temperature on several whole-animal traits that are likely to influence fitness. Incubation temperature not only influenced incubation duration and embryonic mortality, but also affected hatchling size, post-hatch growth rate, and hatchling sprint speed.

Egg Survival and Incubation Time

As in many other reptiles, embryo mortality in *Podarcis muralis* varied considerably with incubation temperature. The upper thermal limit for embryogenesis (35 C) appears to be low relative to the critical thermal maximum of adults (CTMax for adult *P. muralis* = 44.2 C: Bauwens, unpublished data). Physiological constraints seem to determine the upper temperature limit for embryogenesis. Although we do not know what actually caused the high egg mortality in our samples at 32 and 35 C, the high incidence of developmental anomalies at extreme temperatures recorded in many other reptiles (reviewed in Packard and Packard, 1988) suggests a general disruption of highly integrated physiological functions. Although egg survival was highest at the lowest incubation temperature, the prolonged incubation period may induce ecological constraints on successful egg development

in this particular species. Our data, together with those of Cooper (1958), who reported an incubation time of 122-160 days at 18 C, indicate a negative exponential relation between the duration of embryogenesis and incubation temperature. Eggs raised at low temperatures may not hatch before the onset of winter, or juveniles hatching late in the season would have to face the detrimental effects of low fall temperatures and a reduced food supply and may not survive to the next year. In the northernmost population of *P. muralis* at Maastricht (50°51' N latitude in The Netherlands), low environmental temperatures and associated lengthy incubation periods are thought to inflict severe problems on hatching success during some years (Strijbosch et al., 1980).

Hatchling Size

Both egg mass and incubation temperature influenced body size at hatching. In *P. muralis*, large eggs gave rise to large hatchlings. Moreover, these seemed to be in better condition than hatchlings from smaller eggs. Several authors have reported positive relations between egg mass and hatchling size (Ferguson and Brockman, 1980; Ferguson and Snell, 1986; Ferguson et al., 1982). Sinervo and Huey (1990) experimentally reduced egg size of a species of lizard (*Sceloporus*) by removing part of the yolk, and they demonstrated that the resulting hatchlings had smaller SVLs. A substantial part of the variation in egg mass in our sample was due to differences among clutches. The SVL of the mother positively contributed to egg mass, indicating that large females not only produce larger clutches (Barbault and Mou, 1988), but also larger individual eggs. The negative effect of residual female clutch size on egg mass seems in agreement with the notion of a trade-off between egg numbers and egg size, possibly via constraints on total clutch mass (Brockelman, 1975; Smith and Fretwell, 1974). Although all three female traits considered (SVL, condition, clutch size) explained a significant part of the among-clutch variation in egg mass, a substantial part remained unexplained.

In our sample, hatchlings from eggs incubated at 32 and 35 C were on average

smaller than their sibs from lower temperatures. Similar effects of high incubation temperature on hatchling size have been reported in different groups of reptiles (lizards: Beuchat, 1988; Phillips et al., 1990; turtles: Gutzke and Packard, 1987; Packard et al. 1987; crocodiles: Whitehead et al., 1990), and other ectotherms (frogs: Smith-Gill and Berven, 1979; fish: Gray, 1928). Packard and Packard (1988) suggested that embryos developing at high temperatures may have a higher metabolic rate, but a reduced metabolic efficiency (defined as the efficiency of converting energy reserves to tissue). As we did not measure residual yolk mass, we were unable to test this hypothesis in *P. muralis*.

Growth Rate and Sprint Speed of juveniles

Juveniles from eggs incubated at low temperatures (24 and 28 C) exhibited faster post-batch growth than their sibs from higher temperatures. The mechanisms that have caused this difference remain unknown. One possible explanation involves the observed relation between incubation temperature and hatchling sprint speed. *Podarcis muralis* is an active forager that relies on quick sprint bursts to capture the fast moving insects on which it preys (Avery, 1978). High sprint speed may also be advantageous to escape from predators (Christian and Tracy, 1981) and enhance survival (Jayne and Bennett, 1990). Similar unexpected effects of incubation temperature on locomotor capacity, predatory skills and escape behavior have been described in three species of snakes (Burger, 1989, 1990).

The combined effects of large size at hatching and high post-batch growth rate of the lizards incubated at 28 C resulted in these lizards being larger after 2 mo than their sibs incubated at higher temperatures. After 2 mo, the hatchlings incubated at 28 C had outgrown their sibs and thus compensated for their relatively late emergence. Such was, however, not the case for the 24 C hatchlings.

In many lizards, juvenile size is considered an important determinant of fitness. Large size may have several advantages. Large juveniles sprint faster (see also Si-

nervo and Adolph, 1989) and thus may be more successful in hunting prey (Avery et al. 1982), in avoiding predation (Christian and Tracy, 1981; Webb, 1986), and in retaining high social ranks (Garland et al. 1990). In species with high levels of intraspecific competition, large juveniles may have prior access to limited resources (Ferguson et al. 1982). Larger young seem to have better chances to survive their first active season (Ferguson and Fox, 1984; Fox, 1978) and winter (Ferguson and Bohlen, 1978), at least in some years. Finally, in many lizards, females can only reproduce when they have reached a certain minimum SVL (e.g. Barbault and Mou, 1988; Bauwens and Verheyen, 1987), and larger female juveniles may attain this minimum sooner.

Thermal Dependence of Embryogenesis

Our results have implications for the estimation of the optimal temperature of embryogenesis. Temperatures that minimize the time of incubation (32-35°C) were in clear conflict with those that maximize embryo survival, hatchling size, and post-hatch performances (24-28°C). Although hatchling size, post-hatch growth, and juvenile speed were highest at 24°C, incubation time was nearly twice that recorded at 28°C, resulting in a considerable reduction of the time available for post-hatch growth. At 28°C, hatching was only slightly postponed, and juveniles performed better than those incubated at higher temperatures. Hence, the optimal temperature for embryogenesis in *P. muralis* lies within the range 24-32°C, and is probably close to 28°C, the experimental temperature that produced the best balance between development rate, hatching success, and hatchling characteristics. This optimum is low compared to the body temperatures selected by adult *Podarcis muralis* in thermogradients ($x = 33.42^\circ\text{C}$, $1\text{ SE} = 0.15$, $n = 181$: Van Damme, unpublished data), temperatures maintained in the field ($x = 33.83^\circ\text{C}$, $1\text{ SE} = 0.17$: Braña, 1991), and substantially lower than the optimal temperature for sprint speed in adults of this species ($x = 36.8^\circ\text{C}$: Bauwens, unpublished

data). Actually, this may represent a case in favor of the multiple optima hypothesis (Huey, 1982). Discrepancies between optimal temperatures for adult performance and embryo development may induce the lower body temperatures maintained by female *P. muralis* during pregnancy (Braña, unpublished data). Parallel shifts in thermoregulatory set-points have been observed in gravid females of several viviparous lizards (Beuchat 1986, 1988; Garrick, 1974; Van Damme et al., 1986).

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LITERATURE CITED

- ANGEL, F. 1946. Faune de France, Vol. 45. Reptiles et Amphibiens. Libr. Fac. Sci. Paris.
- AVERY, R. A. 1978. Activity patterns, thermoregulation and food consumption in two sympatric lizard species (*Podarcis muralis* and *P. sicula*) from central Italy. *J. Anim. Ecol.* 47:143-158.
- AVERY, R. A., J. D. BEDFORD, AND C. P. NEWCOMBE. 1982. The role of thermoregulation in lizard biology: Predatory efficiency in a temperate diurnal basker. *Behav. Ecol. Sociobiol.* 11:261-267.
- BARBAULT, R. AND Y. P. MOU. 1988. Population dynamics of the common wall lizard, *Podarcis muralis*, in southwestern France. *Herpetologica* 44: 38-47.
- BAUWENS, D. AND R. F. VERHEYEN. 1987. Variation of reproductive traits in a population of the lizard *Lacerta vivipara*. *Holarct. Ecol.* 10:120-127.
- BEUCHAT, C. A. 1986. Reproductive influences on the thermoregulatory behavior of a live-bearing lizard. *Copeia* 1986:971-979.
- . 1988. Temperature effects during gestation in a viviparous lizard. *J. Therm. Biol.* 13:135-142.
- BRAÑA, F. 1991. Summer activity patterns and thermoregulation in the wall lizard, *Podarcis muralis*. *Herpetol. J.* 1:544-549.
- BRAÑA, F., A. BEA, AND M. J. ARRAYAGO. 1991. Egg retention in lacertid lizards: Relationships with reproductive ecology and the evolution of viviparity. *Herpetologica* 47:218-226.
- BROCKELMAN, W. Y. 1975. Competition, the fitness of offspring, and optimal clutch size. *Am. Nat.* 109: 677-699.
- BURGER, J. 1989. Incubation temperature has long-term effects on behavior of young pine snakes (*Pituophis melanoleucus*). *Behav. Ecol. Sociobiol.* 24: 201-207.
- . 1990. Effects of incubation temperature on behavior of young black racers (*Coluber constrictor*). 1971. Temperature and water tolerances of incubating sea turtle eggs. *Br. J. Herpetol.* 4: 196-198.
- CHRISTIAN, K. A. AND C. R. TRACY. 1981. The effect of the thermal environment on the ability of hatchling Galapagos land iguanas to avoid predation during dispersal. *Oecologia (Berl.)* 49:218-223.
- COOPER, J. S. 1958. Observations on the eggs and

- young of the wall lizard (*Lacerta muralis*) in captivity. *Brit. J. Herpetol.* 2:112-121.
- CYREN, O. 1934. Zur Kenntnis der Lacertiden der Iberischen Halbinsel und Makaronesiens. Göteborgs Kgl. Vetensk. vitterh. Samh. Handl. 4:1-64.
- DAMME, R. VAN, D. BAUWENS, A. M. CASTILLA, AND R. F. VERHEYEN. 1989. Altitudinal variation of the thermal biology and running performance in the lizard *Podarcis tiliguerta*. *Oecologia (Berl.)* 80: 516-524.
- DAMME, R. VAN, D. BAUWENS, AND R. F. VERHEYEN. 1986. Selected body temperatures in the lizard *Lacerta vivipara*: Variation within and between populations. *J. Therm. Biol.* 11:219-222.
- DMi'EL, R. 1967. Studies on reproduction, growth, and feeding in the snake *Spalerosophis cliffordi* (Colubridae). *Copeia* 1967:332-346.
- DUFAURE, J. P" AND J. HUBERT. 1961. Table de développement du lézard vivipare: *Lacerta (Zootica) vivipara* Jacquin. *Arch. Anat. mier. Morph. exp.* 50:309-328.
- FERGUSON, G. W" AND C. H. BOHLEN. 1978. Demographic analysis: A tool for the study of natural selection of behavioral traits. Pp. 227-243. *In* N. Greenberg and P. D. Maclean (Eds.), *Behavior and Neurology of Lizards*. U.S. Department of Health, Education and Welfare, National Institute of Mental Health, Rockville, Maryland.
- FERGUSON, G. W" AND T. BROCKMAN. 1980. Geographic differences of growth rate of *Sceloporus* lizards (Sauria: Iguanidae). *Copeia* 1980:259-264.
- FERGUSON, G. W" K. L. BROWN, AND V. G. DEMARCO. 1982. Selective basis for the evolution of variable egg and hatchling size in some iguanid lizards. *Herpetologica* 38:178-188.
- FERGUSON, G. W" AND S. F. FOX. 1984. Annual variation of survival advantage of large juvenile side-blotched lizards, *Uta stansburiana*: Its causes and evolutionary significance. *Evolution* 38:342-349.
- FERGUSON, G. W" AND H. L. SNELL. 1986. Endogenous control of seasonal change of egg, hatchling, and clutch size of the lizard *Sceloporus undulatus garmani*. *Herpetologica* 42:185-191.
- FERGUSON, M. J. W" AND T. JOANEN. 1982. Temperature of egg incubation determines sex in *Alligator mississippiensis*. *Nature* 296:850-853.
1983. Temperature-dependent sex determination in *Alligator mississippiensis*. *J. Zool.* 200: 143-177.
- FITCH, V. A. 1964. Temperature tolerances of embryonic *Eumeces*. *Herpetologica* 20:184-187.
- FOX, S. F. 1978. Natural selection on behavioral phenotypes of the lizard *Utastansburiana*. *Ecology* 59:834-847.
- FOX, W" C. CORDON, AND M. H. FOX. 1961. Morphological effects of low temperatures during the embryonic development of the garter snake, *Thamnophis elegans*. *Zoologica* 46:57-71.
- FRETEY, J. 1975. *Guide des Reptiles et Batraciens de France*. Hatier, Paris.
- GARLAND, T" JR" E. HANKINS, AND R. B. HUEY. 1990. Locomotor capacity and social dominance in male lizards. *Funct. Ecol.* 4:243-250.
- GARRICK, L. D. 1974. Reproductive influences on behavioral thermoregulation in the lizard *Sceloporus cyanogenys*. *Physiol. Behav.* 12:85-91.
- GRAY, J. 1928. The growth of fish. *M*. The effect of temperature on the development of the eggs of *Salmo fario*. *Br. J. Exp. Biol.* 6:125-130.
- GUTZKE, W. H. N" AND G. C. PACKARD. 1987. Influence of the hydric and thermal environments on eggs and hatchlings of bull snakes *Pituophis melanoleucus*. *Physiol. Zool.* 60:9-17.
- HUEY, R. B. 1982. Temperature, physiology, and the ecology of reptiles. Pp. 25-91. *In* C. Gans and F. H. Pough (Eds.), *Biology of the Reptilia*, Vol. 12. Academic Press, London.
- HUEY, R. B" W. SCHNEIDER, G. L. ERIE, AND R. D. STEVENSON. 1981. A field-portable racetrack and timer for measuring acceleration and speed of small cursorial animals. *Experientia* 37:1356-1357.
- JAYNE, B. C" AND A. F. BENNETT. 1990. Selection on locomotor performance capacity in a natural population of garter snakes. *Evolution* 44:1204-1229.
- KABISCH, K" AND W. E. ENGELMANN. 1969. Zur Nahrung von *Lacerta muralis* (Laurenti) in Ostbulgarien. *Zoologische Abhandlungen-Staatliches Museum für Tierkunde in Dresden* 30:89-92.
- LANG, J. W. 1985. Incubation temperature affects thermal selection of hatchling crocodiles. *Am. Zool.* 25:18A.
- LICHT, P" AND W. R. MOBERLY. 1965. Thermal requirements for embryonic development in the tropical lizard *Iguana iguana*. *Copeia* 1965:515-517.
- MERTENS, R. 1947. Die Lurche und Kriechtiere des Rhein-Main-Gebietes. Kramer, Frankfurt am Main.
- MILLER, J. D. 1985. Embryology of marine turtles. Pp. 269-328. *In* C. Gans, F. Billet, and P. F. A. Maderson (Eds.), *Biology of the Reptilia*, Vol. 14. Wiley, New York.
- MROSOVSKY, N" AND C. L. YNTEMA. 1980. Temperature dependence of sexual differentiation in sea turtles: Implications for conservation practices. *Biol. Conserv.* 18:271-280.
- MUTH, A. 1980. Physiological ecology of desert iguana (*Dipsosaurus dorsalis*) eggs: Temperature and water relations. *Ecology* 61:1335-1343.
- ÛSGOOD, D. W. 1978. Effect of temperature on the development of meristic characters in *Natrix fasciata*. *Copeia* 1978:33-37.
- PACKARD, G. C" AND M. J. PACKARD. 1988. The

- physiological ecology of reptilian eggs and embryos. Pp. 523-606. *In* C. Gans and R. B. Huey (Eds.), *Biology of the Reptilia*, Vol. 16B. Liss, New York.
- PACKARD, G. C." M. J. PACKARD, K. MILLER, AND T. J. BOARDMAN. 1987. Influence of moisture, temperature, and substrate on snapping turtle eggs and embryos. *Ecology* 68:983-993.
- PARENT, G. H. 1978. Contribution à la connaissance du peuplement herpetologique de la Belgique. Le caractère d'âge Atlantique de l'aire du lézard des murailles, *Lacerta muralis muralis* (Laurenti) au Benelux. *Nat. Belg.* 59:209-222.
- PHILLIPS, J. A." A. GAREL, G. C. PACKARD, AND M. J. PACKARD. 1990. Influence of moisture and temperature on eggs and embryos of green iguanas (*Iguana iguana*). *Herpetologica* 46:238-245.
- RAND, A. S. 1972. The temperatures of iguana nests and their relation to incubation optima and to nesting sites and season. *Herpetologica* 28:252-253.
- ROLLINAT, R. 1934. *La Vie des Reptiles de la France Centrale*. Delagrave. Paris.
- SEXTON, O. J." AND K. R. MARION. 1974. Duration of incubation of *Sceloporus undulatus* eggs at constant temperature. *Physiol. Zool.* 47:91-98.
- SINERVO, B. 1990. Evolution of thermal physiology and growth rate between populations of the western fence lizard (*Sceloporus occidentalis*). *Oecologia* (Berl.) 83:228-237.
- SINERVO, B." AND S. C. ADOLPH. 1989. Thermal sensitivity of growth rate in hatchling *Sceloporus* lizards: Environmental, behavioral and genetic aspects. *Oecologia* (Berl.) 78:411-419.
- SINERVO, B." AND R. B. HUEY. 1990. Allometric engineering: An experimental test of the causes of interpopulational differences in performance. *Science* 248:1106-1109.
- SMITH, C. C" AND S. D. FRETWELL. 1974. The (optima) balance between size and number of offspring. *Am. Nat.* 108:499-506.
- SMITH-GILL, S. J." AND K. A. BERVEN. 1979. Predicting amphibian metamorphosis. *Am. Nat.* 113:563-585.
- SPARREBOOM, M. 1981. *De Amfibieën en Reptielen van Nederland, België en Luxemburg*. Balkema, Rotterdam.
- STREET, D. 1979. *Reptiles of Northern and Central Europe*. Batsford, London.
- STRIJBOSCH, H" J. J. A. M. BONNEMAYER, AND P. J. M. DIETVORST. 1980. The northernmost population of *Podarcis muralis* (Lacertilia, Lacertidae). *Amphibia-Reptilia* 1:161-172.
- VINEGAR, A. 1973. The effects of temperature on the growth and development of embryos of the Indian python, *Python molurus* (Reptilia: Serpentes: Boidae). *Copeia* 1973:171-173.
- WEBB, G. J. W" AND H. COOPER-PRESTON. 1989. Effects of incubation temperature on crocodiles and the evolution of reptilian oviparity. *Am. Zool.* 29:953-971.
- WEBB, P. V. 1986. Locomotion and predator-prey relationships. Pp. 24-41. *In* M. E. Feder and G. V. Lauder (Eds.), *Predator-prey Relationships: Perspectives and Approaches from the Study of Lower Vertebrates*. University of Chicago Press, Chicago.
- WHITEHEAD, P. J., G. J. W. WEBB, AND R. S. SEYMOUR. 1990. Effect of incubation temperature on development of *Crocodylus johnstoni* embryos. *Physiol. Zool.* 63:949-964.

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