



The sooner the better: reproductive phenology drives ontogenetic trajectories in a temperate squamate (*Podarcis muralis*)

MAXIME LE HENANFF^{1,2*}, SANDRINE MEYLAN^{3,4} and OLIVIER LOURDAIS^{1,5}

¹Centre d'Études Biologiques de Chizé, CNRS, 79360 Villiers en Bois, France

²Université de Poitiers, 40 avenue du Recteur Pineau, 86022 Poitiers, France

³Laboratoire d'Ecologie, Université Pierre et Marie Curie, 7 quai Saint Bernard, Cedex 05, 75252 Paris, France

⁴IUFM de Paris-Université Sorbonne Paris IV, 10 rue Molitor, 75016 Paris, France

⁵School of Life Sciences, Arizona State University, Tempe, AZ 85287-4501, USA

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Understanding variations in individual trajectories is a crucial evolutionary issue. Terrestrial ectotherms from temperate regions typically face thermal constraints and limited activity periods. Developmental conditions (i.e. embryonic life) and reproductive timing (laying date) should induce phenotypic variations and influence subsequent ontogenetic trajectories (growth and survival). We studied these combined influences in an oviparous squamate, the wall lizard (*Podarcis muralis*), comprising a multiple clutch species with natural variations in laying date for the first clutch. We experimentally manipulated maternal basking opportunities during gravidity (3, 6 or 9 h per day) and incubation temperature (23 or 29 °C). Early laying date positively influenced winter survival in both incubation treatments. Survival was significantly lower in cool than warm-incubated individuals (14.8% and 73.6%, respectively) because of delayed hatching date and reduced activity period before winter. Individuals from cool incubation temperature were slightly smaller but had a higher body condition and grew faster during the first month of life. Offspring behaviour was driven by complex interactions between gravidity and incubation treatments. Under cool incubation temperature, defensive behaviour was high, independently of gravidity treatment. Warm incubated individuals showed low defensive response except when maternal basking opportunities were restricted to 3 h. Defensive behaviour at birth had a positive influence on survival in cool-incubated individuals. The results of the present study highlight the long-term influence of hatching date that integrates female reproductive timing and incubation conditions. © 2012 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2013, 108, 384–395.

ADDITIONAL KEYWORDS: cohort variation – long-term effects – phenotypic plasticity – timing of hatching – wall lizard.

INTRODUCTION

Fluctuations in biotic and abiotic conditions are important determinants of phenotypic variation because they can shape individual ontogenetic trajectories and individual performances. For example, early developmental conditions can have immediate effects

on birth weight and early growth (Sæther, 1997; Forchhammer *et al.*, 2001), as well as delayed, long-term effects on survival and breeding performance (Albon, Clutton-Brock & Guinness, 1987; Gaillard *et al.*, 1997; Lindström, 1999; Forchhammer *et al.*, 2001; Lindström & Kokko, 2002). Those effects can result in significant cohort variations (Albon *et al.*, 1987; Gaillard *et al.*, 1997; Descamps *et al.*, 2008) that have been reported in a diversity of taxa-like birds (Reid *et al.*, 2003; Van de Pol *et al.*, 2006), mammals (Albon *et al.*, 1987; Forchhammer *et al.*, 2001;

*Corresponding author.

E-mail: maximelehenanff@gmail.com

Gaillard *et al.*, 2003), and reptiles (Le Galliard, Marquis & Massot, 2010).

Cohort variations in phenotype (morphology, behaviour) and performance (growth, survival) have attracted significant interest in population biology (Albon *et al.*, 1987; Gaillard *et al.*, 1997; Forchhammer *et al.*, 2001; Descamps *et al.*, 2008; Le Galliard *et al.*, 2010). The clarification of proximate determinants of inter-individual variations in ontogenetic trajectories is a central issue (Padilla & Adolph, 1996). Cohort variations can result from reproductive timing (i.e. date of birth) (Feder *et al.*, 2008; Uller & Olsson, 2010; Wapstra *et al.*, 2010) and can profoundly affect individual trajectories (Ghalambor *et al.*, 2007). In addition, early (prenatal) developmental conditions constitute a critical time period for environmental influences (Clark & Galef, 1995; Henry & Uliaszek, 1996; Lindström, 1999; Metcalfe & Monaghan, 2001). Theoretical models predict that adaptive plasticity may occur when the inducing environmental cues offer reliable information, allowing close phenotype–environment matching (Moran, 1992; Reed *et al.*, 2010). Induced phenotypic variation can reflect phenotypic alteration or dynamic compensation and therefore require specific attention in a relevant ecological context (Shine, 2004).

Temperature is the major environmental variable influencing most physiological processes in ectotherms (Huey & Stevenson, 1979; Angilletta, Niewiarowski & Navas, 2002). For example, climatic conditions exert a direct influence on reproductive phenology and notably date of birth (Olsson & Shine, 1997; Qualls & Shine, 2000; Cadby *et al.*, 2010), which is a critical trait for reproductive success (Warner & Shine, 2007). Importantly, hatching date is a complex parameter because it integrates both maternal quality (laying date) and environmental conditions (incubation temperature) that exert a proximate influence on developmental rate (Andrews, 2004). In addition to phenology, thermal conditions during embryonic life have profound effects on offspring phenotype at birth, affecting a diversity of morphological, physiological, and behavioural traits (Deeming & Ferguson, 1991; Shine, Elphick & Harlow, 1997; Wapstra, 2000; Birchard, 2004; Blouin-Demers, Weatherhead & Row, 2004; Watkins & Vraspir, 2006) that can be fitness relevant (Andrews, Mathies & Warner, 2000; Braña & Ji, 2000; Du & Ji, 2003; Andrews, 2008). Thus, it is crucial to understand the relative contribution of phenology and phenotypic plasticity on individual performances and ontogenetic trajectories.

Under temperate climate, activity time of squamates can be particularly constrained by temperature (Adolph & Porter, 1993). Thermal constraints during development are frequent and likely to induce substantial cohort variations. For example, within year

variations can lead to contrasted hatching dates as well as phenotypic changes. Recent correlative studies in viviparous squamates reported that climatic conditions (rainfall and temperature) during development (embryogenesis and early juvenile life) affect offspring performance and induce significant cohort effects (Lourdais *et al.*, 2004; Baron *et al.*, 2010; Le Galliard *et al.*, 2010). Similar effects are expected in oviparous species (Elphick & Shine, 1998). Yet, most studies have focused on hatchling phenotype and early growth (Andrews *et al.*, 2000; Braña & Ji, 2000; Du & Ji, 2003), whereas long-term effects remain poorly studied (Elphick & Shine, 1998; Shine, 2004; Warner & Shine, 2007; Uller & Olsson, 2010).

In the present study, we examined the combined impact of reproductive phenology and developmental conditions in the wall lizard (*Podarcis muralis*) in Western Central France under a temperate climate. This multiple clutch species has an extended reproductive period and females show substantial variation in laying date (M. Le Hénanff, S. Meylan and O. Lourdais, unpubl. data). This context represents a good opportunity for addressing the effects of reproductive timing. In addition, we experimentally manipulated thermal conditions during development (maternal basking opportunities during gravidity and temperature during incubation). We quantified hatchling traits (morphology, thermal preferences, and defensive behaviour) and measured survival and growth over the first year. Our general hypothesis is that, in a constrained environment, phenology should have a prevalent impact on reproductive success. Specifically, we tested the following predictions:

1. Early laying date should positively influence offspring ontogenetic trajectories (growth and survival).
2. Delayed date of birth induced by cool developmental temperature should translate into altered offspring survival and growth.
3. Hatchlings developed under cool conditions should present compensatory responses to minimize the impact of delayed birth and increase individual performances in the post-natal environment.

MATERIAL AND METHODS

SPECIES AND STUDY AREA

The wall lizard *P. muralis* (Laurenti, 1768) is a small-sized Western and Central European lacertid lizard with an adult snout–vent length (SVL) of approximately 50–65 mm. This heliophilic species is an active thermoregulator that generally occupies open and stony habitats where cracks are used as refuges (Van Damme *et al.*, 1992). Winter emergence usually

occurs in February/March, whereas matings begin in April. Reproductive period is long (April to August) and females can lay up to three clutches per year (Mou, 1987). Embryonic stage at oviposition ranges from 25 to 29 in Dufaure & Hubert's (1961) classification (Braña, Bea & Arrayago, 1991). Gravid females have significantly lower preferred body temperature than nongravid females (32.6 °C and 34.0 °C, respectively) (Braña, 1993) but they bask more intensely (Tosini & Avery, 1996). The present study was conducted from spring 2009 until autumn 2010 at the Centre d'Etudes Biologiques de Chizé in Western Central France (46°07'N; 00°25'W) where a large population has been monitored since 2006 (over 1800 individuals marked). The study site is characterized by a temperate oceanic climate. Thermal conditions and notably maximal temperatures fluctuate seasonally and annually (Fig. 1).

HUSBANDRY OF GRAVID FEMALES

Gravid *P. muralis* females were captured during basking or when found under their nocturnal shelter. We only considered first annual clutches to prevent confounding effects such as a possible shift in maternal allocation among clutches. Reproductive status was assessed by abdominal palpation and ultrasounding (MicroMaxx, Sonosite, Inc.). Regular ultrasound monitoring indicates that gravidity period (from folliculogenesis to oviposition) lasts for approximately 2 weeks

(O. Lourdais, pers. observ.). Females that were diagnosed as early vitellogenic were immediately released to avoid captivity-induced reproductive failure. Similarly, females at late stages and very close to laying were excluded. We considered females ($N = 43$) with at least 7 days of exposure to basking treatment (mean \pm SD captivity time was 15.0 ± 6.4 days). Females were housed individually in plastic cages (Fauna Box, L: $41 \times$ W: $23 \times$ H: 17 cm) in a temperature-controlled room set at 20 °C. Cages were illuminated with an Osram Biolux 58W 3700 lm neon tube to provide ultraviolet light. Each cage was individually fitted with a 25-W spotlight at one end to establish a gradient temperature for basking. A basking support was installed to provide full access to the heat source, resulting in a thermal gradient of 21–40 °C. Water was provided *ad libitum* and individuals were fed *ad libitum* with crickets (*Acheta domesticus*) and mealworms (*Tenebrio molitor*) until oviposition. Females were released at the exact capture location 1 day after oviposition.

EXPERIMENTAL DESIGN

Our mark–recapture study showed that females differ in their reproduction timing resulting in substantial variation in first clutch laying dates (mean ordinal date: 135.4, range 111–181; M. Le Hénanff, S. Meylan and O. Lourdais, unpubl. data). This wide range of laying dates represents a good opportunity for

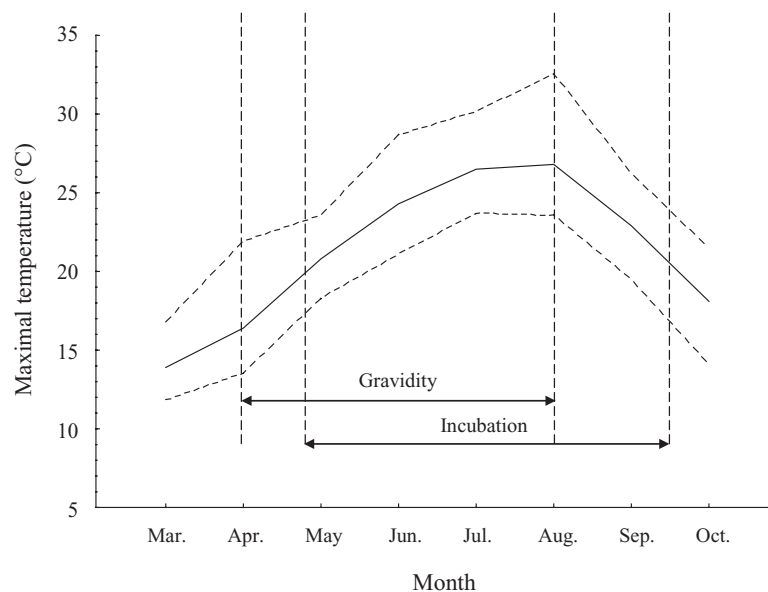


Figure 1. Thermal conditions (shaded air temperature 1.5 m above ground, Météo-France weather station) measured in Niort (46°19'N; 00°28'W) over the period 1990–2010. The full line represents mean monthly maxima and dashed lines represent lower and upper maximal temperatures. Source: Météo France. Relevant reproductive periods (gravidity and incubation) are designated between vertical dashed lines.

addressing the combined effects of timing of reproduction and developmental conditions on individual trajectories.

Most oviparous squamates retain eggs in the oviduct until one third of embryonic development is completed (Shine, 1983). Gravidity is often associated with a more precise maternal thermoregulation (Lourdais, Heulin & DeNardo, 2008). In the present study, we manipulated female basking opportunities during gravidity as well as incubation temperature (Fig. 2). We designed three gravidity treatments (Fig. 2) in which females were allowed to bask for 3 h ($N = 14$), 6 h ($N = 15$) or 9 h ($N = 14$) per day. The ecological relevance of this design is supported by operative temperatures collected in the study site. Using copper models (50 × 20 mm, painted brown), we found that time available at preferred body temperature (T_{set}) was variable, ranging from 1 to 8 h (mean 6.1 h) per day in early spring (M. Le Hénanff, unpubl. data). Gravid females were randomly assigned to one of the three treatments. Each cage was checked twice daily and freshly laid eggs were removed, weighed to the nearest 0.001g and half-buried in moistened vermiculite (2.5 g water/1 g vermiculite). After oviposition, we adopted a split-clutch design: each egg was transferred to one of two temperature-controlled chambers (FOC 225E; Velp Scientifica) with constant temperatures of 23 °C or 29 °C. These temperatures have been used in previous studies and represent contrasted but ecologically relevant incubation conditions (Van Damme *et al.*, 1992; Braña & Ji, 2000,

2007). In the monitored population, females use a diversity of nest sites that can be exposed to important diurnal fluctuations notably when close to ground surface (Lourdais, 2010). However, anthropogenic structures, including concrete pavement sidewalks or pavement roads, are also intensely used notably as communal laying sites (Lourdais, 2010). Such structures typically display very limited daily variations (Lelièvre *et al.*, 2010) but are exposed to important fluctuations (across months and years) that encompass experimental incubation temperatures selected in the present study.

HUSBANDRY OF HATCHLINGS

Hatchlings were sexed by eversion of the hemipenes. We weighed (± 0.001 g) and measured (SVL to the 0.1 mm) each hatchling ($N = 153$). Hatchlings were identified individually and placed in individual cages (same as above). We restricted daily basking period to 8 h. Water was regularly sprayed and available *ad libitum* in a small cup. Lizards were fed with crickets three times a week and were maintained under these conditions until 1 month. At 1 month of age, each individual was weighed, measured and its thermoregulatory and defensive behaviours were investigated (see below).

JUVENILE BEHAVIOUR

After 1 month of age, we recorded thermal preferences using a thermal gradient (temperature range

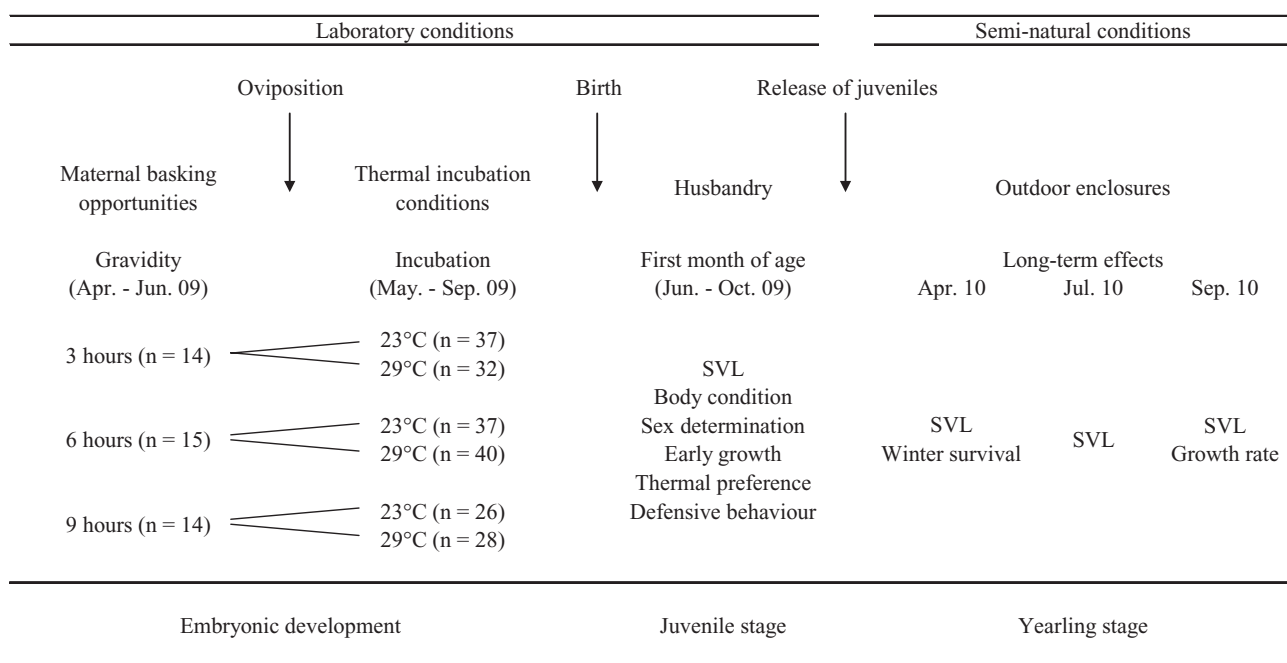


Figure 2. Experimental design used in the present study. SVL, snout–vent length.

20–42 °C; size 15 × 70 cm) placed in a temperature-controlled room (20 °C). Skin surface temperature (T_{sk}) was recorded using an infrared laser thermometer (Raytek Corporation) after 50 min. The measurement procedure was similar to that employed by Andrews (2008) and recommendations from Hare, Whitworth & Cree (2007) (emissivity set at 0.95 and the thermometer was oriented in-line with the lizard's body axis).

The next day, we quantified defensive behaviour using a behavioural procedure adapted from Bonnet *et al.* (2005) and Aubret, Michniewicz & Shine (2011). Before the trial, each individual was placed in a temperature-controlled chamber (FOC 225E; Velp Scientifica) set at 30 °C for at least 30 min to acclimate to the test temperature. With the left hand, we immobilized the whole body of the individual to avoid movements so that only the head was visible. With the right hand, we stimulated the lizard with a paintbrush for 1 min and we counted the number of bites elicited. Using that method a first bite is rapidly induced. Rather than a specific measure of defensive response this trait provides an estimate of stamina because some individuals get quickly exhausted, whereas others will keep on responding (M. Le Hénanff, pers. observ.).

COMMON GARDEN EXPERIMENT

At the age of 1 month, individuals were big enough to be individually identified by heat branding (Vervust & Van Damme, 2009) of ventral scales with disposable medical cautery units (Aaron Medical Change-A-Tip cautery low temperature units; Aaron Medical; http://boviemed.com/products_aaroncauterics_low.asp). Each individual was then randomly assigned to one of our eight outdoor enclosures (4 m × 4 m) and released. Each outdoor enclosure was fitted with underground shelters and central basking places (paving stones). The hatchlings densities and treatment proportions were the same in the enclosures. Individuals were later recaptured in April, July, and September 2010 to estimate wintering survival and growth.

STATISTICAL

We tested the effects of maternal basking opportunities and incubation temperature on phenology (incubation length), clutch characteristics (sex, egg mass), and hatchling morphology, as well as juvenile thermal preferences, defensive behaviour, growth, and survival. For phenology and clutch characteristics analyses, we used linear or generalized mixed models and performed analysis of variance (ANOVA) or analysis of covariance (ANCOVA) for each thermal

treatment with maternal basking opportunities and incubation temperature as fixed factors and female identity as a random factor. Interaction between the two treatments was tested using a two-way ANOVA. To address influence of gravidity and incubation treatments on hatching success and sex-ratio, we performed chi-squared tests by fixing theoretical results at 80% and 50%, respectively (*sensu* Ji & Braña, 1999, with a similar incubation temperatures range).

For hatchling traits analyses, we used linear mixed models and added mother identity as a random factor. We used egg mass as a covariate for analysis of SVL and hatchling body condition. SVL at hatching was a covariate for analysis of early growth. SVL growth was calculated as the difference in SVL divided by time interval. Hatchling body condition was calculated as residuals of the linear regression of body mass according to SVL. Maternal SVL adjusted clutch size (hereafter referred to as maternal investment) was calculated as residuals of the linear regression of clutch size according to SVL. To address long-term effects of developmental conditions on body size and growth, we performed ANOVAs or ANCOVAs using multiple data points for individual lizards (because they were measured consecutively) and we added mother identity as a random factor.

To analyze proximate determinants of survival, we performed linear mixed models and generalized linear mixed models) and used Akaike's information criterion (AIC) based model selection. Because incubation temperatures strongly impact phenological and phenotypical traits in lizards, each group was tested separately. We considered SVL and body condition at time of release, hatchling date, and defensive behaviour. Addition of maternal basking opportunities did not improve the models. We used stepwise backward elimination: we started with all predictors in the model and subsequently removed predictors one by one using AIC to select the best model. The best model is the model with the lowest AIC at the same time as using the fewest number of parameters. Two models differ when the difference in AIC between the two models is higher than 2 (White & Burnham, 1999).

We performed analyses with R software (R Development Core Team) using linear models (stats package), mixed models (nlme package) or generalized mixed models for survival analyses (lme4 package). We checked residuals of the models for normality and homoscedasticity, and computed Tukey's post-hoc tests to determine which treatment combinations were significantly different from the others. $\alpha < 0.05$ was considered statistically significant.

RESULTS

PHENOLOGY: INCUBATION LENGTH AND HATCHING DATE

Laying date was not influenced by maternal basking opportunities ($F_{2,40} = 1.31, P = 0.282$); mean ordinal date: $160.5 \pm 6.3, 150.8 \pm 5.0,$ and 148.2 ± 5.6 (3, 6, and 9 h, respectively, for basking treatments). Time to oviposition was not affected by maternal basking regime ($F_{2,40} = 1.38, P = 0.262$); mean \pm SE: $14.2 \pm 1.7, 16.6 \pm 2.0,$ and 12.7 ± 1.3 days (3, 6, and 9 h, respectively, for basking treatments).

We found that both female laying date ($F_{1,117} = 234.12, P < 0.001$) and incubation temperature ($F_{1,117} = 133.11, P < 0.001$) influenced hatching date with a significant interaction term ($F_{1,115} = 19.30, P < 0.001$) on hatching date. Incubation length was significantly affected by incubation treatment ($F_{1,117} = 18325.71, P < 0.001$; Table 1) but not by maternal basking opportunities ($F_{2,116} = 0.14, P = 0.865$; Table 1). Incubation duration was two-fold longer at cooler temperature (32.6 ± 0.2 days at 29°C versus 65.9 ± 0.3 days at 23°C).

CLUTCH CHARACTERISTICS

Mean clutch size (CS) was 5.5 eggs (range 3–11) and was independent of maternal basking opportunities ($F_{2,40} = 0.91, P = 0.412$). Maternal investment was not affected by maternal basking opportunities ($F_{2,40} = 0.86, P = 0.429$). Mean egg mass was independent of both CS ($F_{1,41} = 0.90, P = 0.348$) and maternal investment ($F_{1,41} = 1.74, P = 0.195$). Mean egg mass was not influenced by maternal basking opportunities ($F_{2,743} = 0.82, P = 0.433$). Neither CS, nor maternal investment influenced hatchling traits and so they were not retained as covariates in subsequent analyses.

Hatching success was independent of maternal basking opportunities ($\chi^2 = 0.61, \text{d.f.} = 2, P = 0.737$), incubation temperature ($\chi^2 = 0.61, \text{d.f.} = 1, P = 0.434$) or their interaction ($\chi^2 = 1.17, \text{d.f.} = 5, P = 0.948$; Table 1). Similarly, offspring sex was not influenced by basking or incubation treatments ($\chi^2, \text{all } P > 0.150$; Table 1). Because sex effects were not the main focus of the present study, males and females were pooled in subsequent analyses.

HATCHLING MORPHOLOGY

SVL at hatching was not affected by maternal basking opportunities ($F_{2,112} = 2.79, P = 0.066$; Table 1) but significantly influenced by incubation treatment. Hatchlings incubated at 23°C had slightly smaller SVL than those kept at 29°C ($F_{1,113} = 4.66, P = 0.033$; Table 1).

Body condition was not dependent on maternal basking opportunities ($F_{2,103} = 0.18, P = 0.835$; Table 1) but influenced by incubation treatment. Hatchlings

Table 1. Influence of maternal basking opportunities and incubation temperatures on clutches and hatchlings traits

Clutches and hatchlings traits	Maternal basking opportunities (h)			Incubation temperature ($^\circ\text{C}$)		Interactions
	3	6	9	23	29	
Incubation duration (days)	49.4 ± 2.3	$F_{2,116} = 0.14$ 48.5 ± 2.2	47.5 ± 2.6	65.9 ± 0.3	$F_{1,117} = 18325.71^{***}$ 32.6 ± 0.2	$F_{2,113} = 0.90$
Hatching success (%)	$76.8 (53/69)$	$\chi^2 = 0.61$ $72.7 (56/77)$	$81.5 (44/54)$	$73.0 (73/100)$	$\chi^2 = 0.61$ $80.0 (80/100)$	$\chi^2 = 1.17$
Proportion of males	$60.4 (32/53)$	$\chi^2 = 4.26$ $41.1 (23/56)$	$34.1 (15/44)$	$43.8 (32/73)$	$\chi^2 = 0.65$ $47.5 (38/80)$	$\chi^2 = 5.26$
SVL at birth (mm)	24.0 ± 0.2	$F_{2,112} = 2.79^{(1)}$ 24.3 ± 0.1	24.3 ± 0.2	24.1 ± 0.1	$F_{1,113} = 4.66^*$ 24.3 ± 0.2	$F_{2,109} = 2.65^\dagger$
Body condition at birth (residuals $\times 10^{-2}$)	0.2 ± 0.5	$F_{2,103} = 0.18$ 0.6 ± 0.6	0.2 ± 0.5	2.2 ± 0.4	$F_{1,104} = 55.09^{***}$ -1.7 ± 0.4	$F_{2,100} = 1.85$
Early growth (mm)	4.2 ± 0.2	$F_{2,90} = 1.39$ 3.9 ± 0.2	3.8 ± 0.2	4.2 ± 0.1	$F_{1,91} = 4.74^*$ 3.7 ± 0.2	$F_{2,87} = 2.67^\dagger$
T_{sk} ($^\circ\text{C}$)	37.7 ± 0.6	$F_{2,96} = 1.10$ 36.2 ± 0.8	37.4 ± 0.8	36.0 ± 0.6	$F_{1,97} = 7.87^{**}$ 38.3 ± 0.5	$F_{2,93} = 0.54$

Data are presented as the mean \pm SE. *** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$; $^\dagger P < 0.10$. SVL, snout-vent length; T_{sk} , skin surface temperature.

Table 2. Influence of maternal basking opportunities and incubation treatment on defensive behaviour in hatchlings wall lizards in Western Central France

Effect tested	ANOVA of the model			
	numDF	denDF	<i>F</i>	<i>P</i>
Maternal basking opportunities	2	109	3.56	0.032
Intercept	1	109	311.68	<i>P</i> < 0.001
Incubation temperature	1	110	4.19	0.043
Intercept	1	110	382.89	<i>P</i> < 0.001
Interaction	2	106	3.65	0.029
Intercept	1	106	314.89	<i>P</i> < 0.001

Thermal treatments were considered as fixed factors, whereas maternal ID was included as a random factor. ANOVA, analysis of variance; num, numerator; den, denominator; DF, degrees of freedom.

incubated at 23 °C were in higher body condition ($F_{1,104} = 55.09$, $P < 0.001$; Table 1) than those incubated at 29 °C.

OFFSPRING BEHAVIOUR AND EARLY GROWTH

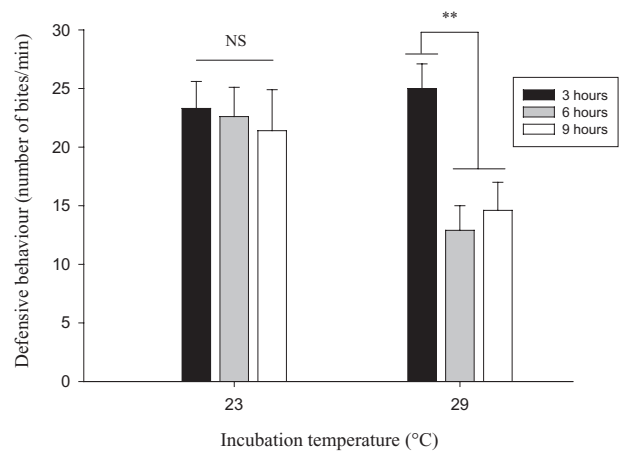
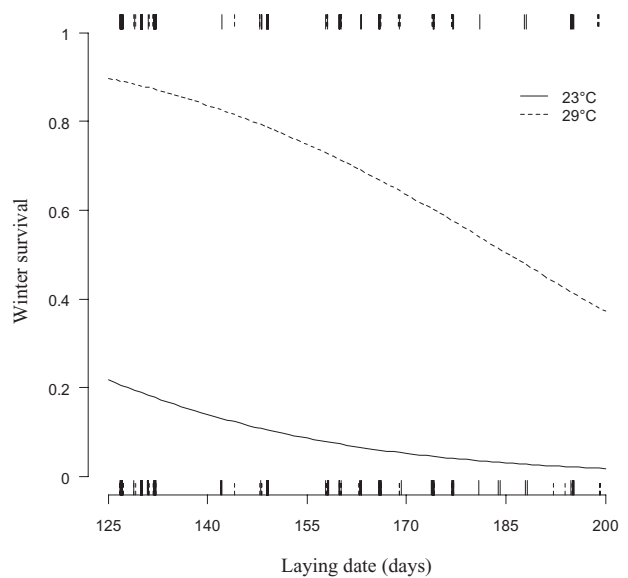
We found no influence of maternal basking opportunities on T_{sk} ($F_{2,96} = 1.10$, $P = 0.336$; Table 1) but a significant impact of incubation temperature ($F_{1,97} = 7.87$, $P = 0.006$; Table 1). The T_{sk} of cool-incubated individuals was 2.3 °C lower compared to warm-incubated ones (36.0 °C versus 38.3 °C).

Defensive behaviour was affected by maternal basking opportunities ($F_{2,109} = 3.56$, $P = 0.032$), incubation temperature ($F_{1,110} = 4.19$, $P = 0.043$), and the interaction between treatments ($F_{2,106} = 3.65$, $P = 0.029$; Table 2). In cool-incubated individuals, defensive behaviour was high, independently of the maternal basking opportunities ($F_{2,44} = 0.13$, $P = 0.875$; Fig. 3). In warm-incubated individuals, defensive behaviour was high only when the maternal basking opportunities were reduced (3 h) ($F_{2,46} = 5.58$, $P = 0.007$; Fig. 3).

SVL growth over the first month of life was negatively influenced by SVL at hatching ($F_{1,92} = 23.97$, $P < 0.001$). When adjusted for SVL at hatching, early growth was not affected by maternal basking opportunities ($F_{2,90} = 1.39$, $P = 0.255$; Table 1) but was highest in hatchlings incubated at 23 °C ($F_{1,91} = 4.74$, $P = 0.032$; Table 1).

LONG-TERM EFFECTS

Incubation temperature significantly affected winter survival ($z = 6.70$, $P < 0.001$). Survival rate of hatch-

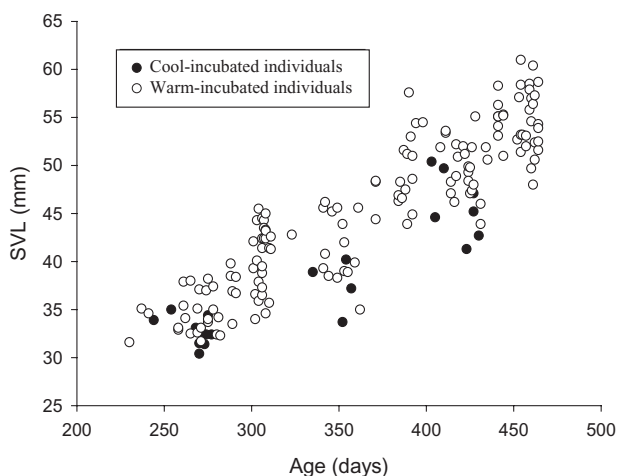
**Figure 3.** Influence of maternal basking opportunities and incubation temperature on defensive behaviour at 1 month of age in juvenile wall lizards in Western Central France. Data are presented as the mean \pm SE. NS, not significant.**Figure 4.** Influences of laying date and incubation temperature on winter survival in juvenile wall lizards in Western Central France. The full line represents warm-incubated individuals and the dashed line represents cool-incubated individuals.

lings incubated at 23 °C was approximately five-fold lower than those incubated at high temperature (14.8% versus 73.6%). Laying date negatively influenced winter survival within each incubation treatment (Fig. 4). Within cool-incubated individuals, the best-fitting model for survival included laying date and defensive behaviour (Table 3). Within warm-incubated individuals, the best-fitting model included laying date and SVL at time of release (Table 3). After adjusting for

Table 3. Proximate determinants of winter survival according to incubation temperature in yearling wall lizards in Western Central France

Parameters tested	d.f.	23 °C		29 °C	
		AIC	ΔAIC	AIC	ΔAIC
SVL1 + BC1 + Lay. + Def. behav.	6	58.32	3.24	84.49	3.42
SVL1 + BC1 + Lay.	5	61.54	6.45	82.94	1.87
SVL1 + BC1 + Def. behav.	5	60.87	5.78	89.22	8.15
SVL1 + Lay. + Def. behav.	5	56.39	1.30	82.63	1.57
BC1 + Lay. + Def. behav.	5	57.07	1.99	86.53	5.46
SVL1 + Lay.	4	60.02	4.93	81.07	0.00
SVL1 + Def. behav.	4	59.87	4.79	87.38	6.31
Lay. + Def. behav.	4	55.09	0.00	84.54	3.47
SVL1	3	–	–	85.65	4.58
Lay.	3	59.33	4.24	83.66	2.59
Def. behav.	3	58.84	3.75	–	–

The function with the lowest Akaike's information criterion (AIC) is the one that best describes the data. The selected model is shown in bold. SVL₁, snout–vent length at 1 month; BC₁, body condition at 1 month; Lay, laying date; Def. behav., defensive behaviour.

**Figure 5.** Influence of age and incubation temperature on body size during post-wintering recaptures of yearling wall lizards in Western Central France. SVL, snout–vent length.

age, we found a significant impact of incubation conditions on body size measured in autumn 2010 ($F_{1,34} = 10.93$, $P = 0.002$; Fig. 5). Cool-incubated individuals were significantly smaller than warm-incubated ones (45.9 ± 1.3 mm and 52.6 ± 0.5 mm, respectively). SVL growth was positively influenced by incubation temperature (1.5 ± 0.1 versus 1.9 ± 0.1 mm month⁻¹; $F_{1,35} = 14.67$, $P < 0.001$).

DISCUSSION

Developmental conditions affect a diversity of traits in squamates, although a significant proportion of the

variation induced can be reversible and a rapid compensation after hatching is known to occur (O'Steen & Janzen, 1999; Shine, 2004; Stahlschmidt & DeNardo, 2009). The consideration of long-term effects is therefore critical (Shine, 2004) and a central question is to understand to what extent phenology or induced phenotypic variation explain individual trajectories (Shine, 2004; Ghalambor *et al.*, 2007). In the present study, we investigated the combined impact of female reproductive timing (laying date) and developmental conditions in a temperate (i.e. time limited) context. We addressed both short-term (morphology) and long-term effects (growth and survival).

Basking treatment had no influence on laying date, which therefore reflected natural variation in female reproductive timing. Similarly, variations in basking opportunities had no impact on offspring morphology. However, early developmental stages are presumably particularly sensitive to perturbations (Shine, 2004; Lorigou *et al.*, 2012). These negative results may be related to the fact that, despite females being exposed to an extended period of basking treatment (15.0 ± 6.4 days on average), they were not captured at the exact same stage of gravidity. Also, contrasted behavioural responses (basking intensity) to treatment may have occurred.

We found that hatching success was high and similar in all treatments combination. Hatching date was strongly dependent on female laying date and incubation treatment. Eggs incubated at 23 °C hatched approximately 1 month later than siblings incubated at 29 °C. As expected, offspring sex was independent of gravidity and incubation treatments (Van Damme

et al., 1992; Ji & Braña, 1999). Hatchlings experiencing cool temperatures were slightly smaller than siblings incubated in warm conditions. Small hatchling body size and delayed hatching date negatively affect individual trajectory and fitness (Warner & Shine, 2007; Uller & Olsson, 2010). In accordance with a previous study on this species (Ji & Braña, 1999), cool-incubated embryos grew faster during their first month of life. Catch-up growth has been studied and reported in a wide range of taxa (Arendt, 1997; Metcalfe & Monaghan, 2001; Radder, Warner & Shine, 2007) and body size has been demonstrated as a major determinant of overwinter survival (Civantos, Salvador & Veiga, 1999; Smith, 2002). Body condition was significantly higher in cool-incubated embryos and can support catch-up growth as observed in other studies (Ji & Braña, 1999; Baron *et al.*, 2010).

Besides phenology and morphology, we found a marked influence of thermal treatment on offspring behaviour. First, incubation temperature influenced thermal preferences at 1 month of age. Cool-incubated individuals had T_{set} approximately 2 °C lower than warm-incubated ones. Such a response to developmental conditions has been previously reported in different species (Blouin-Demers, Kissner & Weatherhead, 2000; Blumberg, Lewis & Sokoloff, 2002; Belliure & Clobert, 2004) and may be advantageous in a cool post-natal environment. Second, our estimate of defensive behaviour was influenced by a complex interaction between gravidity and incubation treatments, with low temperature inducing higher defensive behaviour. In cool-incubated individuals, defensive behaviour was high and independent of maternal basking opportunities. In turn, in warm-incubated individuals, defensive behaviour was high only when maternal basking opportunities were reduced (3 h). Late hatching date coincides with high intraspecific competition (Volkl, 1989; Madsen & Shine, 1998), cool environments, and limited feeding opportunities (Elphick & Shine, 1998). These factors can alter individual performance and affect growth (Olsson & Shine, 1997; Qualls & Shine, 2000). The behavioural modifications reported in the present study (higher defensive behaviour and lower preferred temperatures) may thus represent compensatory embryonic responses to optimize individual performances in a constraining (cool) post-natal environment. Increased defensive behaviour reported in late born hatchlings could be the result of a maternal influence, such as corticosteroid deposition in egg yolk (Thompson, 1957; Takahashi *et al.*, 1988; Mousseau & Fox, 1998; Meylan, de Fraipont & Clobert, 2004; Meylan & Clobert, 2005).

Although thermal treatment had no impact on hatching success we found a strong influence on subsequent growth and survival. Individuals incubated at 23 °C had substantially low survival rate (14.8%)

compared to those experiencing warm conditions (73.6%), most likely because of the negative effects of the timing of hatching. Hatching date drives activity period before wintering (Olsson & Shine, 1997; Uller & Olsson, 2010). Extended activity in early hatched individuals can result in increased food intake, growth, and energy stores, as well as enhanced winter survival (Bauwens, 1981; Olsson & Shine, 1997, 1998; Warner & Shine, 2007). Not only is the activity period available for growth reduced in late hatched individuals, but also it is altered by cool post-natal environmental temperatures (Fig. 1). Early hatched individuals are likely to experience long-term benefit that can be considered a 'silver-spoon effect' (Grafen, 1988; Madsen & Shine, 2000; Qualls & Shine, 2000).

Importantly, survival was negatively influenced by female laying date within the two incubation groups (early laying date favouring survival). A previous study has reported that improved offspring performances can result from phenological maternal effects (Wapstra *et al.*, 2010). Laying date can be considered as correlate of female quality (Olsson & Shine, 1997), with high-quality individuals capable of starting reproduction early in the season when environmental constraints (temperature & food resource) are stronger. Beside laying date, we observed a positive influence of body size at the time of release (warm incubation treatment) or defensive behaviour (cool incubation) on survival. Our results suggest that the phenotypic determinants of offspring quality are not constant but depend on date of birth and associated constraints (either biotic or abiotic). Defensive behaviour resulted from complex interactions between gravidity and incubation treatments. Defensive behaviour was higher in cool-incubated individuals and positively related to survival, thereby supporting for a compensatory response to low incubation temperature as reported in several oviparous reptiles (Du *et al.*, 2010). The proximate mechanisms underlying this relation are not clear and are worthy of specific study. Because lizards were not exposed to predation, defensive behaviour at birth could be of particular importance with respect to both interspecific and intraspecific interactions (Civantos, 2000; Lind & Cresswell, 2005) by lizards in terms of more efficient food acquisition during the critical period before winter (Civantos, 2000). Finally, we found a significant influence of incubation treatment on annual growth rate and body size at 1 year of age. Growth was altered in the cool-incubated individuals, whereas these individuals exhibited catch-up growth during the first month of life. As a result, warm-incubated individuals were significantly longer than surviving cool-incubated ones at 1 year of age. Body size at maturity influences reproductive performances in lizards (Uller & Olsson, 2010) and the developmental effects reported in the present study are

likely to entail such long-term impact on individual performances and fitness.

Overall, the results reported in the present study highlight the complex interactions between female reproductive timing (laying date) and developmental conditions (gravidity and incubation) and their influence on offspring ontogenetic trajectories. In a constrained environment, early laying date is beneficial by favouring offspring survival. Although thermal treatment had no impact on hatching success, induced variation in date of birth resulted in both numerical cohort effects (differences in survival) and delayed quality cohort effects (altered growth rates) (Gaillard *et al.*, 2003; Le Galliard *et al.*, 2010). Finally, the findings of the present study suggest possible compensatory responses to cool incubation temperatures. Further studies are required to explore in more detail the links between female reproductive timing, embryonic responses, and population dynamics.

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