

# Timing of locomotor impairment and shift in thermal preferences during gravidity in a viviparous lizard

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## Summary

1. Locomotor impairment and shift in thermal preferences during gestation have been documented in some lizards, but few studies have investigated their timing. Here, endurance capacity, sprint speed and selected body temperature of gravid females of the viviparous lizard *Lacerta vivipara* (Jacquin) were measured weekly before and after parturition.

2. Significant temporal variation of endurance and sprint speed was detected. A marked decrease in locomotor abilities occurred 2 weeks before parturition (c. 35% for endurance and 25% for sprint speed). A rapid recovery was observed a few days after parturition for endurance, while sprint speed recovered more slowly.

3. A physical impairment due to body mass was detected for endurance capacity, but not for sprint speed. The recovery of locomotor abilities after parturition was independent of the intensity of reproductive investment. Mass-independent variation in locomotor performances might be explained by physiological consequences of reproduction independent of the physical burden.

4. Females basking under laboratory conditions selected low body temperatures during the final month of gestation ( $29.8\text{ }^{\circ}\text{C} \pm 0.12\text{ SE}$ ) and a drastic increase occurred in the few days following parturition ( $33.4\text{ }^{\circ}\text{C} \pm 0.13\text{ SE}$ ).

5. These results call for a more detailed investigation of the mechanisms underlying trade-offs between reproduction, locomotion and thermoregulation in lizards.

*Key-words:* Costs of reproduction, *Lacerta vivipara*, locomotion, reproductive burden, thermoregulation

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## Introduction

A reduction in the reproductive value associated with current reproduction has been observed in many species and has been called costs of reproduction (Reznick 1985). In squamates, reproductive costs in females might result from a reduction in sprint speed, jumping distance or endurance capacity (among other locomotor abilities) associated with gravidity (Shine 1980). The role of locomotor performances has been emphasized because locomotion can act as an intermediate between the physiology, morphology and behaviour of an individual and the components of its lifetime reproductive success (Arnold 1983; Bennett & Huey 1990; Garland & Losos 1994; Irschick & Garland 2001). Locomotor performances depend on metabolic capacities, musculature strength and body shape of individuals (e.g. Bauwens *et al.* 1995; Garland 1993). Locomotor performances set physiological limits on ecologically

relevant tasks, such as foraging, predator avoidance or mate-searching abilities (Bennett & Huey 1990), although empirical evidences of this link are still scant (Garland & Losos 1994; Irschick & Garland 2001). Therefore, a reduction in locomotor performances could impact the future reproductive value of gravid females (e.g. Miles, Sinervo & Frankino 2000).

Reproductive trade-offs involve several physiological components, such as hormones with pleiotropic effects, resource allocations or the physical mass burdening (Shine 1980; Schwarzkopf 1994; Sinervo 1999). For example, both physical and physiological modifications associated with gestation can decrease locomotor performances. Increased body mass raises the energetic costs of transport, reduces body manoeuvrability and diminishes ventilation abilities in many lizards (Schwarzkopf 1994; Miles *et al.* 2000). These effects are likely to result in a 'physical burden' on locomotor capacities during gestation (Shine 1980). Physiological modifications associated with reproduction, such as changes in steroid profiles, can also influence locomotor performances in the short term, for example through

direct effects on metabolic pathways, and in the long term, for example through a muscle attrition process. These effects are likely to result in a 'physiological burden' on locomotor capacities during and after gestation (review in Olsson, Shine & Bak-Olsson 2000).

Locomotor costs of reproduction can also be influenced by the thermoregulation behaviour of gravid females. In most lizards, locomotor performances reach maximum values over a species-specific optimal thermal breadth (Huey & Kingsolver 1989). Typically, lizards basking freely achieve body temperatures within this range, provided thermoregulation is not constrained by the environment (e.g. van Damme, Bauwens & Verheyen 1987). However, body temperature is also strongly linked with embryonic development, implying possible conflicts between multiple thermal optima during gravidity (Huey & Kingsolver 1989). It has been found that female lizards usually exhibit different body temperatures during pregnancy through behavioural preferences or through constraints on basking activities (e.g. Brana 1993; Mathies & Andrews 1997). Such shifts in thermoregulation could affect locomotor abilities in the wild, reducing or enhancing the locomotor costs of reproduction depending on whether body temperature increases or decreases during gestation.

Although some studies have identified changes in locomotion and thermoregulation associated with reproduction in reptiles, the timing and proximate determinants of these variations have been more rarely examined. Comparisons between gravid and postparturient females have indicated that performances are smaller before than after parturition (review in Schwarzkopf 1994). However, such changes may have fewer ecological consequences if they occur only during a short time period. To overcome this problem, we collected weekly repeated measurements of locomotor performances and thermal preferences on gravid females of the Common Lizard *Lacerta vivipara* (Jacquin), a viviparous ground-dwelling species. We addressed three problems successively. First, we analysed temporal changes in sprint speed and endurance capacity from 1 month before parturition to 2 weeks after parturition, a time scale much larger than previous studies. This allowed us to observe both the impairment of locomotor capacities during gestation, and the recovery process after parturition. Second, we studied the effects on locomotor changes of variations in body mass during gestation and parturition. If changes in locomotor performances during reproduction are driven by a 'physical burden', most temporal variations in locomotion could be explained by body mass changes (Olsson *et al.* 2000). In contrast, a 'physiological burden' on locomotion during reproduction would imply that locomotor performances varied independently from changes in body mass. Third, we also observed shifts in thermal preferences under laboratory conditions, therefore excluding most environmental constraints on thermoregulation (Huey 1974).

## Materials and methods

### COLLECTION AND MAINTENANCE OF FEMALES

A sample of 19 gravid female Common Lizards was collected in the Cévennes (South France) between 25 and 28 May 2001 in one local population (44°25' N, 3°46' E). Individuals were measured for length and body mass to the nearest millimetre and micrometre, respectively. Animals were transferred to the Ecological Research Station of Foljuif (Seine-et-Marne) on the 29 May. We then maintained females under standard conditions in individual terraria (25 × 15 × 15 cm<sup>3</sup>). Terraria were heated on one side with an incandescent bulb (25 W) from 09.00 to 12.00 h and from 14.00 to 17.00 h local time which provided a gradient from room temperature (19–24 °C night–day) to 35–37 °C, encompassing the thermal breadth of the Common Lizard (van Damme, Bauwens & Verheyen 1986). Animals were fed every fourth day with a moth larva (*Pyralis* sp.) or a large cricket (*Acheta domestica*). After parturition, postpartum females were isolated from offspring, measured for body mass, fed once with one moth larva, and then maintained under the same conditions. Relative clutch mass (ratio of clutch mass to postparturition body mass) and clutch size were measured. Photoperiod was naturally imposed and one fluorescent UV-light bulb was added every 4 days (Iguana Light 5.0 UV-B, ZooMed, 40 W, San Luis Obispo, USA).

### MEASUREMENT OF LOCOMOTOR PERFORMANCES

Locomotor performances (endurance, sprint speed) and selected body temperatures were characterized during seven 8-day intervals from 18 June to 8 August. Data were collected in the following daily order: endurance (3 days after feeding), thermoregulation (with food provided *ad libitum*) and sprint speed. Endurance and sprint speed were measured by the same person. All measurements were completed on lizards heated during 30 min at 32 °C (± 1 °C).

Endurance was measured by running each lizard on a horizontal, circular treadmill covered with cork to ensure traction (external diameter 61 cm, internal diameter 41 cm). The treadmill was maintained between 30 and 31 °C with two heat lamps (120 W). The lizard was stimulated to run at a constant speed (*c.* 0.66 km h<sup>-1</sup>) and motivated after each stop with soft brush taps behind the tail. The running was stimulated until exhaustion of the animal, as estimated from the loss of a righting response after strong stimulations on the tail (Sorci *et al.* 1995; Clobert *et al.* 2000). Endurance was measured during the morning (9.00–12.00 h local time) in a random order, and calculated as the time elapsed during the trial (to the closest second). The number of stops per unit distance was recorded to index the 'motivation' of each lizard during a locomotor trial, as advised by

some authors (Tsuji *et al.* 1989; Bennett & Huey 1990; Sorci *et al.* 1995). Body mass was measured at completion of running. These measurements of endurance capacity have been found to be repeatable (repeated measurements on yearlings in 2000,  $r = 0.87$ ,  $F_{44,45} = 10.42$ ,  $P < 0.001$ ,  $n = 45$  individuals,  $N = 90$  observations; Lessells & Boag 1987).

A sprint speed value was obtained on a 1-m length linear racetrack covered with cork from four repeated trials spaced by 30 min. The length of racetrack was preferred to shorter intervals because we wanted to measure sprint speed along an ecologically relevant flight distance for the species, as estimated from two previous studies (Bauwens & Thoen 1981; Lecomte, Clobert & Massot 1993). The lizard was run on 30 cm to avoid the initial acceleration phase (Huey & Hertz 1984), and then chased along the racetrack with a soft brush. Taps were given with the brush when the lizard stopped, and the total number of taps was recorded. The highest sprint speed of the four trials and the corresponding number of stimulations were retained for analysis. Body mass was measured at the end of the running. The four sprint speed measurements obtained during the seven measurements all indicated significant repeatability ( $r > 0.23$ ,  $P < 0.006$ ).

#### MEASUREMENT OF SELECTED BODY TEMPERATURE

Selected body temperature was measured on pairs of females housed in large terraria ( $130 \times 47 \times 35 \text{ cm}^3$ ) heated on one side with an incandescent bulb (40 W) from 09.00 to 17.00 h local time. The thermal gradient ranged from room temperature (19–20 °C) at the end of the terrarium to 40 °C under the bulb. We thought that pooling two individuals did not bias our measurements because Patterson & Davies (1978) observed that Common Lizards tested alone or in groups had similar body temperatures. Furthermore, we found no resemblance in daily averages of body temperatures among individuals within terraria ( $F_{9,44} = 0.45$ ,  $P = 0.90$ ). We reduced costs of thermoregulation by providing food and water *ad libitum*, and by arranging under the heat lamp a substrate used for basking and hiding (15 cm long, 5 cm wide). Lizards were placed in the terraria the evening before measurements to permit acclimation, and observations were obtained from repeated sampling every 45 min from 9.30 to 12.30, and from 14.15 to 16.30 h local time. Cloacal temperature was measured with a K-thermocouple thermometer (Hanna Instruments, K-thermocouple 1.5 mm, 0.2 °C accuracy, Ann Harbor, USA). The repeatability of this protocol between two successive days has been established on adults ( $r = 0.66$ ,  $P = 0.002$ ,  $n = 20$ ,  $N = 40$  observations).

#### STATISTICAL ANALYSES

All analyses were performed with the SAS statistical software, and repeated measurements were analysed

with covariance models using PROC MIXED (Littell *et al.* 1996). We used the Shapiro–Wilk tests of normality of residuals and Bartlett tests of variance homogeneity. Endurance data were log-transformed to meet these assumptions. A covariance structure was selected from the suite provided by the statistical procedure using the Akaike Criterion Index (Littell *et al.* 1996). To test differences between pairs of sessions, we used the adjusted Tukey's multiple comparison for differences of least-square means.

The effect of time varying covariates on locomotor performances was not analysed with a standard regression, because this method assumes independence among observations from the same individual (Diggle, Liang & Zeger 1994). Rather, we conducted a regression accounting for the repeated-measure design using a covariance structure in PROC MIXED. To disentangle the between- and within-subject effects of body mass and 'motivation' (number of stops per unit distance) on locomotor changes, we calculated for each covariate the mean per individual over the sessions (between-subject component) and the difference from the mean for each session (within-subject component; Neuhaus & Kalbfleisch 1998). We then used locomotor performance as a response variable in a regression including the mean and deviation of all predictor variables as factors.

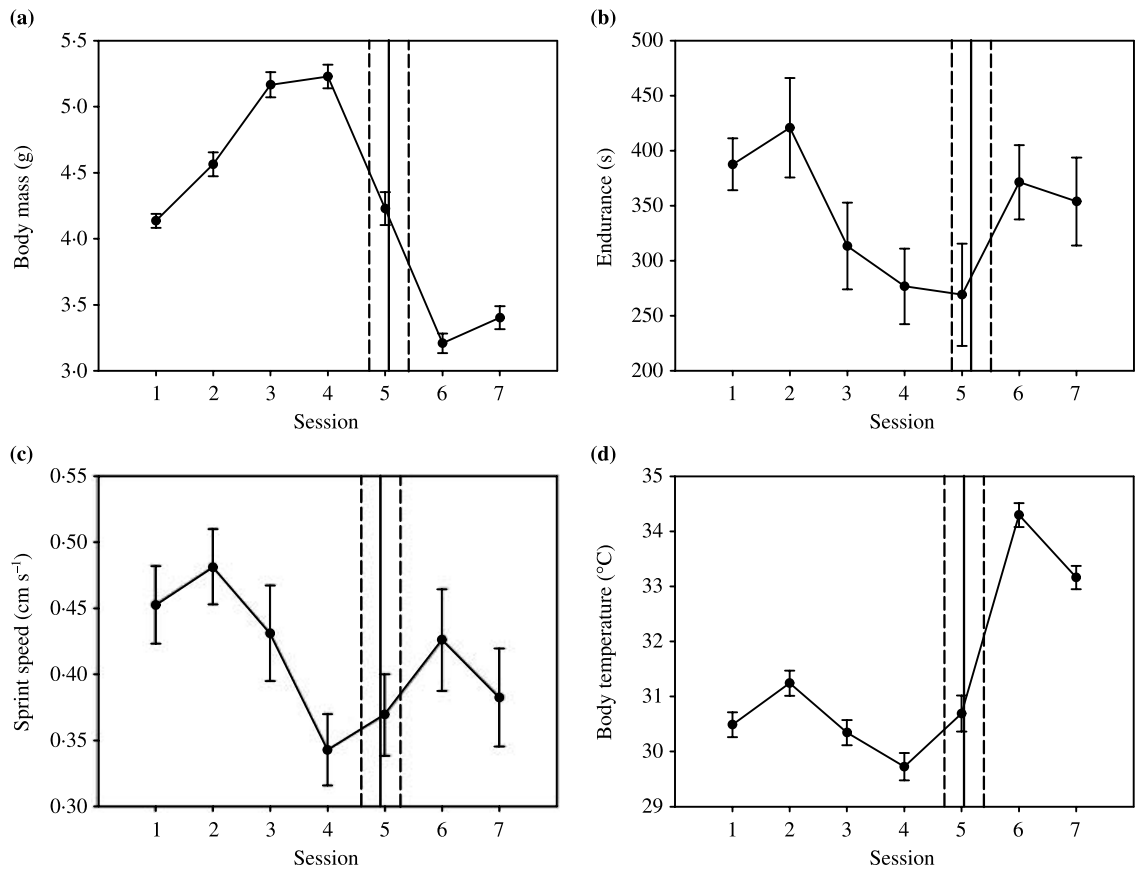
## Results

#### TIMING OF THE REPRODUCTIVE BURDEN

Body length did not change during measurements, and body mass was used to index reproductive burden. Body mass varied significantly during gestation ( $F_{6,108} = 26.98$ ,  $P < 0.001$ ,  $N = 133$  observations, Fig. 1a). Body mass increased from the start of the measurements (adjusted Tukey's multiple comparison, all  $P < 0.001$ ), and reached a plateau in the last week before parturition (sessions 3 and 4 in Fig. 1a). Mass decreased strongly at parturition, resulting in the loss of 53% ( $\pm 3$  SE) extra-mass relative to postparturition levels (average date: 21 July  $\pm 3$  days SD; clutch size:  $5.7 \pm 0.4$  SE).

#### TIMING OF THE LOCOMOTOR IMPAIRMENT

A significant temporal variation for both endurance and sprint speed was detected (log-transformed endurance,  $F_{6,108} = 5.38$ ,  $P < 0.001$ ,  $N = 133$  observations; sprint speed,  $F_{6,108} = 5.65$ ,  $P < 0.001$ , Fig. 1b,c). Endurance capacity decreased from the first two measurements to the fifth measurement, and then quickly returned close to its initial state (Tukey's tests,  $P < 0.05$  between sessions 1–2 and 5 and between session 5 and sessions 6–7, Fig. 1b). Endurance capacity reached a minimum level during the last week of gestation ( $250 \text{ s} \pm 46.4$  SE). This reduction equalled approximately 35% of the values observed at the start of gestation and following parturition (initial value:  $387 \text{ s} \pm 23.6$  SE, postparturition



**Fig. 1.** Timing of reproductive burden, locomotor impairment and shift in thermal preferences in the Common Lizard: (a) individual body mass (g,  $\pm$  SE) of gravid females; (b) female endurance capacity (time (s) spent on the racetrack,  $\pm$  SE); (c) sprint speed ( $\text{cm s}^{-1}$ ,  $\pm$  SE); and (d) average daily temperature ( $^{\circ}\text{C}$ ,  $\pm$  SE). An 8-day time lag separated each session. The average parturition date ( $\pm$  SD) is indicated as a line in each frame.

value:  $371 \text{ s} \pm 33.7 \text{ SE}$ ). Sprint speed decreased from the first three measurements to the fourth measurement (Tukey's test,  $P < 0.05$  between session 1–3 and 4, between session 2 and sessions 4–5, Fig. 1c). Sprint speed reached minimum values during the last week of gestation ( $0.34 \text{ m s}^{-1} \pm 0.03 \text{ SE}$ ), a relative reduction corresponding to 25% of the initial value ( $0.45 \text{ m s}^{-1} \pm 0.03 \text{ SE}$ ).

We found a significant repeatability of individual differences in locomotor performances over the seven sessions (log-transformed endurance, intraclass correlation coefficient:  $r = 0.30$ ,  $F_{18,114} = 3.98$ ,  $P < 0.0001$ ; sprint speed,  $r = 0.55$ ,  $F_{18,114} = 9.69$ ,  $P < 0.0001$ ). Therefore, individual differences in locomotor performances were consistent despite variability within each individual during gestation. This would not have been expected if the directions and intensities of locomotor changes were different among individuals.

#### PROXIMATE DETERMINANTS OF LOCOMOTOR IMPAIRMENT

The number of stops per unit distance varied significantly among sessions for endurance ( $F_{6,108} = 2.54$ ,  $P = 0.02$ ), but not for sprint speed ( $F_{6,108} = 1.62$ ,  $P = 0.15$ ). In the case of endurance, the number of stops was lower during late gestation compared with other sessions

(sessions 1–3:  $0.46 \text{ stops round}^{-1} \pm 0.04 \text{ SE}$ , session 4:  $0.65 \text{ stops round}^{-1} \pm 0.09 \text{ SE}$ , session 5:  $0.83 \text{ stops round}^{-1} \pm 0.15 \text{ SE}$ , sessions 6–7:  $0.49 \text{ stops round}^{-1} \pm 0.05 \text{ SE}$ ).

We estimated the proximate determinants of locomotor impairment using the first five sessions (see Table 1). Regression of endurance with time, body mass and number of stops showed that both body mass and number of stops contributed to the temporal variation. Endurance was negatively correlated with body mass, indicating that an increase in body mass was associated with a decrease in endurance capacity. Also, the number of times the lizard stopped per unit distance was negatively correlated with endurance capacity. The residual endurance obtained from the joint regression of endurance on body mass and number of stops was still varying between sessions: residual endurance decreased progressively from the first to the fifth measurement, although only the comparison between sessions 2 and 5 was significant (Tukey's test,  $P = 0.04$ ).

Sprint speed variations were different from those in endurance capacity on two points (Table 1). First, body mass had no significant effect on sprint speed. However, as for endurance data, the number of stops correlated negatively with sprint speed. Second, most temporal variation of sprint speed remained unexplained by 'motivational' changes or mass increase. Residual sprint

**Table 1.** Effect of body mass, 'motivation' (stops per unit distance) and session on repeated measures of locomotor performances during impairment (five first sessions). Bracketed terms are slopes ( $\pm$  SE) of the regression. Similar results were obtained when body size was controlled for in the analysis

|                                | Endurance                                    | Sprint speed                         |
|--------------------------------|--|--------------------------------------|
| <b>Between-subject effects</b> |  |                                      |
| Body mass                      | $F_{1,16} = 3.95^{\dagger} (-0.09 \pm 0.04)$ | $F_{1,16} = 0.44 (-0.01 \pm 0.02)$   |
| Number of stops                | $F_{1,16} = 6.68^* (-0.52 \pm 0.20)$         | $F_{1,16} = 3.12 (-0.14 \pm 0.08)$   |
| <b>Within-subject effects</b>  |  |                                      |
| Body mass                      | $F_{1,70} = 11.6^{***} (-0.31 \pm 0.09)$     | $F_{1,70} = 0.83 (-0.01 \pm 0.02)$   |
| Number of stops                | $F_{1,70} = 9.31^{***} (-0.33 \pm 0.11)$     | $F_{1,70} = 4.55^* (-0.03 \pm 0.01)$ |
| Session                        | $F_{4,70} = 3.08^*$                          | $F_{4,70} = 5.59^{***}$              |

$^{\dagger}0.05 < P < 0.10$ ,  $^*P < 0.05$ ,  $^{**}P < 0.01$ ,  $^{***}P < 0.001$ .

speed from the model incorporating the number of stops and body mass decreased after the second session, and reached a minimum during the fourth session (Tukey's tests between session 2 and sessions 3–4,  $P < 0.02$ ). Therefore, locomotor impairment for sprint speed was concomitant with, but apparently not driven by, the mass burden.

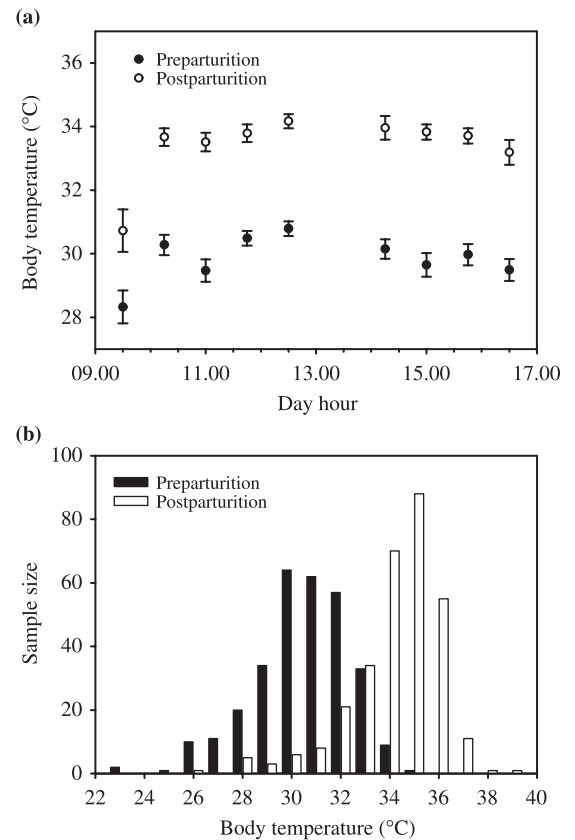
#### LOCOMOTOR RECOVERY

An analysis of locomotor recovery was conducted using the closest preparturition and postparturition measurements. We found an increase of endurance and sprint speed after parturition, although it was only marginally significant for sprint speed (endurance,  $F_{1,18} = 16.69$ ,  $P = 0.0007$ ; sprint speed,  $F_{1,18} = 4.30$ ,  $P = 0.053$ ). Endurance increased from  $196.7 \text{ s} \pm 21.4 \text{ SE}$  before parturition to  $365.7 \text{ s} \pm 42.6 \text{ SE}$ , a proportional 46% recovery. Sprint speed increased from  $0.35 \text{ m s}^{-1} \pm 0.03 \text{ SE}$  before parturition to  $0.39 \text{ m s}^{-1} \pm 0.03 \text{ SE}$ , only a 10% proportional recovery. The number of stops was not significantly different before and after parturition for endurance ( $F_{1,18} = 0.49$ ,  $P = 0.49$ ) or sprint speed ( $F_{1,18} = 1.66$ ,  $P = 0.21$ ).

If the locomotor recovery is due to the physical relaxation associated with parturition, we should find a correlation between locomotor changes and mass loss. Differences between locomotor performances after and before parturition were therefore regressed against the individual mass loss. There was no correlation between the change in endurance and sprint speed on one side and the change in body mass during parturition on the other side (endurance:  $r = -0.13$ ,  $F_{1,17} = 0.30$ ,  $P = 0.59$ ; sprint speed:  $r = 0.06$ ,  $P = 0.81$ ). Relative clutch mass (RCM) and total clutch size were also not correlated with endurance recovery (endurance, RCM:  $r = -0.31$ ,  $P = 0.20$ ; clutch size:  $r = 0.11$ ,  $P = 0.66$ ), or sprint speed recovery (RCM:  $r = -0.22$ ,  $P = 0.36$ ; clutch size:  $r = -0.16$ ,  $P = 0.52$ ).

#### SELECTED BODY TEMPERATURE

Body temperature was affected by the hour of the day (ANOVA,  $F_{8,1116} = 25.02$ ,  $P < 0.0001$ , lizard identity as a



**Fig. 2.** Thermoregulation before and after parturition in the Common Lizard: (a) mean selected body temperature ( $^{\circ}\text{C}$ ,  $\pm$  SE) of females before (sessions 3–4) and after parturition (sessions 6–7) during the day ( $N = 38$  observations per day hour); and (b) probability distribution of body temperatures before and after parturition after excluding the first daily measurement.

random effect,  $n = 19$  individuals,  $N = 1197$  observations). Both gravid and postparturient females had lower body temperatures at the start of the day (Fig. 2a). Because we were interested in body temperatures of active lizards, we excluded data from the first observation, which could be confounded with emergence time. We then used the daily average body temperature to measure the selected body temperature. A repeated measurement analysis on this variable detected highly

**Table 2.** Thermal preferences before (sessions 3–4) and after parturition (sessions 6–7) following on the conventions of Bauwens *et al.* (1995). The preferred body temperature (PBT) was estimated as the median of the thermal distribution. The temperature breadth was estimated as the central 80% of body temperature observations (TB). Minimum and maximum body temperatures observed are also indicated.  $N = 342$  observations

|                    | Average temperature ( $^{\circ}\text{C} \pm \text{SE}$ ) | PBT ( $^{\circ}\text{C}$ ) | TB ( $^{\circ}\text{C}$ ) | $T_{\min}$ ( $^{\circ}\text{C}$ ) | $T_{\max}$ ( $^{\circ}\text{C}$ ) |
|--------------------|--|----------------------------|---------------------------|-----------------------------------|-----------------------------------|
| Before parturition | 29.8 $\pm$ 0.12  | 29.5                       | 5.3 (27.0, 32.3)          | 21.6                              | 34.8                              |
| After parturition  | 33.4 $\pm$ 0.13  | 34.1                       | 4.8 (30.7, 35.5)          | 22.5                              | 38.4                              |

significant temporal variation ( $F_{6,108} = 43.31$ ,  $P < 0.0001$ ). The temporal change followed a two-step pattern (Fig. 1d): gravid females selected lower temperatures before parturition (average: 30.5  $^{\circ}\text{C} \pm 0.15$  SE for sessions 1–4) than after parturition (average: 33.7  $^{\circ}\text{C} \pm 0.13$  SE for sessions 6–7; Tukey's contrasts between first and second period, all  $P < 0.001$ ).

The daily variance in body temperature, a measure of the stability of thermoregulation, was not different among sessions (Bartlett's test,  $\chi^2 = 6.47$ ,  $\text{df} = 6$ ,  $P = 0.37$ ). This homogeneity of variance was explained by the fact that both maximum and minimum daily temperatures shifted during pregnancy (maximum,  $F_{6,108} = 25.22$ ,  $P < 0.0001$ ; minimum,  $F_{6,108} = 19.44$ ,  $P < 0.0001$ ). The minimum and maximum daily temperatures increased following parturition (preparturition minimum: 27.9  $^{\circ}\text{C} \pm 0.28$  SE, postparturition: 31.8  $^{\circ}\text{C} \pm 0.34$  SE; maximum: 32  $^{\circ}\text{C} \pm 0.19$ , and 35.4  $^{\circ}\text{C} \pm 0.15$  SE, respectively). To summarize, gravidity was associated with a downward shift in thermal preferences affecting the whole thermal distribution, and a drastic upward shift occurred after parturition (Fig. 2b, Table 2).

## Discussion

We observed a significant reduction in locomotor performances during mass burdening. Relative to postparturition values, the reduction was on the same order of magnitude as for sprint speed (*c.* 10–40%) and endurance data (*c.* 40–60%) of other lizards (review in Schwarzkopf 1994). Also, as in most studies (Shine 1980; Bauwens & Thoen 1981; Garland 1985; Cooper *et al.* 1990; Schwarzkopf & Shine 1992; Qualls & Shine 1997), parturition was associated with an increase in performance abilities. However, sprint speed performances recovered more slowly. Concomitant with these locomotor changes, we observed a shift in selected body temperatures: females selected lower average body temperature during gestation than after parturition.

### SIGNIFICANCE OF LOCOMOTOR CHANGES

Temporal variations in locomotor performances during gestation could originate from (1) gestation effects (Olsson *et al.* 2000), (2) seasonal variations in locomotor performances independently of gestation, (3) acclimation to laboratory conditions, or (4) training and fatigue effects (Garland *et al.* 1987). Training and acclimation effects on locomotion have little support

in lizards (Garland *et al.* 1987; Gleeson 1979; Snell *et al.* 1988). Also, it is unlikely that our trials have been deleterious, because measurements were obtained at sufficiently spaced intervals, and we even observed significant increases in performances at some stages. The second option is more difficult to reject because locomotor performance could vary independently from reproductive burden. However, the matching between mass burdening, timing of parturition and temporal variations of locomotor abilities has very little chance of being accidental. A more rigorous proof could be obtained by comparing gravid females with non-gravid females from the same populations, or by manipulating reproductive effort of adult females (e.g. Miles *et al.* 2000).

### LOCOMOTOR IMPAIRMENT AND RECOVERY

Our results show that gravid females suffered from a reduction in locomotor performances during late gestation, recovered quickly their endurance capacities after parturition, but recovered their sprint speed abilities more slowly. There was a significant individual effect on locomotor performances, suggesting parallelism in locomotor changes among individuals. To our knowledge, similar investigations on the timing of locomotor costs of reproduction in squamates have only been incidental. Indeed, most studies have compared pre- and postparturition locomotion to measure recovery (defined as the increase in locomotor performances during parturition), while the impairment phase (defined as the decrease in locomotor performances during gravidity) has been generally disregarded. Seigel, Huggins & Ford (1987) found a decreasing pattern of locomotor performances during gravidity in one snake species, with a minimum for endurance during late gestation and for sprint speed during mid-gestation. In contrast, Olsson *et al.* (2000) observed a reduction in sprint speed performance of female skinks only after parturition. In one oviparous lizard, endurance capacity decreased continuously during gestation, as estimated from covariation with the size of the follicle (Miles *et al.* 2000). Also, Sinervo, Hedges & Adolph (1991) reported that sprint speed increased significantly with time after oviposition, suggesting long-lasting recovery of sprint speed ability. Such variations of locomotor performances before and after parturition may occur in many species, and may be one reason for inconsistencies across studies in the ability to detect

locomotor costs of reproduction (Schwarzkopf 1994). For example, sprint speed could decrease during gestation and recover extremely slowly after parturition, if investment in reproduction reduces condition and musculature. In this scenario, the recovery of locomotor performances observed at parturition would be low, and we might wrongly conclude that the costs of reproduction are small, while, when measured long before parturition, they might turn out to be strong.

#### PROXIMATE DETERMINANTS OF LOCOMOTOR CHANGES

Studies on impairment and recovery are likely to yield similar results if change in locomotor ability is explained only by the physical mass burdening of gravid females. In our study, we were able to investigate the effects of body mass, 'motivation' (number of stops) and independent time-varying factors on locomotion. First, we observed a decrease in 'motivation' during gestation, and found a negative correlation between the number of stops and locomotor performances. Such an effect could illustrate a covariation between locomotor capacities and behavioural factors (Schwarzkopf & Shine 1992; Garland & Losos 1994). Second, locomotor recovery was independent of reproductive effort, but body mass affected endurance capacity during impairment. This suggests that the endurance impairment could be driven by the physical burden of reproduction. Higher body mass can increase the energetic costs of transport and decrease body manoeuvrability or ventilation capacity, all of which are important for sustained aerobic efforts during endurance trials (Garland & Losos 1994). The fact that sprint speed, an anaerobic performance, does not decrease for similar reasons is not completely surprising. Indeed, comparative studies within and among species have found that sprint speed relates mostly to muscular structure and body shape, while endurance capacity depends upon body mass and aerobic metabolism (Bennett & Huey 1990). Finally, time-varying factors independent from body mass or 'motivation' affected sprint speed and endurance, especially during recovery. This suggests some important physiological effects of gestation not associated directly to the physical burden, such as modifications due to hormones or musculature shape (e.g. Olsson *et al.* 2000). These patterns call for a more detailed investigation of the physiological mechanisms underlying trade-offs between reproduction and locomotion.

#### SELECTED BODY TEMPERATURE

Females selected lower average body temperature during gestation than after parturition, and body temperatures after parturition were similar to values reported in other populations (Patterson & Davies 1978; van Damme *et al.* 1986, 1987; van Damme, Bauwens & Verheyen 1990; Bauwens *et al.* 1995). Similar modifica-

tions associated with reproduction have been observed in other lizards (Shine 1980; Beuchat 1986; Daut & Andrews 1993), with body temperature being higher during gestation in some cases (Stewart 1984; Brana 1993).

The lower body temperature during gestation was achieved by a downward shift in the thermal distribution (Stewart 1984; Beuchat 1986). Field data on this species also indicated a decrease in body temperature during gravidity (Heulin 1987; van Damme *et al.* 1987). Our results show that this modification partly results from an active selection. The stringent association between thermal preferences and the timing of parturition also suggests that both are linked (Patterson & Davies 1978; van Damme *et al.* 1987). Furthermore, thermal requirements were independent from the physical burden. This contradicts the hypotheses that body temperature is lower during gestation because of a reduction in warming speed due to mass burdening (Claussen & Art 1981), or because of a hypoxia due to impairment of ventilation ability (Beuchat 1986). In fact, this pattern might be explained by endocrinological modifications. For example, progesterone levels are affected by gestation and change the selected body temperature (Garrick 1974). Also, abrupt modifications in corticosterone profiles at parturition could induce the rapid thermal shift observed in our study (de Fraipont *et al.* 2000).

A shift in selected temperatures during gravidity can be adaptive if thermoregulation affects mothers and offspring fitness differently. Body temperatures higher than 31–32 °C optimize energy acquisition and fat storage (van Damme, Bauwens & Verheyen 1991), ability to escape predators (van Damme *et al.* 1990) and gestation speed (Mathies & Andrews 1997). Therefore, gravid females should select body temperatures similar to postparturient females. However, thermal environment can also modify embryonic success and life-history traits of neonates (e.g. Mathies & Andrews 1997; Angilletta, Winters & Dunham 2000). In cell cultures of the Common Lizard, embryos developed optimally around 27 °C *in vitro*, which is lower than the preferred adult body temperature during summer (Maderson & Bellairs 1962). Therefore, the body temperature of mothers during embryological development (*c.* 30 °C) was intermediate between *in vitro* and maternal optima. This might indicate that maternal behaviour helps to resolve a parent–offspring conflict on thermoregulation.

#### THERMOREGULATION AND LOCOMOTION

According to our thermal measurements, gravid females should spend less time basking during the day, should be less active during warmer periods and should be more cryptic. These behavioural modifications associated with gestation have indeed been observed in the Common Lizard (Bauwens & Thoen 1981; Lecomte *et al.* 1993). Usually, however, such changes from flight to cryptic strategies have been attributed to predation (Brodie 1989; Cooper *et al.* 1990; Schwarzkopf & Shine

1992). Our data indicate that thermal requirements might be another reason, although the distinction between thermal and antipredation strategies warrants further studies. The two strategies are complementary here because a cryptic behaviour decreases both visibility toward predators (Bauwens & Thoen 1981) and basking (Lecomte *et al.* 1993).

Locomotor costs of reproduction will depend on performances realized under natural conditions rather than on locomotor abilities measured under laboratory conditions (Hertz, Huey & Garland 1988; Irschick & Garland 2001). This means that shifts in body temperature have to be accounted for. Because gravid females selected lower body temperatures during late gestation, locomotor costs of reproduction are likely to be higher than predicted by our laboratory study. For example, sprint speed increases with body temperature up to an optimal thermal range of 32–35 °C in this species (van Damme *et al.* 1990), which is higher than the thermal preferences displayed during gestation. Therefore, measurements of locomotor abilities should be obtained under a larger range of body temperatures in the future. Of particular interest is the problem of whether differences between gravid and postparturient females are consistent across a thermal range.

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