Mating Does Not Influence Reproductive Investment, in a Viviparous Lizard

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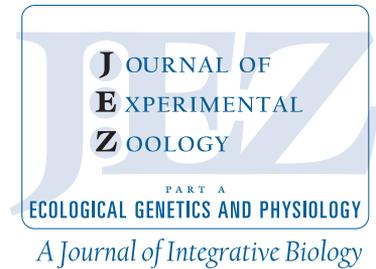
ABSTRACT
Mating is crucial for females that reproduce exclusively sexually and should influence their investment into reproduction. Although reproductive adjustments in response to mate quality have been tested in a wide range of species, the effect of exposure to males and mating per se has seldom been studied. Compensatory mechanisms against the absence of mating may evolve more frequently in viviparous females, which pay higher direct costs of reproduction, due to gestation, than oviparous females. To test the existence of such mechanisms in a viviparous species, we experimentally manipulated the mating opportunity of viviparous female lizard, *Lacerta* (*Zootoca*) *vivipara*. We assessed the effect of mating on ovulation, postpartum body condition and parturition date, as well as on changes in locomotor performances and body temperatures during the breeding cycle. Female lizards ovulated spontaneously and mating had no influence on litter size, locomotor impairment or on selected body temperature. However, offspring production induced a more pronounced locomotor impairment and physical burden than the production of undeveloped eggs. Postpartum body condition and parturition dates were not different among females. This result suggests that gestation length is not determined by an embryonic signal. In the common lizard, viviparity is not associated with facultative ovulation and a control of litter size after ovulation, in response to the absence of mating. *J. Exp. Zool. 315:458–464, 2011.* © 2011 Wiley-Liss, Inc.

Reproductive investment strategies involve trade-offs over resource allocation to number and quality of offspring versus self growth and maintenance; they are crucial determinants of female lifetime reproductive success (Roff, 2002). Mating is crucial for female fitness in species with exclusively sexual reproduction. Reproductive adjustments in response to mate quality, such as differential allocation, have been tested in a wide range of species (Sheldon, 2000; Harris and Uller, 2009). However, mating per se may be much more important for female fitness than mating with

a better or a lower quality male. Surprisingly, the effect of exposure to males and mating per se has seldom been studied. Some species are spontaneous ovulators, whereas others are facultative ovulators that do not invest in reproduction at all when they are not stimulated by mating. Facultative ovulation is common in many mammals (for review see Kauffman and Rissman, 2006), but relevant data for squamate reptiles are scarce (for lizards, see Crews et al., '86; and for snakes, see Mendonça and Crews, '90; DeNardo and Autumn, 2001; Mathies et al., 2004).

An absence of mating may influence reproductive investment at different times in the reproductive cycle, depending on the reproductive mode. Viviparity (live-bearing) enables adaptive maternal manipulations of offspring phenotypes during gestation and facilitates postfertilization adjustments of reproductive effort (Bernardo, '96)–two key advantages that can favor this reproductive mode over oviparity (egg-laying). Evolutionary transitions from oviparity to viviparity have occurred more than 100 times and relatively recently in squamate reptiles (Blackburn, 2006). Contrary to mammals, in most viviparous squamate reptiles, mother–embryo exchange of organic nutrients is of reduced importance: females supply most of them directly into the egg yolk (lecithotrophy, Blackburn, '98a). Therefore, follicle and egg production requires almost comparable investment in oviparous and viviparous females. On the other hand, viviparous females retain their eggs for a longer period than oviparous females, and this long period of gestation is associated with significant locomotor and thermoregulatory costs (Olsson et al., 2000; Ladyman et al., 2003; Le Galliard et al., 2003; Shine, 2003; Lin et al., 2008). Viviparous females, therefore, pay a higher direct cost of reproduction than oviparous females. We, therefore, expect compensatory mechanisms against the absence of mating to evolve more frequently in viviparous females, including facultative ovulation but also adjustments of reproductive effort postovulation. Reproductive adjustments could indeed occur after ovulation through selective expulsion or resorption (as observed in mammals, Morton et al., '82).

We set up an experiment to test whether female common lizards *Lacerta* (*Zootoca*) *vivipara* are facultative ovulators and whether the expected postovulation adjustments exist. We manipulated mating opportunities in the laboratory and assessed the influence of the absence of mating on ovulation (number of eggs) as well as on changes in locomotor performances and behavior during the breeding cycle. Pregnant females select lower body temperatures during gestation, due to a trade-off between their optimal temperature and the one of their embryos, and have a lower endurance capacity (Le Galliard et al., 2003). Therefore, we measured the selected body temperature and endurance capacity once before the manipulation of mating opportunities and several times after this treatment, i.e., during gestation and once after parturition. We expected that unmated females would not ovulate if common lizards are facultative ovulators, or would produce smaller litters than mated females, if females can expel or resorb some unfertilized eggs. We also expected stronger changes in locomotor performances and body temperatures in mated than in unmated females.

MATERIAL AND METHODS

Model Species

L. vivipara is a small (50–70 mm adult snout-vent length, SVL) ground-dwelling lizard widely distributed across Eurasia. We studied a viviparous strain originating from natural populations of the Massif Central mountain range (South-eastern France) maintained before hibernation in outdoor enclosures at our field station (CEREEP, 48°17′N, 2°41′E, Central France). For females, mating occurs 0–3 days after hibernation, and reproductive investment (vitellogenesis) occurs on average during the first three weeks (Bauwens and Verheyen, '85). During gestation, a primitive chorioallantoic placenta allows respiratory, aqueous and mineral exchanges between mother and embryos (Panigel, '56; Stewart et al., 2009). Parturition occurs when embryos are fully developed, after an average gestation period of 2 months. The mean litter size is five (range from 1 to 12) including undeveloped eggs (fertilized or unfertilized eggs where only yolk is visible), stillborn and live offspring. Live offspring hatch immediately and are autonomous.

Experimental Conditions

Adult females and males were maintained before hibernation in separate outdoor enclosures at our field station. Enclosures were surrounded by plastic walls to prevent lizards from escaping (see Fitze et al., 2008 for a description of field enclosures). The start of the mating period was determined in mixed-sex populations located in the same meadow. Once mating was detected in the mixed-sex populations, individuals were captured (from 2nd to 7th of April), weighed (to the nearest milligram), measured for SVL (to the nearest millimeter), and transferred to the laboratory for mating. Females and males were maintained in separate rooms during this period. Females ($n = 30$) were randomly allocated to one of the two treatment groups: mated or unmated group (Fig. 1). Females of the two treatment groups did not differ in initial SVL ($F_{1,28} = 0.11$, $P = 0.74$) or body condition ($F_{1,27} = 1.63$, $P = 0.21$, body mass with SVL as a covariate). Mating experiments were conducted from 8th to 15th of April following the protocol of Fitze et al. (2008, 2010): females were released into large boxes (2,500 cm^2) and thereafter a randomly selected male was introduced. Mating trials were observed for 1 hr and males were removed after 1 hr or, if mating lasted longer, 5 min after the end of the copulation. Unmated females were handled in the same way as mated females, but no males were introduced in their box. After the mating experiments, females were released in their outdoor enclosures. They were recaptured during the first week of May and then maintained under standardized laboratory conditions until parturition (Le Galliard et al., 2003). Two females probably died in the

Figure 1. Experimental design. Females were experimentally mated or not. Within each treatment, we observed only a few nonreproductive females. Within reproductive females, we observed: mated females that produced offspring, mated females that produced undeveloped eggs and unmated females that produced undeveloped eggs.
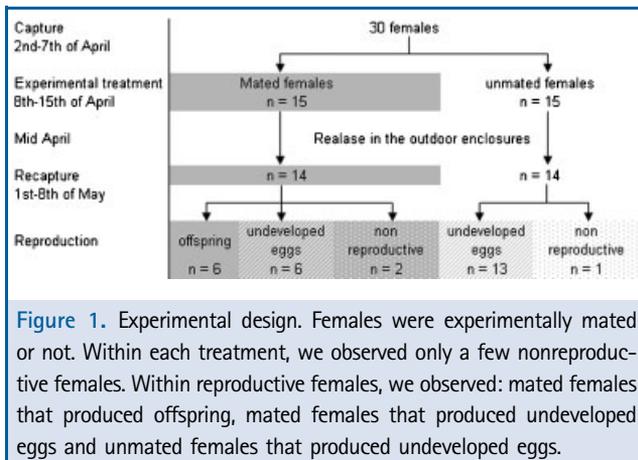
enclosures and were not recaptured (Fig. 1). Females were weighed every 4 days before parturition and once immediately after parturition. The authors attest the adherence to the *National Institutes of Health Guide for Care and Use of Laboratory Animals.*

Direct Costs of Reproduction and Investment in Reproduction

We assessed the costs of reproduction with indirect measures: endurance capacity, selected body temperature and postpartum body condition, and we assessed the investment in reproduction with litter size and the mass loss during parturition. Endurance capacity was measured four times on average once every three weeks from the start of the experiment to 8 days after parturition (SD = 4.7 days). Endurance was calculated as the time spent running until exhaustion on a treadmill following the protocol of Le Galliard et al. (2003). Body temperature was measured for females housed individually in large terrariums (130 × 47 × 35 cm), using a K-thermocouple thermometer ($\pm 0.2°C$ accuracy) inserted into the cloaca every hour from 13:00 to 17:00 local time. The selected body temperature was assessed once before (14 days, SD = 5.29 days) and once after parturition (7 days, SD = 4.71 days), and was calculated as the mean of all measures. At parturition, the number of offspring or eggs was counted and females were weighted. We could not avoid the desiccation of the eggs and thus could not weigh them accurately. Instead we calculated the mass loss during parturition, defined as the difference between female body mass before and after parturition (females were weighed on average 4.5 days before parturiton, SD = 3.0 days). This measure thus included the mass of the litter, embryonic annexes and water lost during parturition. A female was considered reproductive if she gave birth to offspring or laid eggs.

Statistical Analyses

Two females were not recaptured in May and thus could not be included in the analyses. The experiment resulted in nonreproductive females producing no eggs (2 mated and 1 unmated), unmated females producing undeveloped (unfertilized) eggs (n=13), mated females producing offspring (n=6), and mated females producing undeveloped (unfertilized or fertilized) eggs (n=6, see Fig. 1). First, we analyzed differences between the experimental groups of mated (n=12) and unmated females (n=13). Because some mated females did not produce offspring (Fig. 1), we analyzed differences between the three groups of mated females that produced offspring (n=6), mated females that produced undeveloped eggs (n=6) and unmated females that produced undeveloped eggs (n=13). Finally, we also tested the effect of producing offspring by comparing females that produced offspring (n=6) and females that produced undeveloped eggs (n=19). For the analyses of litter size, we excluded two females that produced undeveloped eggs (1 mated and 1 unmated) because their clustered eggs could not be counted. Repeated measures of endurance capacity (log-transformed to normalize the data) and mean selected body temperatures were analyzed with mixed-effects linear models for repeated measures in R 2.12.1 statistical software (http://cran.r-project.org/). Repeated measures were modeled with the *lme* procedure and with the compound symmetry covariance structure (Pinheiro and Bates, 2000). The covariance structure was selected from a list of variance–covariance models by the Akaike Index Criterion (AIC) (Pinheiro and Bates, 2000). The model included fixed effects of treatment, time and their interaction, and a random effect of subject identity. Mass loss during parturition, litter size and postpartum body mass were compared between groups using linear models and standard ANOVA tests (*lm* procedure) with female SVL as a covariate. Parturition dates were compared between groups using linear models and the *lm* procedure. In all cases, the assumptions of normality and homogeneity of variances were fulfilled. Results are presented as mean$\pm$standard error.

RESULTS

Reproductive Traits

There were no significant differences between treatments in the probability of being reproductive (Fisher's exact test, $P = 1$). Litter size was 4.92 ± 0.80 for unmated females producing undeveloped eggs, 3.40 ± 0.51 for mated females producing undeveloped eggs and 6.50 ± 1.23 for mated females producing offspring. Litter sizes were not significantly different between the groups (Table 1). Mass loss during parturition was significantly different between females producing offspring and females producing undeveloped eggs (Table 1). Mass loss during parturition was on average $54.9\pm8.8\%$ of postpartum body mass for females that produced offspring and only $28.4\pm3.2\%$ for females that produced undeveloped eggs. Female postpartum body conditions (body mass statistically corrected for female SVL) and parturition dates did not significantly differ between groups (Table 1).

Locomotor Performances and Basking Behavior

Repeated measures of endurance capacity indicated temporal changes during reproduction independent of the experimental

Table 1. Reproductive traits.

	Experimental groups: effect of mating	Effect of offspring production	Effect of mating and offspring production
Litter size			
Treatment	$F_{1,20} = 0.05$, $P = 0.8260$	$F_{1,20} = 2.38$, $P = 0.1390$	$F_{2,19} = 2.53$, $P = 0.1059$
SVL	$F_{1,20} = 1.80$, $P = 0.1943$	$F_{1,20} = 1.61$, $P = 0.2188$	$F_{1,19} = 2.93$, $P = 0.1031$
Mass loss during parturition			
Treatment	$F_{1,22} = 1.15$, $P = 0.2949$	**$F_{1,22} = 11.97$, $P = 0.0022$**	**$F_{2,21} = 6.28$, $P = 0.0073$**
SVL	$\underline{F_{1,22} = 3.59, P = 0.0714}$	$\underline{F_{1,22} = 4.27, P = 0.0507}$	**$F_{1,21} = 4.48$, $P = 0.0464$**
Postpartum body mass			
Treatment	$F_{1,22} = 0.48$, $P = 0.4939$	$F_{1,22} < 0.01$, $P = 0.9790$	$F_{2,21} = 0.37$, $P = 0.6967$
SVL	**$F_{1,22} = 13.97$, $P = 0.0011$**	**$F_{1,22} = 13.03$, $P = 0.0016$**	**$F_{1,21} = 13.29$, $P = 0.0015$**
Parturition date			
Treatment	$F_{1,23} = 1.15$, $P = 0.2956$	$F_{1,23} < 0.01$, $P = 0.9976$	$F_{2,22} = 0.85$, $P = 0.4402$

We compared litter size, mass loss during parturition, postpartum body mass and parturition dates between different groups (see Fig. 1). First, we compared mated and unmated females to assess the effect of mating (experimental treatment). Second, we compared females that produced offspring and females that produced undeveloped eggs to assess the effect of offspring production, irrespective of the mating status. Finally, we compared mated females that produced offspring, mated females that produced undeveloped eggs and unmated females that produced undeveloped eggs to assess the effect of mating and of offspring production simultaneously. In models containing SVL, interactions between treatment and SVL were not significant ($P > 0.42$). Significant results are in bold ($P < 0.05$) and marginally significant results are underlined ($P < 0.10$).

Table 2. Locomotor performances and thermoregulation.

|	Experimental groups: effect of mating	Effect of offspring production	Effect of mating and offspring production
Endurance capacity			
Treatment	$F_{1,23} = 0.23$, $P = 0.6383$	$F_{1,23} = 0.70$, $P = 0.4121$	$F_{2,22} = 0.34$, $P = 0.7181$
Time	**$F_{3,64} = 11.42$, $P < 0.0001$**	**$F_{3,64} = 18.44$, $P < 0.0001$**	**$F_{3,61} = 12.32$, $P < 0.0001$**
Time × Treatment	$F_{3,64} = 1.16$, $P = 0.3332$	**$F_{3,64} = 3.60$, $P = 0.0180$**	$\underline{F_{6,61} = 1.96, P = 0.0849}$
Body temperatures			
Treatment	$F_{1,23} = 0.20$, $P = 0.6575$	$F_{1,23} = 1.81$, $P = 0.1912$	$F_{2,22} = 2.12$, $P = 0.1438$
Time	**$F_{1,19} = 82.70$, $P < 0.0001$**	**$F_{1,19} = 115.87$, $P < 0.0001$**	**$F_{1,18} = 84.13$, $P < 0.0001$**
Time × Treatment	$F_{1,19} = 0.06$, $P = 0.8137$	$F_{1,19} = 0.64$, $P = 0.4336$	$F_{2,18} = 0.74$, $P = 0.4903$

We compared repeated measures of endurance capacity and body temperatures between different groups (see Table 1 for more explanations). Models included a random effect of subject identity. Significant results are in bold ($P < 0.05$) and marginally significant results are underlined ($P < 0.10$).

treatment (Table 2). Endurance capacity decreased from the first to the third session of measure (contrast $= -101.4 \pm 33.1$ sec, $P = 0.0031$, see Fig. 2), followed by a significant recovery after parturition (contrast $= 277.2 \pm 35.0$ sec, $P < 0.0001$). There was an effect of offspring production, but not of mating, on the temporal changes in endurance capacity (Table 2). Females producing offspring showed a more pronounced locomotor impairment at the end of gestation (Fig. 2). Body temperature was only affected by the time of the measure (Table 2). Parturition was associated with a significant increase in selected body temperature ($29.48 \pm 0.31°C$ before versus $33.26 \pm 0.28°C$ after parturition,

Table 2). This shift in selected body temperatures was not dependent on mating or on offspring production.

DISCUSSION

Our study showed that common lizards are spontaneous ovulators whose litter size is not influenced by the absence of mating. Reproductive costs associated with gestation were also independent of the mating treatment. Thus, in the common lizard, viviparity is not associated with facultative ovulation, and viviparity does not allow an effective control of litter size, after ovulation, in response to the absence of mating opportunities.
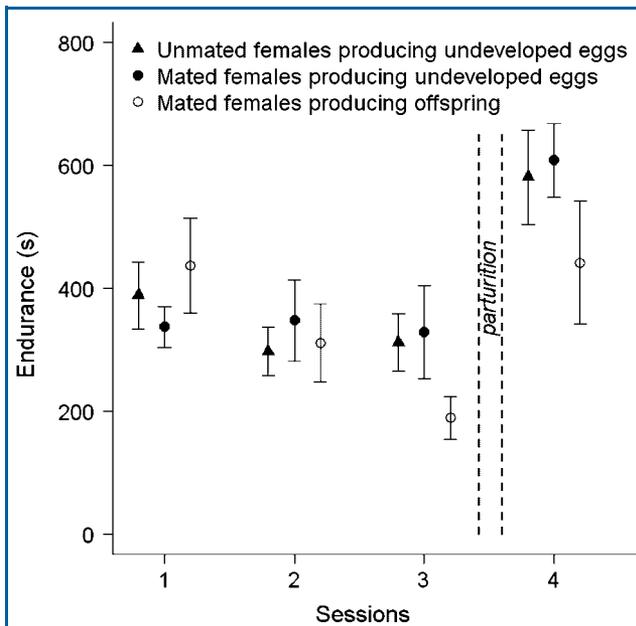
Figure 2. Locomotor impairment. Endurance capacity of females (mean running time ± SE) during gestation (sessions 1, 2 and 3) and after parturition (session 4). Data are shown for unmated females producing undeveloped eggs ($n = 13$), mated females producing undeveloped eggs ($n = 6$) and mated females producing offspring ($n = 6$).

The lack of compensatory mechanisms might be explained by the relative recentness with which viviparity has evolved in this species (i.e., 0.5–2 mybp according to Surget-Groba et al., 2001). However, offspring production induced a more pronounced locomotor impairment and physical burden of reproduction than the production of undeveloped eggs.

Reproduction in the Absence of Mating

Female lizards mate directly after emergence, and vitellogenesis, which is controlled by an endogenous cycle, starts shortly thereafter (Gavaud, '83). We observed that mating has no effect on the onset of vitellogenesis and on ovulation. In squamates, ovulation can be induced by mating or male presence (Crews et al., '86; Mendonça and Crews, '90; DeNardo and Autumn, 2001; Mathies et al., 2004). However, these data are not sufficient to understand the phylogenetic constraints and the ease with which induced ovulation can evolve in this group. In the common lizard, the investment in reproduction may be controlled by other factors and/or at a different time scale. For example, litter size may be influenced by female food consumption after hibernation (when vitellogenesis starts) and also by conditions experienced before vitellogenesis (e.g., Marquis et al., 2008). Common lizards are thought to use a mixed-strategy in which they fuel reproduction with both stored and recently acquired

resources (Avery, '75; Massot and Clobert, '95; Mugabo et al., 2011; Bleu et al., unpublished results). According to previous observations, litter size is a function of multiple mating (Fitze et al., 2005; Eizaguirre et al., 2007). Our study suggests that multiple mating is unlikely to affect follicle recruitment; however, it may increase fertilization success. Since we observed no difference in litter sizes between the different groups, we can conclude that females did not abort or resorb their unfertilized and undeveloped eggs. This finding is in line with the fact that, contrary to mammals, there is no clear-cut evidence in viviparous squamates, indicating that pregnant females are able to resorb unviable eggs and embryos from the uterus (Blackburn, '98b; Girling, 2002; Blackburn et al., 2003). However, it may occur in some particular species (Bonnet et al., 2008). That being said, we did not check for qualitative adjustments of the reproductive investment. It is possible that females did not invest the same amount of nutrients in their eggs, as observed in studies of differential allocation on egg mass (e.g., Uller et al., 2005), yolk hormonal content (e.g., Gil et al., 2004; Tschirren et al., 2004) or other compounds of the egg yolk (e.g. antioxidant, Williamson et al., 2006).

Unmated and mated females displayed similar reduced locomotor performances and selected lower body temperatures during gestation. These locomotor and behavioral changes during gestation are associated with a decrease in the ability to escape predators and to forage. Thus, both unmated and mated females may suffer from increased mortality costs in the field (Irschick et al., 2008; but see Bauwens and Thoen, '81). However, we also found that females carrying offspring compared to females producing undeveloped eggs had a stronger locomotor impairment during late gestation, probably due to their heavier litters. The weight of fertilized eggs, containing developing embryos, increases in the course of pregnancy, because a large amount of water accumulates in the eggs (Dufaure and Hubert, '61). Apparently, there was no such accumulation in undeveloped eggs. We found no significant difference in postpartum body condition. This result is important because the postpartum amount of resources of a female affects its future survival (Sorci et al., '96) and its subsequent investment in reproduction (capital breeding, Bleu et al., unpublished results). Altogether, our results, therefore, indicate that unmated female common lizards pay both the cost of missing a reproduction opportunity and most of the typical direct costs of reproduction. This double cost of not mating may generate a strong positive selection for insurance of fertilization, which may explain why females mate with multiple partners in this species (Laloi et al., 2004; Fitze et al., 2005; Uller and Olsson, 2005).

Implications of the Absence of Reproductive Adjustments

The risk of an absence of mating depends on factors such as age, body size and social conditions, in particular the population density (Massot et al., '92; Richard et al., 2005). *L. vivipara* population densities across Eurasia are highly variable and

densities can be very low in marginal habitats (e.g., Herczeg et al., 2003). Lizards used in this experiment were native from high-density populations where around 700 adults and yearlings co-occur within a ha of natural habitat (Massot et al., '92). In these populations, most of the 3 year old and older females are mated (Massot et al., 2011) and still they may produce litters of exclusively undeveloped eggs (2.7% in 1630 litters, Massot, pers. comm.). Thus, our experiment, which may be more representative of low-density populations, is still relevant in high-density populations. The inability of adjusting reproductive effort in response to mating could be an important demographic factor, especially in small populations, since it may increase local extinction risk. The inability of adjusting reproductive effort may also affect the colonization of new habitats, since newly founded populations show low densities and since unmated females paying the costs of reproductive investment may have reduced lifetime reproductive success. This drawback may become especially important since rapid habitat changes, e.g. induced by climate warming (Massot et al., 2008), may limit the colonization ability of the species.

Finally, this finding also has implications for the understanding of the evolution of viviparity. It has been suggested that the thin eggshell of viviparous eggs may allow exposure of the maternal uterus to chemical signals of embryonic origin (Guillette, '93). Embryonic signals may allow maternal recognition of pregnancy and may have played a role in the increase of egg retention length during transitions from oviparity to viviparity (Guillette, '93). The fact that undeveloped eggs were retained until normal parturition date suggests that there is no embryonic signal for maternal recognition of pregnancy, or at least that this signal does not determine gestation length. Maternal effects during pregnancy on offspring phenotypes have been demonstrated to exist in the common lizards (e.g., Massot and Clobert, '95; Meylan and Clobert, 2005). However, further studies are needed to clarify the existence and the role of embryonic signals on their mother.

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