

Reproductive allocation strategies: a long-term study on proximate factors and temporal adjustments in a viviparous lizard

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Abstract Optimisation of reproductive investment is crucial for Darwinian fitness, and detailed long-term studies are especially suited to unravel reproductive allocation strategies. Allocation strategies depend on the timing of resource acquisition, the timing of resource allocation, and trade-offs between different life-history traits. A distinction can be made between capital breeders that fuel reproduction with stored resources and income breeders that use recently acquired resources. In capital breeders, but not in income breeders, energy allocation may be decoupled from energy acquisition. Here, we tested the influence of extrinsic (weather conditions) and intrinsic (female characteristics) factors during energy storage, vitellogenesis and early gestation on reproductive investment, including litter mass, litter size, offspring mass and the litter size and offspring mass trade-off. We used data

from a long-term study of the viviparous lizard, *Lacerta (Zootoca) vivipara*. In terms of extrinsic factors, rainfall during vitellogenesis was positively correlated with litter size and mass, but temperature did not affect reproductive investment. With respect to intrinsic factors, litter size and mass were positively correlated with current body size and postpartum body condition of the previous year, but negatively with parturition date of the previous year. Offspring mass was negatively correlated with litter size, and the strength of this trade-off decreased with the degree of individual variation in resource acquisition, which confirms theoretical predictions. The combined effects of past intrinsic factors and current weather conditions suggest that common lizards combine both recently acquired and stored resources to fuel reproduction. The effect of past energy store points out a trade-off between current and future reproduction.

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Introduction

Reproductive allocation decisions are of central interest in evolutionary ecology as they determine lifetime reproductive success and some of the costs associated with reproduction (Roff 2002). It is possible to distinguish the allocation of resources to reproduction (i.e. how much to invest in reproduction) and the allocation of reproductive resources between the size and number of offspring. The energy invested into reproduction by a female depends on the total amount of energy available, and reproductive investment as well as allocation rules are under maternal and/or environmental (e.g. climatic) controls. In animals, there are capital breeding species that fuel reproduction with stored resources and income breeding species that use recently acquired resources (Stephens et al. 2009). Thus, in capital breeders, pre-reproductive resource stores or environmental conditions experienced during the energy storage period, such as food availability, should correlate with future reproductive investment (Doughty and Shine 1997, 1998; Bonnet et al. 2001; Lourdais et al. 2002; Reading 2004) or future reproductive success (Festa-Bianchet 1998). However, the capital and income breeding strategies describe only the extremes of a continuum (e.g. Houston et al. 2007). Thus, females may adjust their energy allocation strategy at multiple points in the reproductive cycle. In particular, adjustment of offspring size or litter size may occur during gestation in viviparous (i.e. live-bearing) species via embryo resorption or nutritional transfer. In viviparous lizards, for example, food and thermal conditions experienced by the mother during gestation can affect offspring mass at birth (e.g. Shine and Downes 1999; Swain and Jones 2000). A second aspect of reproductive investment decisions is the existence of trade-offs between reproduction and other life-history traits, including trade-offs between different reproductive events. In particular, current fecundity can be traded-off with future fecundity. For example, a high investment in reproduction decreases the probability to breed again and thus increases the interbreeding interval (e.g. Bonnet et al. 2001; Hadley et al. 2007), or a lower investment in reproduction increases survival later in life (e.g. Clutton-Brock et al. 1983; Massot et al. 2011). In line with this trade-off hypothesis, experiments in mammals (Koivula et al. 2003), lizards (e.g. Cox and Calsbeek 2010) and birds (e.g. Richner and Tripet 1999; Hanssen et al. 2005) demonstrate that a higher reproductive effort results in a decrease in survival or fecundity the following year.

Finally, females can also adjust how the energy is allocated into each offspring (e.g. offspring mass), i.e. how the trade-off between litter size and offspring mass is solved. Females may vary in their resource stores and resource acquisition efficiency (Doughty and Shine 1997;

Glazier 1999). The van Noordwijk and de Jong's model (1986) suggests that trade-offs will be weaker if variation in resources acquisition is high relative to variation in resources allocation. Furthermore, the pattern of energy allocation to offspring mass may follow distinct pathways. It is often assumed that females decide in a sequential manner, first deciding on how much to invest into reproduction, and then on how much to invest in litter size versus offspring mass (e.g. Charnov et al. 1995). However, investment and allocation decisions may also be simultaneous, genetically linked or correlated, as suggested by an old theoretical model (Winkler and Wallin 1987) and by evidence from natural populations (Christians 2000; Uller et al. 2009).

Long-term studies are especially suited to disentangle the effects of past and present, and extrinsic and intrinsic factors on both total reproductive investment and reproductive allocation in litter size versus offspring mass. Squamate reptiles (i.e. lizards and snakes) are good model species for such studies because they often lack parental care (Shine 2005), and thus reproductive investment is completed during vitellogenesis and gestation in viviparous species. Moreover, potential factors affecting the investment in reproduction are well identified. In many squamates, body size influences reproductive output, such that larger females invest more in reproduction than smaller females (e.g. Shine 2005). Some squamates are typical capital breeders, but others may also use mixed capital and income strategies (e.g. Bonnet et al. 2001; Houston et al. 2007). Weather conditions are also of particular importance for reproduction because they directly affect habitat quality and food availability and also because foraging performances are linked to the ability to maintain optimal body temperatures (Le Galliard et al. 2012). Thus, we expect that reproductive decisions should be largely dependent on pre-reproductive resource stores, food availability and weather conditions in squamates. Moreover, because parturition dates affect the duration of the energy storage period, early breeders may be able to capitalise more resources than late breeders for the next reproductive event. In this study, we used 13 years of field data on the viviparous common lizard, *Lacerta (Zootoca) vivipara*, to test the effects of extrinsic factors (temperature and rainfall during the current and previous year) and intrinsic factors [current body size, previous postpartum body condition (PBC), previous parturition date] on reproductive output. From previous studies on the common lizard we know the following. First, life-history traits are sensitive to variation in air temperature and rainfall (Chamaillé-Jammes et al. 2006; Marquis et al. 2008; Le Galliard et al. 2010). Second, stored lipids decrease during vitellogenesis (Avery 1974), and vitellogenesis occurs during a short period of 3 weeks after winter emergence (Bauwens and Verheyen 1985), which are

features of capital breeders. Third, females can assimilate food during vitellogenesis (Avery 1975), and there are maternal effects during gestation (e.g. Massot and Clobert 1995; Marquis et al. 2008), which are features of income breeders.

Previous studies on *L. vivipara* addressed the effects of current weather (Marquis et al. 2008; Le Galliard et al. 2010) and of social interactions (Le Galliard et al. 2008) on reproductive investment, but none investigated the relative importance of past and present factors. We therefore specifically tested the importance of the previous year's weather conditions and female condition on reproductive investment. If common lizards are true capital breeders, we predict that weather conditions during energy storage, PBC and/or parturition date of the previous year should affect reproductive investment (litter mass, litter size and offspring mass). A correlation of reproductive investment decisions with weather conditions during vitellogenesis and/or gestation would suggest income breeding. Finally, an intermediate situation would suggest a mixed strategy. We expect the strength of the litter size and offspring mass trade-off to depend on the variation in resource acquisition and resource allocation as predicted by the van Noordwijk and de Jong's model (1986).

Materials and methods

Model species

Lacerta (Zootoca) vivipara is a small [adult snout–vent length (SVL) 50–70 mm] ground-dwelling lizard that is widely distributed across Eurasia. We studied viviparous populations located in the Massif Central mountain range (south-eastern France) where the reproductive cycle is annual (Fig. 1). In this area, adults start to become active around mid-April (males) or early May (females). Emergence of the females from hibernation is highly synchronised, with mating occurring 0–3 days after emergence and reproductive investment (vitellogenesis) occurring on average during the first 3 weeks of May for the Massif Central populations). During gestation, a primitive chorioallantoic placenta allows respiratory, aqueous and mineral exchanges between mother and embryos (Panigel 1956; Stewart et al. 2009). Parturition occurs after an average gestation period of 2 months, i.e. in late July to mid-August. Mean litter size is five (range 1–12), including both nonviable offspring (fertilised or unfertilised eggs where only yolk is visible, undeveloped embryos and stillborns) and live offspring. Live offspring hatch immediately after parturition and are thereafter autonomous. Adult females replenish their lipid stores during the

summer immediately after parturition and gradually enter into hibernation in September (Avery 1974; Bauwens 1981).

Population survey and rearing conditions

Longitudinal data on reproductive strategies were obtained from a long-term mark–recapture survey conducted each year from 1990 to 2002 in a population at Mont-Lozère (1,420 m a.s.l., 44°23'03"N, 3°52'40"E) that consists of two adjacent habitats with different structures (Clobert et al. 1994). Adult females were captured on average 1 month before parturition (June), identified or marked by toe-clipping and kept in the laboratory until parturition (rearing conditions as in Massot and Clobert 1995). After parturition, litter size was recorded, and females and their live offspring were weighed. Females were then released together with their live offspring at the original capture location 3–5 days after parturition. We recorded litter size for all litters (litters containing exclusively viable offspring and litters containing nonviable offspring), and we calculated litter mass and offspring mass only for litters containing exclusively viable offspring (because we could not avoid the desiccation of the nonviable offspring and thus could not weight them accurately). Litter mass was the sum of all offspring body masses, and offspring mass was litter mass divided by litter size.

Weather

Temperature and rainfall data were recorded by Météo-France at a meteorological station situated at a similar altitude, 50 km south of the study site (Mont Aigoual, 1,567 m a.s.l., 44°07'N, 3°35'E; see Chamaillé-Jammes et al. 2006; Marquis et al. 2008). We used daily maximum temperature and daily cumulative amount of precipitation as descriptors of thermoregulation opportunities and habitat humidity (Huey 1982). For each year, we calculated

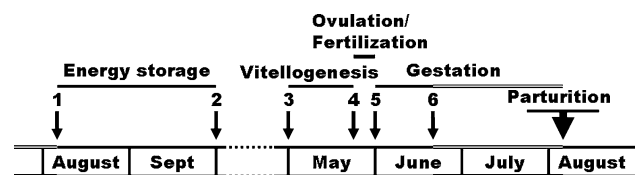


Fig. 1 Reproductive cycle of the common lizard [*Lacerta (Zootoca) vivipara*] at Mont Lozère. During the course of our study, lizards were captured during mid-gestation in June and maintained in the laboratory until parturition (hollow lines). We calculated average weather conditions (1) during energy storage [from parturition (date 1: 8 August) to the start of hibernation (date 2: 30 September)], (2) during vitellogenesis [from 1 May (date 3) to 21 May (date 4)], and (3) during gestation before capture and maintenance in the laboratory [from 1 June (date 5) to capture (date 6: 21 June)]

mean values for different periods of the reproductive cycle, namely (1) during the previous summer activity season (energy storage period), (2) during vitellogenesis and (3) during the early gestation period in natura (see Fig. 1 for more details). Correlations between these variables are reported in Electronic Supplementary Material (ESM) 1. We tested the effects of temperature during energy storage and temperature during early gestation both separately and together to address potential colinearity issues caused by a significant correlation between these variables. Effects were all robust, and colinearity was therefore not a strong issue in our analyses.

Offspring mass and litter size trade-off

We also modelled the trade-off between offspring mass and litter size in more detail. Correlations were run between offspring mass and residual litter size for each year (Pearson correlations). We also ran correlations on log-transformed variables to make the results comparable with those reported in recent publications (e.g. Christians 2000). Van Noordwijk and de Jong's model (1986) predicts that more negative correlations should be found when variation in resource acquisition is low compared to variation in resource allocation. Christians (2000) adapted the van Noordwijk and de Jong's model (1986) to the litter size and offspring mass trade-off by calculating the variation in resource acquisition as the variation in total reproductive investment, i.e. variation in clutch or litter mass. Thus, as suggested by Christians (2000), we calculated the allocation as $[\log(\text{offspring mass})/(\log(\text{litter mass}))]$ and the investment as $[\log(\text{litter mass})]$. Then, to avoid the confounding effect of maternal size, we used the residuals of a linear regression of these variables (investment or allocation) against maternal SVL (Christians 2000; Brown 2003). We calculated the variances of these residuals to estimate the variation in female investment and in female allocation. These variances were calculated for each year. We expect a negative relationship between the ratio of allocation variance to investment variance and the Pearson's correlation coefficient between offspring mass and litter size.

Statistical analyses

All statistical models were implemented in R 2.14.1 statistical software (<http://www.cran.r-project.org/>). We analysed variation in the litter mass, litter size, and offspring mass at birth of litters containing exclusively viable offspring ($n = 157$) and variation in litter size of all litters (i.e. litters containing exclusively viable offspring and litters containing nonviable offspring, $n = 239$) with mixed-effects linear models, including year as a random effect (Pinheiro and Bates 2000) (lme procedure). The annual

sample sizes are reported in ESM 2. Fifty females were captured several times in two successive years, and the measurements performed on them cannot be assumed to be independent. To ensure that there was no problem of pseudo-replication (only some females appeared several times in the dataset), we also performed the same statistical analyses with two random effects: year and female identity (lmer procedure). Both analyses yielded very similar results (see ESM 3 and 4 for the results with two random effects).

A first random-effect model was fitted to assess inter-annual variation. Then, a mixed-effect model was fitted to test for intrinsic effects. In this model, we included, as explanatory variables, PBC of the previous reproductive season [PBC ($t - 1$)], parturition date of the previous reproductive season [parturition ($t - 1$)] and female SVL during the current reproductive season [SVL (t)]. Body condition was calculated as residuals of a linear regression of body mass against SVL. We also added a habitat effect (there are two habitats in our study site, see "Population survey and rearing conditions") because previous studies have reported spatial differences in life-history traits between these two habitats (Clobert et al. 1994). For offspring mass, we modelled a potential trade-off with litter size. Since litter size and maternal SVL are correlated (Pearson's $r = 0.66$, $P < 0.0001$), we included relative litter size in the model (residuals of a linear regression of litter size against maternal SVL). To test for potential differences between litters containing exclusively viable offspring and litters containing at least one nonviable offspring, we included a categorical effect ("success") when analysing all litters. The full model included additive and first-order interaction terms. A first minimum adequate model was selected using both backward elimination and forward selection of higher order interactions based on the Akaike Index Criterion (AIC). Finally, additive effects of weather conditions were added to the first minimum adequate model. A second minimum adequate model was then selected using the same procedure as mentioned above. We report only significant effects using F tests based on restricted maximum likelihood conditional estimates of variance. Estimates \pm standard errors (SE) are shown for fixed effects and the 95 % confidence intervals (CI) are given for random effects.

Results

Reproductive data for 239 females, including 157 exclusively viable litters and 82 litters containing nonviable offspring, were collected over a 13-year period. We found no effect of temperature or habitat in any of the models tested (Table 1). The mass and size of litters containing

exclusively viable offspring were positively correlated with rainfall during vitellogenesis (Table 1; Fig. 2), as well as with current female body size and with female PBC the previous year (Fig. 3a). However, offspring mass was only explained by residual litter size (litter size corrected by the maternal body size; Table 1). The size of all litters (litters containing exclusively viable offspring and litters also containing nonviable offspring) increased with rainfall during vitellogenesis and female body size, but was additionally influenced by the interaction between the parturition date the previous year, PBC the previous year and litter success of the current year (Table 1). In fact, consistent with the analysis reported above, the interaction between parturition date and PBC the previous year was not significant for litters containing exclusively viable offspring (partial test with “successful” litters: $F_{1,141} = 1.54$, $P = 0.22$). This interaction was significant for litters containing nonviable offspring (partial test with “unsuccessful” litters: $F_{1,66} = 7.73$, $P = 0.0071$; Fig. 3b). In these unsuccessful litters, PBC had a positive effect on litter size for females giving birth late in the season but not for early breeders (Fig. 3b).

Inter-annual variation was estimated using mixed-effects linear models with reproduction year as the random effect. Annual factors explained between 15.93 and 27.67 % of the total inter-annual standard deviation in reproductive traits (Table 2). Intrinsic factors (body size and condition) explained a large part of the inter-annual variation in litter size (for litters containing exclusively viable offspring and all litters) and litter mass (Table 2), but inter-annual variation in offspring mass remained unchanged when significant intrinsic factors (residual litter size) were included in the model (Table 2). The effect of rainfall during vitellogenesis, which was significant for litter mass and litter size, explained all remaining inter-annual variation in these two reproductive traits (Table 2).

In litters containing exclusively viable offspring, the correlations between residual litter size and offspring body mass were negative in all years (7 years were not significant; Table 3), and there was an annual variation in the strength of the correlation (Table 3). Our analysis confirmed the existence of a strong, negative relationship between the variance ratio and the correlation between litter size and offspring mass (Fig. 4; Pearson's $r = -0.860$,

Table 1 Effects of intrinsic and extrinsic factors on reproductive traits

Effects ^a	Estimate	<i>F</i>	<i>df</i>	<i>P</i>
Litter mass				
SVL (<i>t</i>)	0.058 ± 0.005	149.62	1,143	<0.0001
PBC (<i>t</i> – 1)	0.132 ± 0.050	7.10	1,143	0.0086
Rainfall during vitellogenesis	0.015 ± 0.005	9.45	1,10	0.0117
Size of litters containing exclusively viable offspring				
SVL (<i>t</i>)	0.311 ± 0.029	118.28	1,143	<0.0001
PBC (<i>t</i> – 1)	0.748 ± 0.299	6.26	1,143	0.0135
Rainfall during vitellogenesis	0.089 ± 0.030	8.86	1,10	0.0139
Size of all litters				
SVL (<i>t</i>)	0.306 ± 0.024	167.47	1,219	<0.0001
PBC (<i>t</i> – 1)	1.268 ± 0.473	8.94	1,219	0.0031
Parturition (<i>t</i> – 1)	–0.030 ± 0.019	1.74	1,219	0.1881
Success	–0.357 ± 0.178	0.44	1,219	0.5093
PBC (<i>t</i> – 1) × parturition (<i>t</i> – 1)	0.239 ± 0.078	9.34	1,219	0.0025
PBC (<i>t</i> – 1) × success	–0.496 ± 0.577	4.54	1,219	0.0341
Parturition (<i>t</i> – 1) × success	0.019 ± 0.025	0.35	1,219	0.5525
PBC (<i>t</i> – 1) × parturition (<i>t</i> – 1) × success	–0.192 ± 0.089	4.62	1,219	0.0327
Rainfall during vitellogenesis	0.090 ± 0.025	12.94	1,10	0.0049
Offspring mass				
Residual litter size ^b	–0.008 ± 0.001	59.66	1,144	<0.0001

SVL, snout-vent length; PBC, postpartum body condition

^a Final models were selected starting with full models. These included intrinsic factors [SVL (*t*), current body size; PBC (*t* – 1), PBC of the previous reproductive season; Parturition (*t* – 1), parturition date of the previous reproductive season; Success, litter success] and extrinsic factors (habitat, rainfall and temperatures during energy storage, vitellogenesis and gestation. See Fig. 1 for details. Random effects are presented in Table 2

^b Residual litter size was calculated as the residuals of a linear regression between litter size and maternal SVL

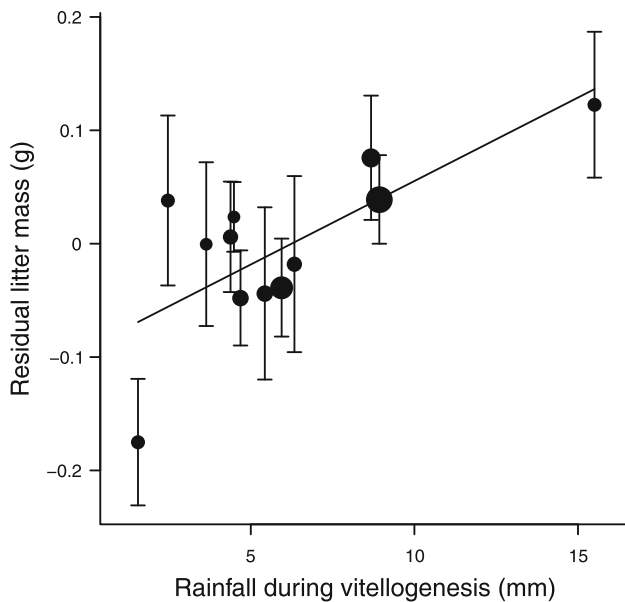


Fig. 2 Variation in litter mass. Residual litter mass (residuals of litter mass from a linear regression against maternal snout–vent length (SVL) and previous postpartum body condition (PBC); see Table 1) is shown as the mean \pm standard error (SE) per year. Size of filled circles is proportional to sample size (range = 10–21). Solid line represents model predictions from Table 1. The slope estimate was robust to the exclusion of the year with the highest rainfall (slope = 0.016 ± 0.007 , $F_{1,9} = 2.18$, $P = 0.057$)

95 % CI -0.960 to -0.566 , $P = 0.0003$). These results are in line with analyses based on log-transformed values of offspring mass and litter size (ESM 5).

Discussion

In this study we tested how weather conditions and female characteristics may affect reproductive investment at different time scales, especially with regard to the relative importance of past and present factors. Our major results are that reproductive investment is positively correlated with current rainfall and female condition the year before, and is negatively correlated with the parturition date of the previous reproduction. Our data also indicate that adjustments of the reproductive investment occurred via the number of offspring and that offspring mass was subsequently traded-off with litter size.

Reproduction and weather conditions

We investigated the effects of weather conditions on reproductive investment because they can have direct or indirect effects. First, weather conditions can directly influence the metabolism and physiology of an animal. In particular, in ectotherms, it is known that temperatures

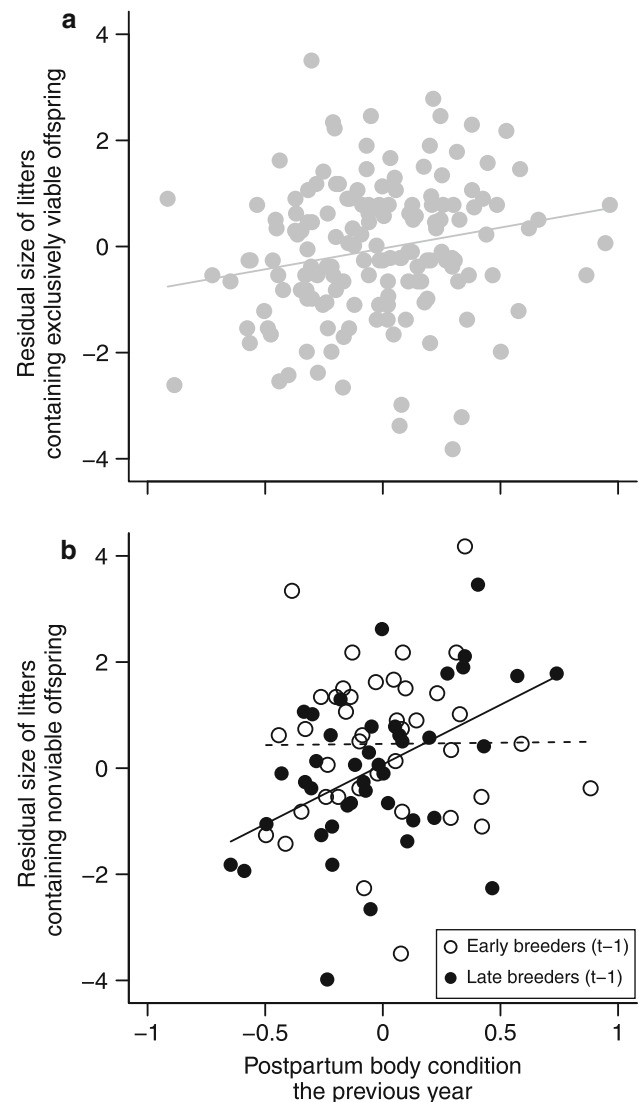


Fig. 3 Variation in litter size. **a** PBC of the previous year was correlated with the size of litters containing exclusively viable offspring ($n = 157$). Solid line indicates model predictions (Table 1). **b** PBC of the previous year was correlated with the size of litters containing nonviable offspring for late-breeding females, but not for early-breeding females. Model predictions are represented using a dashed line for early breeding females (parturition date < mean parturition date) and a solid line for late breeders (parturition date > mean parturition date). Slopes estimates obtained from the model in Table 1 were positive and significant for late breeders ($n = 42$, slope = 2.225 ± 0.648 , $P = 0.0007$) but not significantly different from zero in early breeders ($n = 40$, slope = 0.063 ± 0.690 , $P = 0.93$). Data for litter sizes are residuals of a linear regression between litter size and maternal SVL

influence directly maternal activity (opportunity to feed), the efficiency of food assimilation (e.g. Adolph and Porter 1993) and, during gestation, embryonic development (see below). Yet, in this study, we found no effect of temperature on litter size, litter mass and offspring mass at birth. Previous laboratory experiments in viviparous squamates

Table 2 Annual variations in reproductive traits

Intrinsic factors ^a	σ_{Annual}	σ_{Residual}	ICC	LRT	<i>P</i>
Litter mass					
Annual variation	0.09 [0.05–0.19]	0.29 [0.25–0.32]	24.50	4.95	0.0260
Intrinsic factors	0.05 [0.0–0.15]	0.21 [0.18–0.23]	18.15	1.17	0.2786
Final best model	~0 ^c	0.21 [0.18–0.23]	0		
Size of litters containing exclusively viable offspring					
Annual variation	0.61 [0.32–1.16]	1.59 [1.42–1.79]	27.67	7.89	0.0050
Intrinsic factors	0.20 [0.03–1.38]	1.25 [1.11–1.40]	13.94	0.35	0.5542
Final best model	~0	1.23 [1.10–1.38]	0		
Size of all litters					
Annual variation	0.63 [0.35–1.13]	1.68 [1.53–1.84]	27.32	13.24	0.0003
Intrinsic factors	0.33 [0.14–0.76]	1.26 [1.15–1.39]	20.64	3.25	0.0716
Final best model	~0	1.24 [1.16–1.39]	0		
Offspring mass^b					
Annual variation	0.0035 [0.0010–0.0125]	0.0187 [0.0167–0.0210]	15.93	1.03	0.3109
Intrinsic factors	0.0030 [0.0009–0.0103]	0.0160 [0.0142–0.0179]	15.90	1.08	0.2994

Values between square brackets indicate the confidence interval

σ_{annual} , year effect standard deviation, σ_{residual} , residual standard deviation; ICC, intraclass correlation coefficient (% of total standard deviation); LRT, likelihood ratio test

^a Estimates of year random effect for litter mass, size of exclusively viable litters, offspring mass, and size of all litters. Estimates are given as standard deviations (SD) calculated from a random model with no fixed effect (“annual variation” model), a mixed effect model with significant intrinsic factors (“intrinsic factors” model) and a mixed effect model with significant intrinsic and extrinsic factors (“final best model”; Table 1)

^b Effects of extrinsic factors were not significant for offspring mass

^c ~0 indicates an estimate at the boundary of the parameter space

found effects of temperature or basking opportunities during gestation on offspring mass (Shine and Harlow 1993; Doughty and Shine 1998; Swain and Jones 2000;

Wapstra 2000; Hare and Cree 2010). Experiments in the laboratory may not reflect the natural variations of thermal conditions and may also reduce the possibility of a

Table 3 Annual variation in the offspring mass and litter size trade-off

Years	<i>n</i>	Pearson’s <i>r</i> ^a	95 % confidence interval	<i>P</i>	Variance ratio ^b
1991	11	−0.415	−0.813 to 0.246	0.204	0.0190
1992	10	−0.313	−0.787 to 0.394	0.379	0.0152
1993	21	−0.493*	−0.762 to −0.078*	0.023*	0.0189*
1994	18	−0.226	−0.627 to 0.269	0.366	0.0133
1995	13	−0.713*	−0.908 to −0.267*	0.006*	0.0246*
1996	15	−0.611*	−0.855 to −0.143*	0.016	0.0195*
1997	12	−0.870*	−0.963 to −0.592*	<0.001*	0.0451*
1998	11	−0.475	−0.837 to 0.174	0.140	0.0169
1999	11	−0.705*	−0.917 to −0.182*	0.015*	0.0246*
2000	12	−0.319	−0.755 to 0.312	0.312	0.0163
2001	10	−0.305	−0.784 to 0.402	0.392	0.0138
2002	13	−0.451	−0.802 to 0.133	0.122	0.0148

The trade-off was investigated in litters containing exclusively viable offspring (*n* = 157)

* Correlation is significant at *P* < 0.05

^a Pearson’s *r* correlation coefficient was calculated between offspring mass and residual litter size for each year (see ESM 5 for results on log-transformed values)

^b Following Christian (2000), we calculated the variance ratio as the ratio of the variance in allocation {i.e. var[log(offspring mass)/log(litter mass)]} to the variance in investment {i.e. var[log(litter mass)]}

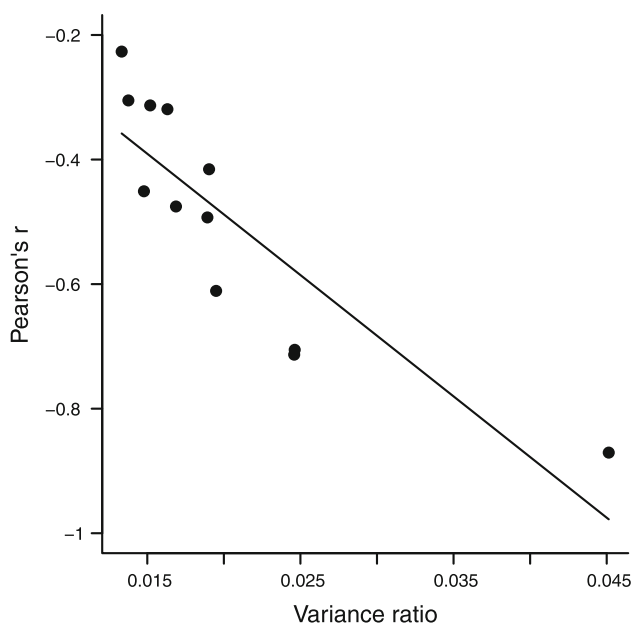


Fig. 4 Variation in the offspring mass and number trade-off. There is a negative correlation between the Pearson's correlation coefficient (r), calculated between offspring mass and residual litter size, and the variance ratio, calculated as the ratio of the variance in allocation to the variance in investment (see Table 3). Note that this negative correlation is still significant if we exclude the highest variance ratio (Pearson's $r = -0.918$, 95 % confidence interval -0.979 to -0.707 , $P < 0.0001$)

maternal response to compensate such variations. Some field studies have been conducted, and different results have been found, with some authors finding no effect of temperature during gestation on offspring size at birth (*Vipera aspis* Lourdais et al. 2004; *Niveoscincus ocellatus*, Cadby et al. 2010) and other authors finding an effect of temperature during gestation on offspring mass at birth but only at some altitudes (*Niveoscincus ocellatus*, Uller et al. 2011). Thus, under natural conditions, females may be able to compensate for poor climatic conditions—for example, by active thermoregulation—and may thus not be so strongly constrained by thermal conditions (Webb et al. 2006). In particular, when there is strong selection to produce larger offspring, females may be strongly selected to compensate for poor thermal conditions (for example, despite an increased predation risk) (Uller et al. 2011).

Second, weather conditions can have indirect effects on females since they influence habitat quality. Weather conditions influence environmental productivity and thus food availability: more rainfall can be associated with a higher productivity and a higher reproductive investment (e.g. Jordan and Snell 2002). In this case, the positive effect of rainfall during vitellogenesis on reproductive investment may indicate income breeding for the common lizard. This result shows that rainfall may be more important for successful breeding than thermal conditions. However, the

confirmation of underlying mechanisms and of income breeding will require direct tests of resource use either by measuring body composition and resource allocation with isotopic analysis (e.g. Warner et al. 2008) or by manipulating the food intake during vitellogenesis (e.g. Lourdais et al. 2003). We also observed that weather conditions experienced during gestation had no effect on reproductive investment, confirming previous findings (Marquis et al. 2008; Bleu et al. 2011). Finally, we observed that weather conditions experienced during energy storage, here taken to correspond to the summer activity of the previous year, had no effect on reproductive investment. Thus, this period may not be limiting for females. This result is in line with an experimental manipulation in the common lizard: manipulation of food intake after parturition during the summer revealed no major effect of food availability on reproductive investment the following year (Mugabo et al. 2011).

Reproduction and intrinsic factors

Body size was positively correlated with current reproductive investment. Body size may limit a female's reproductive output due to size-dependent availability of abdominal space (Qualls and Shine 1995). Furthermore, larger lizards are usually more efficient foragers (González-Suárez et al. 2011) and thus have more resources to allocate to reproduction than smaller lizards, leading to a positive relationship between body size, fat body reserves and reproductive investment (Avery 1974, 1975).

We also investigated the effects of PBC and parturition date of the previous year on current reproduction. PBC indicates the resource stores of the female after reproduction, and parturition date the previous year determines the length of the energy storage period. We found a positive effect of PBC the previous year on current reproductive investment. This result may suggest capital breeding as in other species (e.g. Doughty and Shine 1997; Festa-Bianchet 1998). However, such a long-term effect of body condition is somewhat surprising since lizards can store resources during the summer after reproduction and may thus compensate for a low PBC. The lack of compensation suggests that feeding rate is positively correlated with body condition and that a low PBC probably indicates a low individual quality. In addition, we found a state-dependent effect of the parturition date of the previous year on current reproductive investment for females that produced litters containing nonviable offspring. In these cases, litter size was constrained by PBC of the previous year when females gave birth late in the previous season, but not when females gave birth early in the previous season. This illustrates that earlier breeding and parturition may be advantageous for subsequent reproduction for some females.

The effect of previous PBC on current reproductive investment suggests a trade-off between successive reproductive events because a low PBC is associated with a stronger reproductive effort in the common lizard (Le Galliard et al. 2010). The mechanisms of such trade-offs are being increasingly studied. First, there may be a simple energetic link between the two reproductive events (Roff 2002): females that used more energy have fewer resources for the next season and may not be able to compensate for this difference. However, more complex scenarios are also possible. Resources allocated to reproduction are not available for other functions, which may thus be down-regulated as a consequence of a high reproductive investment, leading to a lower investment in reproduction the following year. For example, a reduction of the investment in the immune system may increase the risks of infection and thus decrease the condition of the female and consequently its reproductive investment. Major functions that can be down-regulated are the immune system (e.g. Gustafsson et al. 1994; Hanssen et al. 2005; French et al. 2007; Cox et al. 2010), the oxidative defence (e.g. Alonso-Alvarez et al. 2004) and growth (e.g. Landwer 1994). Reduction in growth may be an important cost in species where female size is positively correlated with female fecundity, as typically observed in squamates but also in other species (e.g. in a crustacean; Berglund and Rosenqvist 1986). In this study we did not measure growth, but we used female current size as a covariate in the statistical models. Thus, we have corrected our analyses for potential differences in growth and quantified the effects of PBC and parturition date independently from their potential effects on growth. Future studies should attempt to measure these different functions to understand their relative importance.

Offspring mass and litter size trade-off

More than two decades ago, van Noordwijk and de Jong (1986) suggested that trade-offs will be more difficult to detect if variation in resources acquisition is high relative to variation in resources allocation. We tested this hypothesis on the litter size and offspring mass trade-off. We found a strong correlation between the variance ratio (i.e. the ratio of allocation variance to investment variance) and the strength of the litter size and offspring mass trade-off, confirming the prediction of the van Noordwijk and de Jong's model (1986). Previous studies in different species and situations also confirmed this prediction. Christians (2000) explained inter-specific variation in the strength of the trade-off between different bird species of the same order. This prediction has also been confirmed at the intra-specific level between years or different populations of the same species in scorpions (Brown 2003) and in lizards (Jordan and Snell 2002). In the common lizard, Uller and

Olsson (2005) compared field and laboratory data for a given year. They showed that the strength of the trade-offs was higher under laboratory conditions, i.e. when variation in resources acquisition was presumably lower. Our study on a multi-annual data set from a natural population also confirms the van Noordwijk and de Jong's model (1986).

Despite annual variations in the strength of the litter size–offspring mass trade-off, we did not detect any variation in offspring mass that was independent of this trade-off. In particular, offspring mass was not influenced by previous female reproduction nor by weather conditions before, during or after vitellogenesis. Thus, our data indicate that adjustments of the reproductive investment occurred via the number of offspring and that offspring mass was subsequently traded-off with litter size. This result confirms that the litter size and offspring mass trade-off is the major determinant of offspring mass (see also Bleu et al. 2012). Actually, an increased food intake caused by better weather conditions may not be invested in offspring mass (Massot and Clobert 1995); these extra resources may instead be invested in female somatic growth, resulting in higher PBC (Gregory 2006; Le Galliard et al. 2010).

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Conflict of interest None.

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