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### ► To cite this version:

Josefa Bleu, Jean-François Le Galliard, Patrick S. Fitze, Sandrine Meylan, Jean Clobert, et al.. Reproductive allocation strategies: a long-term study on proximate factors and temporal adjustments in a viviparous lizard. *Oecologia*, 2013, 171 (1), pp.141-151. 10.1007/s00442-012-2401-1 . hal-03193611

**HAL Id: hal-03193611**

**<https://hal.science/hal-03193611>**

Submitted on 8 Apr 2021

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

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25 The final publication is available at [www.springerlink.com](http://www.springerlink.com)

26 Citation: J. Bleu, J.-F. Le Galliard, P. S. Fitze, S. Meylan, J. Clobert & M. Massot (2013)

27 Reproductive allocation strategies: a long-term study on proximate factors and temporal

28 adjustments in a viviparous lizard. *Oecologia*. 171: 141-151. [doi:10.1007/s00442-012-2401-1](https://doi.org/10.1007/s00442-012-2401-1).

29 Abstract

30 Optimisation of reproductive investment is crucial for Darwinian fitness, and detailed long-term  
31 studies are especially suited to unravel reproductive allocation strategies. Allocation strategies  
32 depend on the timing of resource acquisition, the timing of resource allocation, and trade-offs  
33 between different life-history traits. A distinction can be made between capital breeders that fuel  
34 reproduction with stored resources and income breeders that use recently acquired resources. In  
35 capital breeders, but not in income breeders, energy allocation may be decoupled from energy  
36 acquisition. Here, we tested the influence of extrinsic (weather conditions) and intrinsic (female  
37 characteristics) factors during energy storage, vitellogenesis, and early gestation on reproductive  
38 investment, including litter mass, litter size, offspring mass and the litter size and offspring mass  
39 trade-off. We used data from a long-term study of the viviparous lizard, *Lacerta (Zootoca)*  
40 *vivipara*. In terms of extrinsic factors, rainfall during vitellogenesis was positively correlated  
41 with litter size and mass, but temperatures did not affect reproductive investment. With respect  
42 to intrinsic factors, litter size and mass were positively correlated with current body size and  
43 postpartum body condition of the previous year, but negatively with parturition date of the  
44 previous year. Offspring mass was negatively correlated with litter size, and the strength of this  
45 trade-off decreased with the degree of individual variation in resource acquisition, which  
46 confirms theoretical predictions. The combined effects of past intrinsic factors and current  
47 weather conditions suggest that common lizards combine both recently acquired and stored  
48 resources to fuel reproduction. The effect of past energy store points out a trade-off between  
49 current and future reproduction.

50

51 **Keywords:** capital breeder, energy allocation, phenotypic plasticity, viviparity, trade-off.

52

## 53 **INTRODUCTION**

54 Reproductive allocation decisions are of central interest in evolutionary ecology as they  
55 determine lifetime reproductive success and some of the costs associated with reproduction (Roff  
56 2002). It is possible to distinguish the allocation of resources to reproduction (i.e. how much to  
57 invest in reproduction) and the allocation of reproductive resources between the size and number  
58 of offspring. The energy invested into reproduction by a female depends on the total amount of  
59 energy available, and reproductive investment as well as allocation rules are under maternal  
60 and/or environmental (e.g. climatic) controls. In animals, there are capital breeding species that  
61 fuel reproduction with stored resources and income breeding species that use recently acquired  
62 resources (Stephens et al. 2009). Thus, in capital breeders pre-reproductive resource stores or  
63 environmental conditions experienced during the energy storage period, such as food  
64 availability, should correlate with future reproductive investment (Doughty and Shine 1997,  
65 1998; Bonnet et al. 2001; Lourdais et al. 2002; Reading 2004) or future reproductive success  
66 (Festa-Bianchet 1998). However, the capital and income breeding strategies describe only the  
67 extremes of a continuum (e.g. Houston et al. 2007). Thus, females may adjust their energy  
68 allocation strategy at multiple points in the reproductive cycle. In particular, adjustment of  
69 offspring size or litter size may occur during gestation in viviparous (i.e. live-bearing) species  
70 via embryo resorption or nutritional transfer. In viviparous lizards, for example, food and thermal  
71 conditions experienced by the mother during gestation can affect offspring mass at birth (e.g.  
72 Shine and Downes 1999; Swain and Jones 2000). A second aspect of reproductive investment  
73 decisions is the existence of trade-offs between reproduction and other life-history traits,  
74 including trade-offs between different reproductive events. In particular, current fecundity can  
75 be traded-off with future fecundity. For example, a high investment in reproduction decreases  
76 the probability to breed again and thus increases the inter-breeding interval (e.g. Bonnet et al.

77 2001; Hadley et al. 2007), or a lower investment in reproduction increases survival later in life  
78 (e.g. Clutton-Brock et al. 1983; Massot et al. 2011). In line with this trade-off hypothesis,  
79 experiments in mammals (Koivula et al. 2003), lizards (e.g. Cox and Calsbeek 2010) and birds  
80 (e.g. Richner and Tripet 1999; Hanssen et al. 2005) demonstrate that a higher reproductive effort  
81 results in a decrease in survival or fecundity the following year.

82 Finally, females can also adjust how the energy is allocated into each offspring (e.g. offspring  
83 mass), i.e. how the trade-off between litter size and offspring mass is solved. Females may vary  
84 in their resource stores and resource acquisition efficiency (Doughty and Shine 1997; Glazier  
85 1999). The van Noordwijk and de Jong's model (1986) suggests that trade-offs will be weaker  
86 if variation in resources acquisition is high relative to variation in resources allocation.  
87 Furthermore, the pattern of energy allocation to offspring mass may follow distinct pathways. It  
88 is often assumed that females decide in a sequential manner, first deciding how much to invest  
89 into reproduction, and then, how much to invest in litter size versus offspring mass (e.g. Charnov  
90 et al. 1995). However, investment and allocation decisions may also be simultaneous, genetically  
91 linked, or correlated, as suggested by an old theoretical model (Winkler and Wallin 1987) and  
92 by evidence from natural populations (Christians 2000; Uller et al. 2009).

93 Long-term studies are especially suited to disentangle the effects of past and present, and  
94 extrinsic and intrinsic factors on both total reproductive investment and reproductive allocation  
95 in litter size versus offspring mass. Squamate reptiles (i.e. lizards and snakes) are good model  
96 species for such studies because they often lack parental care (Shine 2005), and thus reproductive  
97 investment is completed during vitellogenesis and gestation in viviparous species. Moreover,  
98 potential factors affecting the investment in reproduction are well identified. In many squamates,  
99 body size influences reproductive output, such that larger females invest more in reproduction  
100 than smaller females (e.g. Shine 2005). Some squamates are typical capital breeder but others  
101 may also use mixed capital and income strategies (e.g. Bonnet et al. 2001; Houston et al. 2007).

102 Weather conditions are also of particular importance for reproduction because they directly  
103 affect habitat quality and food availability and also because foraging performances are linked to  
104 the ability to maintain optimal body temperatures (Le Galliard et al. in press). Thus, we expect  
105 that reproductive decisions should be largely dependent on pre-reproductive resource stores,  
106 food availability and weather conditions in squamates. Moreover, because parturition dates  
107 affect the duration of the energy storage period, early breeders may be able to capitalise more  
108 resources than late breeders for the next reproductive event. In this study, we used 13 years of  
109 field data on the viviparous common lizard, *Lacerta (Zootoca) vivipara*, to test the effects of  
110 extrinsic factors (temperature and rainfall during the current and previous year) and intrinsic  
111 factors (current body size, previous postpartum body condition (PBC), previous parturition date)  
112 on reproductive output. From previous studies on the common lizard we know the following.  
113 First, life-history traits are sensitive to variation in air temperature and rainfall (Chamaillé-  
114 Jammes et al. 2006; Marquis et al. 2008; Le Galliard et al. 2010). Second, stored lipids decrease  
115 during vitellogenesis (Avery 1974) and vitellogenesis occurs during a short period of 3 weeks  
116 after winter emergence (Bauwens and Verheyen 1985), which are features of capital breeders.  
117 Third, females can assimilate food during vitellogenesis (Avery 1975) and there are maternal  
118 effects during gestation (e.g. Massot and Clobert 1995; Marquis et al. 2008), which are features  
119 of income breeders.

120 Previous studies on *L. vivipara* addressed the effects of current weather (Marquis et al. 2008; Le  
121 Galliard et al. 2010) and of social interactions (Le Galliard et al. 2008) on reproductive  
122 investment, but none investigated the relative importance of past and present factors. We  
123 therefore specifically tested the importance of the previous year's weather conditions and female  
124 condition on reproductive investment. If common lizards are true capital breeders, we predict  
125 that weather conditions during energy storage, PBC and/or parturition date of the previous year  
126 should affect reproductive investment (litter mass, litter size and offspring mass). A correlation

127 of reproductive investment decisions with weather conditions during vitellogenesis and/or  
128 gestation would suggest income breeding. Finally, an intermediate situation would suggest a  
129 mixed strategy. We expect the strength of the litter size and offspring mass trade-off to depend  
130 on the variation in resource acquisition and resource allocation as predicted by the van  
131 Noordwijk and de Jong's model (1986).

## 132 ***MATERIAL AND METHODS***

### 133 **Model species**

134 *Lacerta (Zootoca) vivipara* is a small (50-70 mm adult snout-vent length, SVL) ground-dwelling  
135 lizard that is widely distributed across Eurasia. We studied viviparous populations located in the  
136 Massif Central mountain range (south-eastern France) where the reproductive cycle is annual  
137 (Fig. 1). In this area, adults start to become active around mid-April (males) or early May  
138 (females). Emergence of the females from hibernation is highly synchronised, with mating  
139 occurring 0-3 days after emergence and reproductive investment (vitellogenesis) occurring on  
140 average during the first 3 weeks after emergence (Bauwens and Verheyen 1985) (first 3 weeks  
141 of May for the Massif Central populations). During gestation, a primitive chorioallantoic  
142 placenta allows respiratory, aqueous and mineral exchanges between mother and embryos  
143 (Panigel 1956; Stewart et al. 2009). Parturition occurs after an average gestation period of 2  
144 months, i.e. in late July to mid-August. Mean litter size is five (range 1-12), including both  
145 nonviable offspring (fertilised or unfertilised eggs where only yolk is visible, undeveloped  
146 embryos, and stillborns) and live offspring. Live offspring hatch immediately after parturition  
147 and are thereafter autonomous. Adult females replenish their lipid stores during the summer  
148 immediately after parturition and gradually enter into hibernation in September (Avery 1974;  
149 Bauwens 1981).

### 150 **Population survey and rearing conditions**

151 Longitudinal data on reproductive strategies were obtained from a long-term mark-recapture  
152 survey conducted each year from 1990 to 2002 in a population at Mont-Lozère (1,420 m a.s.l.,  
153 44°23'03''N, 3°52'40''E) that consists of two adjacent habitats with different structures (Clobert  
154 et al. 1994). Adult females were captured on average 1 month before parturition (June), identified  
155 or marked by toe-clipping, and kept in the laboratory until parturition (rearing conditions as in  
156 Massot and Clobert 1995). After parturition, litter size was recorded, and females and their live  
157 offspring were weighed. Females were then released together with their live offspring at the  
158 original capture location 3-5 days after parturition. We recorded litter size for all litters (litters  
159 containing exclusively viable offspring and litters containing nonviable offspring), and we  
160 calculated litter mass and offspring mass only for litters containing exclusively viable offspring  
161 (because we could not avoid the desiccation of the nonviable offspring and thus could not weight  
162 them accurately). Litter mass was the sum of all offspring body masses, and offspring mass was  
163 litter mass divided by litter size.

#### 164 **Weather**

165 Temperature and rainfall data were recorded by Météo-France at a meteorological station  
166 situated at a similar altitude, 50 km south of the study site (Mont Aigoual, 1,567 m a.s.l., 44°07'  
167 N, 3°35' E, see Chamaillé-Jammes et al. 2006; Marquis et al. 2008). We used daily maximum  
168 temperature and daily cumulative amount of precipitation as descriptors of thermoregulation  
169 opportunities and habitat humidity (Huey 1982). For each year, we calculated mean values for  
170 different periods of the reproductive cycle, namely (1) during the previous summer activity  
171 season (energy storage period), (2) during vitellogenesis, and (3) during the early gestation  
172 period *in natura* (see Fig. 1 for more details). Correlations between these variables are reported  
173 in Electronic Supplementary Material (ESM) 1. We tested the effects of temperature during  
174 energy storage and temperature during early gestation both separately and together to address



175 potential colinearity issues caused by a significant correlation between these variables. Effects  
176 were all robust, and colinearity was therefore not a strong issue in our analyses.

### 177 **Offspring mass and litter size trade-off**

178 We also modelled the trade-off between offspring mass and litter size in more detail. Correlations  
179 were run between offspring mass and residual litter size for each year (Pearson correlations). We  
180 also ran correlations on log-transformed variables to make the results comparable with those  
181 reported in recent publications (e.g. Christians 2000). Van Noordwijk and de Jong's model  
182 (1986) predicts that more negative correlations should be found when variation in resource  
183 acquisition is low compared to variation in resource allocation. Christians (2000) adapted the  
184 van Noordwijk and de Jong's model (1986) to the litter size and offspring mass trade-off by  
185 calculating the variation in resource acquisition as the variation in total reproductive investment,  
186 i.e. variation in clutch or litter mass. Thus, as suggested by Christians (2000), we calculated the  
187 allocation as  $(\log(\text{offspring mass})/(\log(\text{litter mass})))$  and the investment as  $(\log(\text{litter mass}))$ .  
188 Then, to avoid the confounding effect of maternal size, we used the residuals of a linear  
189 regression of these variables (investment or allocation) against maternal SVL (Christians 2000;  
190 Brown 2003). We calculated the variances of these residuals to estimate the variation in female  
191 investment and in female allocation. These variances were calculated for each year. We expect  
192 a negative relationship between the ratio of allocation variance to investment variance and the  
193 Pearson's correlation coefficient between offspring mass and litter size.

194

195

### 196 **Statistical analyses**

197 All statistical models were implemented in R 2.14.1 statistical software ([http://cran.r-](http://cran.r-project.org/)  
198 [project.org/](http://cran.r-project.org/)). We analysed variation in the litter mass, litter size, and offspring mass at birth of  
199 litters containing exclusively viable offspring ( $n = 157$ ) and variation in litter size of all litters

200 (i.e. litters containing exclusively viable offspring and litters containing nonviable offspring,  $n$   
201 = 239) with mixed-effects linear models, including year as a random effect (Pinheiro and Bates  
202 2000) (*lme* procedure). The annual sample sizes are reported in ESM 2. Fifty females were  
203 captured several times in two successive years, and the measurements performed on them cannot  
204 be assumed independent. To be sure that there is no problem of pseudo-replication (only some  
205 females appeared several times in the dataset) we also did the same statistical analyses with two  
206 random effects: year and female identity (*lmer* procedure). Both analyses yielded very similar  
207 results (see ESM 3 and 4 for the results with two random effects).

208 A first random-effect model was fitted to assess inter-annual variation. Then, a mixed-effect  
209 model was fitted to test for intrinsic effects. In this model, we included, as explanatory variables,  
210 PBC of the previous reproductive season [PBC(t-1)], parturition date of the previous  
211 reproductive season [parturition(t-1)], and female SVL during the current reproductive season  
212 [SVL(t)]. Body condition was calculated as residuals of a linear regression of body mass against  
213 SVL. We also added a habitat effect (there are two habitats in our study site, see “population  
214 survey and rearing conditions”) because previous studies have reported spatial differences in life  
215 history traits between these two habitats (Clobert et al. 1994). For offspring mass, we modelled  
216 a potential trade-off with litter size. Since litter size and maternal SVL are correlated (Pearson’s  
217  $r = 0.66$ ,  $P < 0.0001$ ), we included relative litter size in the model (residuals of a linear regression  
218 of litter size against maternal SVL). To test for potential differences between litters containing  
219 exclusively viable offspring and litters containing at least one nonviable offspring, we included  
220 a categorical effect (“success”) when analysing all litters. The full model included additive and  
221 first-order interaction terms. A first minimum adequate model was selected using both backward  
222 elimination and forward selection of higher order interactions based on the Akaike Index  
223 Criterion (AIC). Finally, additive effects of weather conditions were added to the first minimum  
224 adequate model. A second minimum adequate model was then selected using the same procedure

225 as mentioned above. We report only significant effects using F tests based on restricted maximum  
226 likelihood conditional estimates of variance. Estimates  $\pm$  standard errors (SE) are shown for fixed  
227 effects and the 95% confidence intervals (CI) are given for random effects.

## 228 **RESULTS**

229 Reproductive data for 239 females, including 157 exclusively viable litters and 82 litters  
230 containing nonviable offspring, were collected over a 13-year period. We found no effect of  
231 temperature or habitat in any of the models tested (Table 1). The mass and size of litters  
232 containing exclusively viable offspring were positively correlated with rainfall during  
233 vitellogenesis (Table 1, Fig. 2), as well as with current female body size and with female PBC  
234 the previous year (Fig. 3a). However, offspring mass was only explained by residual litter size  
235 (litter size corrected by the maternal body size, Table 1). The size of all litters (litters containing  
236 exclusively viable offspring and litters also containing nonviable offspring) increased with  
237 rainfall during vitellogenesis and female body size, but was additionally influenced by the  
238 interaction between the parturition date the previous year, PBC the previous year and litter  
239 success of the current year (Table 1). In fact, consistent with the analysis reported above, the  
240 interaction between parturition date and PBC the previous year was not significant for litters  
241 containing exclusively viable offspring (partial test with “successful” litters:  $F_{1,141} = 1.54$ ,  $P =$   
242  $0.22$ ). This interaction was significant for litters containing nonviable offspring (partial test with  
243 “unsuccessful” litters:  $F_{1,66} = 7.73$ ,  $P = 0.0071$ , Fig. 3b). In these unsuccessful litters, PBC had  
244 a positive effect on litter size for females giving birth late in the season but not for early breeders  
245 (Fig. 3b).

246 Inter-annual variation was estimated using mixed-effects linear models with reproduction year  
247 as random effect. Annual factors explained between 15.93 and 27.67 % of the total inter-annual  
248 standard deviation in reproductive traits (Table 2). Intrinsic factors (body size and condition)

249 explained a large part of the inter-annual variation in litter size (for litters containing exclusively  
250 viable offspring and all litters) and litter mass (Table 2), but inter-annual variation in offspring  
251 mass remained unchanged when significant intrinsic factors (residual litter size) were included  
252 in the model (Table 2). The effect of rainfall during vitellogenesis, which was significant for  
253 litter mass and litter size, explained all remaining inter-annual variation in these two reproductive  
254 traits (Table 2).

255 In litters containing exclusively viable offspring, the correlations between residual litter size and  
256 offspring body mass were negative in all years (7 years not significant, Table 3) and there was  
257 an annual variation in the strength of the correlation (Table 3). Our analysis confirmed the  
258 existence of a strong, negative relationship between the variance ratio and the correlation  
259 between litter size and offspring mass (Figure 4, Pearson's  $r = -0.860$ , range =  $[-0.960; -0.566]$ ,  
260  $P = 0.0003$ ). These results are in line with analyses based on log transformed values of offspring  
261 mass and litter size (ESM 5).

## 262 ***DISCUSSION***

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

### 270 **Reproduction and weather conditions**

271 We investigated the effects of weather conditions on reproductive investment because they can  
272 have direct or indirect effects. First, weather conditions can directly influence the metabolism

273 and physiology of an animal. In particular, in ectotherms, it is known that temperatures influence  
274 directly maternal activity (opportunity to feed), the efficiency of food assimilation (e.g. Adolph  
275 and Porter 1993) and, during gestation, embryonic development (see below). Yet, in this study,  
276 we found no effect of temperatures on litter size, litter mass and offspring mass at birth. Previous  
277 laboratory experiments in viviparous squamates found effects of temperature or basking  
278 opportunities during gestation on offspring mass (Shine and Harlow 1993; Doughty and Shine  
279 1998; Swain and Jones 2000; Wapstra 2000; Hare and Cree 2010). Experiments in the laboratory  
280 may not reflect the natural variations of thermal conditions and also may reduce the possibility  
281 of a maternal response to compensate such variations. Some field studies have been conducted,  
282 and different results have been found, with some authors finding no effect of temperature during  
283 gestation on offspring size at birth (*Vipera aspis* Lourdais et al. 2004; *Niveoscincus ocellatus*,  
284 Cadby et al. 2010) and other authors finding an effect of temperature during gestation on  
285 offspring mass at birth but only at some altitudes (*Niveoscincus ocellatus*, Uller et al. 2011).  
286 Thus, under natural conditions, females may be able to compensate for poor climatic conditions  
287 – for example, by active thermoregulation - and may thus not be so strongly constrained by  
288 thermal conditions (Webb et al. 2006). In particular, when there is strong selection to produce  
289 larger offspring, females may be strongly selected to compensate for poor thermal conditions  
290 (for example, despite an increased predation risk) (Uller et al. 2011).

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

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

### 308 **Reproduction and intrinsic factors**

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

315 We also investigated the effects of PBC and parturition date of the previous year on current  
316 reproduction. PBC indicates the resource stores of the female after reproduction, and parturition  
317 date the previous year determines the length of the energy storage period. We found a positive  
318 effect of PBC the previous year on current reproductive investment. This result may suggest  
319 capital breeding as in other species (e.g. Doughty and Shine 1997; Festa-Bianchet 1998).  
320 However, such a long-term effect of body condition is somewhat surprising since lizards can  
321 store resources during the summer after reproduction and may thus compensate for a low PBC.  
322 The lack of compensation suggests that feeding rate is positively correlated with body condition

323 and that a low PBC indicates probably a low individual quality. In addition, we found a state-  
324 dependent effect of the parturition date of the previous year on current reproductive investment  
325 for females that produced litters containing nonviable offspring. In these cases, litter size was  
326 constrained by PBC of the previous year when females gave birth late in the previous season,  
327 but not when females gave birth early in the previous season. This illustrates that earlier breeding  
328 and parturition may be advantageous for subsequent reproduction for some females.

329 The effect of previous PBC on current reproductive investment suggests a trade-off between  
330 successive reproductive events, because a low PBC is associated with a stronger reproductive  
331 effort in the common lizard (Le Galliard et al. 2010). The mechanisms of such trade-offs are  
332 increasingly studied. First, there may be a simple energetic link between the two reproductive  
333 events (Roff 2002): females that used more energy have fewer resources for the next season and  
334 may not be able to compensate this difference. However, more complex scenarios are also  
335 possible. Resources allocated to reproduction are not available for other functions, which may  
336 thus be down-regulated as a consequence of a high reproductive investment, leading to a lower  
337 investment in reproduction the following year. For example, a reduction of the investment in the  
338 immune system may increase the risks of infection and thus decrease the condition of the female  
339 and consequently its reproductive investment. Major functions that can be down-regulated are  
340 the immune system (e.g. Gustafsson et al. 1994; Hanssen et al. 2005; French et al. 2007; Cox et  
341 al. 2010), the oxidative defence (e.g. Alonso-Alvarez et al. 2004) and growth (e.g. Landwer  
342 1994). Reduction in growth may be an important costs in species where female size is positively  
343 correlated with female fecundity, as typically observed in squamates but also in other species  
344 (e.g. in a crustacean, Berglund and Rosenqvist 1986). In this study we did not measured growth,  
345 but we used female current size as a covariate in the statistical models. Thus, we have corrected  
346 our analyses for potential differences in growth and quantified the effects of PBC and parturition

347 date independently from their potential effects on growth. Future studies should attempt to  
348 measure these different functions to understand their relative importance.

### 349 **Offspring mass and litter size trade-off**

350 More than two decades ago, van Noordwijk and de Jong (1986) suggested that trade-offs will be  
351 more difficult to detect if variation in resources acquisition is high relative to variation in  
352 resources allocation. We tested this hypothesis on the litter size and offspring mass trade-off. We  
353 found a strong correlation between the variance ratio (i.e. the ratio of allocation variance to  
354 investment variance) and the strength of the litter size and offspring mass trade-off, confirming  
355 the prediction of the van Noordwijk and de Jong's model (1986). Previous studies in different  
356 species and situations also confirmed this prediction. Christians (2000) explained inter-specific  
357 variation in the strength of the trade-off between different bird species of the same order. This  
358 prediction has also been confirmed at the intra-specific level between years or different  
359 populations of the same species in scorpions (Brown 2003) and in lizards (Jordan and Snell  
360 2002). In the common lizard, Uller and Olsson (2005) compared field and laboratory data for a  
361 given year. They showed that the strength of the trade-offs was higher under laboratory  
362 conditions, i.e. when variation in resources acquisition was presumably lower. Our study on a  
363 multi-annual data set from a natural population also confirms the van Noordwijk and de Jong's  
364 model (1986).

365 Despite annual variations in the strength of the litter size-offspring mass trade-off, we did not  
366 detect variation in offspring mass that was independent of this trade-off. In particular, offspring  
367 mass was not influenced by previous female reproduction nor by weather conditions before,  
368 during or after vitellogenesis. Thus, our data indicate that adjustments of the reproductive  
369 investment occurred via the number of offspring and that offspring mass was subsequently  
370 traded-off with litter size. This result confirms that the litter size and offspring mass trade-off is  
371 the major determinant of offspring mass (see also Bleu et al. 2012). Actually, an increased food



372 intake caused by better weather conditions may not be invested in offspring mass (Massot and  
373 Clobert 1995), these extra resources may instead be invested in female somatic growth, resulting  
374 in higher PBC (Gregory 2006; Le Galliard et al. 2010).

## 375 **ACKNOWLEDGMENTS**

376 We are grateful to the students who helped collect data and to the *Parc National des Cévennes*  
377 and the *Office National des Forêts* for providing good conditions during fieldwork. We thank  
378 *Météo-France* for providing the weather data used in this study. Financial support was received  
379 from the *Agence Nationale de la Recherche* (grant 07-JCJC-0120 to J.F.L.G and grant 07-  
380 BLAN-0217 to M. M. and J. C.), the Spanish Ministry of Education and Science (CGL2005-  
381 01187, CGL2008-01522, and Programa Ramón y Cajal to P. S. F.), the Swiss National Science  
382 Foundation (PPOOP3\_128375) and the *Ministère de l'Éducation Supérieure et de la Recherche*  
383 (Ph.D grant to J. B.). The authors declare that they have no conflict of interest.

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558



559 **TABLES**

560 **Table 1. Effects of intrinsic and extrinsic factors on reproductive traits.** Final models were selected  
 561 starting with full models. These included intrinsic factors [current body size: SVL(t), PBC of the previous  
 562 reproductive season: PBC(t-1), parturition date of the previous reproductive season: Parturition(t-1), litter  
 563 success: Success], and extrinsic factors (habitat, rainfall and temperatures during energy storage,  
 564 vitellogenesis and gestation, see Fig. 1 for details). Residual litter size was calculated as the residuals of  
 565 a linear regression between litter size and maternal SVL. Random effects are presented in Table 2.

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

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

567

568 **Table 2. Annual variations of reproductive traits.** Estimates of year random effect for litter mass, size  
 569 of exclusively viable litters, offspring mass, and size of all litters. Estimates are given as standard  
 570 deviations (SD) calculated from a random model with no fixed effect (“annual variation” model), a mixed  
 571 effect model with significant intrinsic factors (“intrinsic factors” model) and a mixed effect model with  
 572 significant intrinsic and extrinsic factors (“final best model”, Table 1).

	$\sigma_{\text{annual}}$	$\sigma_{\text{residual}}$	ICC	LRT	P
<b>Litter mass</b>					
Annual variation	0.09 [0.05 ; 0.19]	0.29 [0.25 ; 0.32]	24.50	4.95	0.0260
Intrinsic factors	0.05 [0.01 ; 0.15]	0.21 [0.18 ; 0.23]	18.15	1.17	0.2786
Final best model	~ 0	0.21 [0.18 ; 0.23]	0		
<b>Size of litters containing exclusively viable offspring</b>					
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		
<b>Size of all litters</b>					
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 <sup>a</sup>	1.24 [1.16 ; 1.39]	0		
<b>Offspring mass<sup>b</sup></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

573 Values between square brackets indicate the confidence interval.

574  $\sigma_{\text{annual}}$  = year effect standard deviation,  $\sigma_{\text{residual}}$  = residual standard deviation, ICC = intraclass correlation  
 575 coefficient (% of total standard deviation), LRT = likelihood ratio test.

576 <sup>a</sup> ~ 0 indicates an estimate at the boundary of the parameter space.

577 <sup>b</sup> Effects of extrinsic factors were not significant for offspring mass

578

579 **Table 3. Annual variation in the offspring mass and litter size trade-off.** The trade-off was  
580 investigated in litters containing exclusively viable offspring (n = 157). Pearson's r correlation coefficient  
581 was calculated between offspring mass and residual litter size for each year (see ESM 5 for results on  
582 log-transformed values). Following on Christians (2000), we calculated the variance ratio as the ratio of  
583 the variance in allocation [i.e. var{log(offspring mass)/log(litter mass)}] to the variance in investment  
584 [i.e. var{log(litter mass)}].  
585

<b>Year</b>	<b>n</b>	<b>Pearson's r</b>	<b>95% confidence interval</b>	<b>P</b>	<b>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
<b>1993</b>	<b>21</b>	<b>-0.493*</b>	<b>-0.762 to -0.078</b>	<b>0.023*</b>	<b>0.0189*</b>
1994	18	-0.226	-0.627 to 0.269	0.366	0.0133
<b>1995</b>	<b>13</b>	<b>-0.713*</b>	<b>-0.908 to -0.267</b>	<b>0.006*</b>	<b>0.0246*</b>
<b>1996</b>	<b>15</b>	<b>-0.611*</b>	<b>-0.855 to -0.143</b>	<b>0.016*</b>	<b>0.0195*</b>
<b>1997</b>	<b>12</b>	<b>-0.870*</b>	<b>-0.963 to -0.592</b>	<b>&lt; 0.001*</b>	<b>0.0451*</b>
1998	11	-0.475	-0.837 to 0.174	0.140	0.0169
<b>1999</b>	<b>11</b>	<b>-0.705*</b>	<b>-0.917 to -0.182</b>	<b>0.015*</b>	<b>0.0246*</b>
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

586 \* Correlation is significant at P < 0.05

587

## **FIGURE LEGENDS**

**Figure 1. Reproductive cycle of the common lizard 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).

**Figure 2. Variation in litter mass.** Residual litter mass (residuals of litter mass from a linear regression against maternal SVL and previous postpartum body condition (PBC), see Table 1) is shown as means ( $\pm$  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 =  $0.016 \pm 0.007$ ,  $F_{1,9} = 2.18$ ,  $P = 0.057$ ).

**Figure 3. Variation in litter size.** a) Postpartum body condition (PBC) of the previous year was correlated with the size of litters containing exclusively viable offspring ( $n = 157$ ). The 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 =  $2.225 \pm 0.648$ ,  $P = 0.0007$ ) but not significantly different from zero in early breeders ( $n = 40$ , slope =  $0.063 \pm 0.690$ ,  $P = 0.93$ ). Data for litter sizes are residuals of a linear regression between litter size and maternal SVL.

**Figure 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  $r = -0.918$ , range =  $[-0.979; -0.707]$ ,  $P < 0.0001$ ).

**FIGURES**

Figure 1

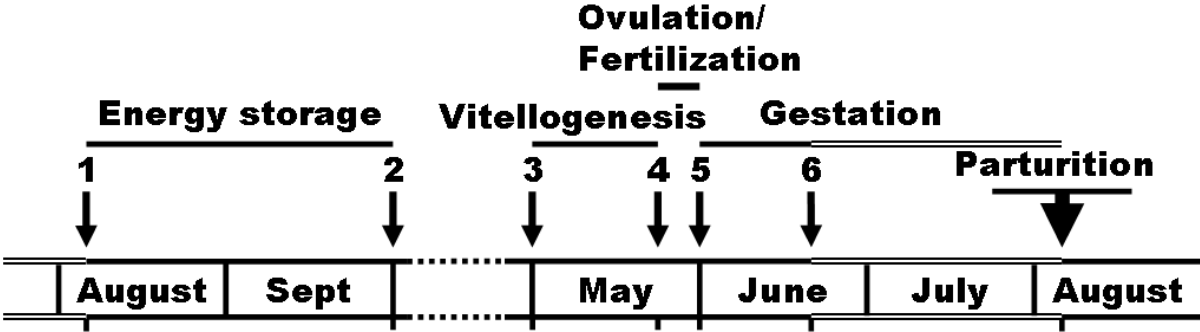


Figure 2

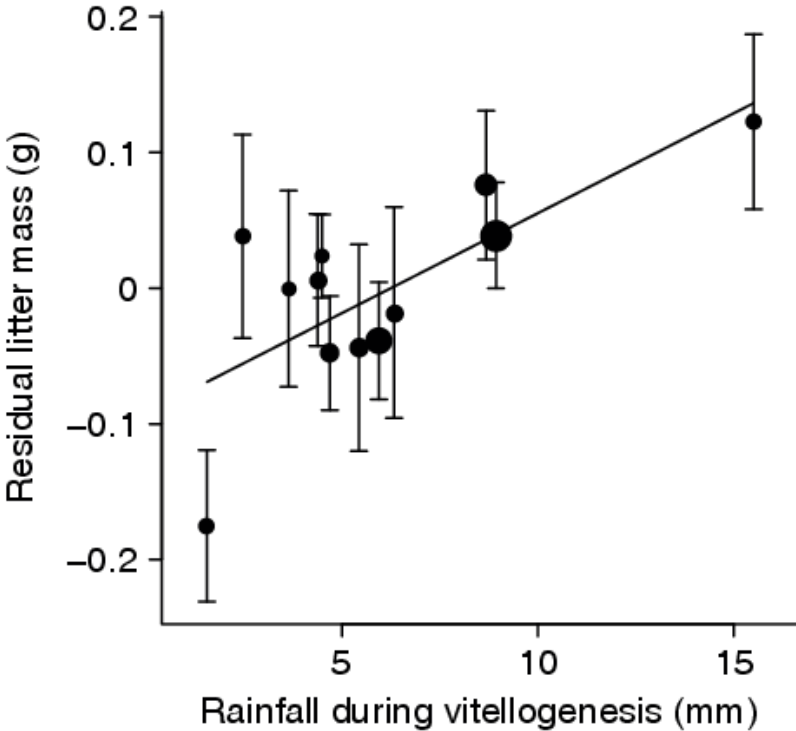


Figure 3

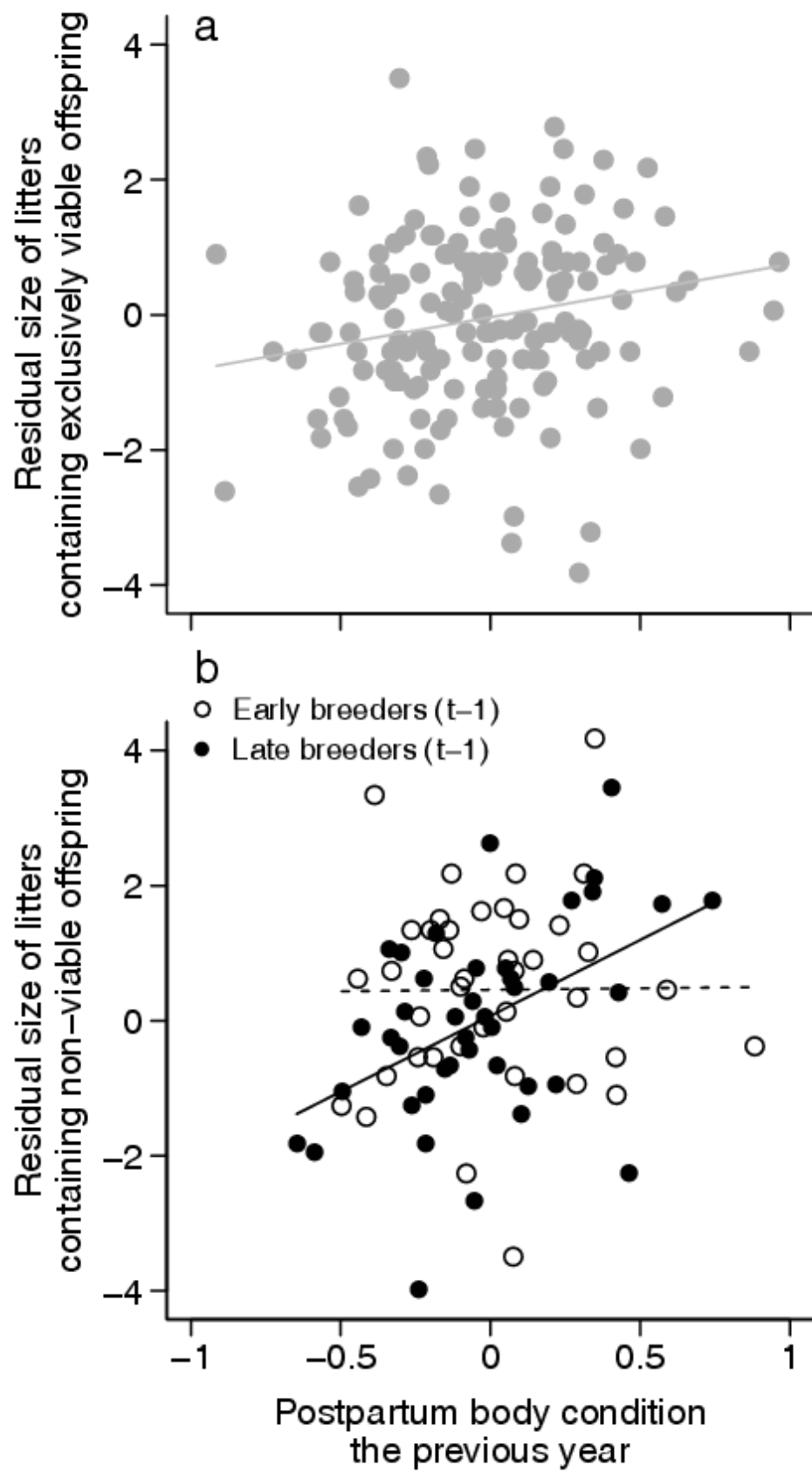


Figure 4

