



Mother-offspring conflict for water and its mitigation in the oviparous form of the bimodal lizard *Zootoca vivipara*

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**Mother-offspring conflict for water varies across altitude
and is mitigated in the oviparous form of the bimodal lizard
*Zootoca vivipara***

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93**in the oviparous form of the bimodal lizard *Zootoca vivipara***

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Abstract

Parent-offspring conflicts are widespread in nature given that resources are often limited. Recent evidence has shown that water can trigger such conflict during pregnancy in viviparous squamate species (lizards and snakes) and thus questions the role of water in the evolution of reproductive modes. Here, we examined the impact of water restriction during gravidity in the oviparous form of the bimodal common lizard (*Zootoca vivipara*), using the same protocol previously used in the viviparous form. Females were captured in early gravidity from six populations across a 600 m altitudinal gradient to investigate if environmental conditions (altitude, water access and temperature) may exacerbate responses to water restriction. Females were significantly dehydrated after water restriction, irrespective of their reproductive status (gravid *versus* non-reproductive), relative reproductive effort (relative clutch mass), and treatment timing (embryonic development stage). Female dehydration together with reproductive performance varied along altitude, likely due to long term acclimation or local adaptation. This moderate water-based intergenerational conflict in gravid females sharply contrasts to previous findings in the viviparous form, suggesting a potential implication in the reversion from viviparity to oviparity. Therefore, oviparity may constitute a water-saving reproductive mode which might help mitigate intensive temperature-driven population extinctions at low altitudes.

Keywords. Altitude, mother-offspring conflicts, dehydration, ectotherm, parity mode, reproduction

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Introduction

Life history trade-offs, by shaping the allocation of resources within and between generations, are central to the evolution of reproductive strategies (Stearns, 1992; Harshman & Zera, 2007; Kölliker *et al.*, 2015). Intergenerational trade-offs refer to parental allocation strategies to the offspring and may lead to *parent-offspring conflicts* (POCs) when resources become scarce (Trivers, 1974). POCs have been used to model the evolution of parental care, optimal parental investment, life history strategies (Godfray, 1995; Haig, 2010; Kölliker *et al.*, 2015), and even the evolution of reproductive modes (Zeh & Zeh, 2000; Crespi & Semeniuk, 2004; Pollux *et al.*, 2014).

In animals, parity modes range from oviparity (egg-laying) to viviparity (live-bearing) and are unimodal in many animal families and orders (e.g., birds or eutherian mammals). Yet, squamate reptiles (i.e., lizards and snakes) display exceptional diversity in reproductive strategies by covering the whole spectrum of reproductive modes from some species laying eggs in early developmental stages to others bearing embryos with complex placental structures (Blackburn, 2006; Van Dyke, Brandley, & Thompson, 2014). The different selective forces involved in the evolution of viviparity in squamates remain debated as shown by recent phylogenetic and comparative studies (Pyrön & Burbrink, 2014; Blackburn, 2015; Shine, 2015). An accepted view is that viviparity evolved from oviparity more than 110 times independently (Blackburn, 2006) given the general selective advantage associated with extended maternal care (Shine, 2014). In ectotherms, it is often advantageous for the mother to control stable and optimal thermal conditions of development through behavioural means (Li *et al.*, 2009; Llorioux *et al.*, 2013b; Llorioux, Lisse, & Lloridais, 2013a; Foucart, Heulin, & Lloridais, 2018). However, prolonged egg retention may generate an arms race between maternal investment and embryonic resource acquisition [the ‘Viviparity conflict hypothesis’ (Crespi & Semeniuk, 2004)]. Such elevated costs of pregnancy may preclude the transition

from oviparity to viviparity and explain intermediate stages of retention as observed in many oviparous squamates (Andrews, 2004; Blackburn, 2015). Additionally, pregnancy costs may explain reverse transitions from viviparity to oviparity as recently hypothesized (Recknagel, Kamenos, & Elmer, 2018; Gao *et al.*, 2019; Horreo, Suarez, & Fitze, 2020). That said, how water shapes the evolution of reproductive strategies remains an open question, and our objective was to determine whether a mother-offspring conflict for water would differ between reproductive modes.

The vast majority of reptile species are lecithotrophic, meaning that mothers invest nutrients into the yolk prior to ovulation (Fig. 1) and embryos rely on this store of nutrients for their growth and development (Blackburn & Stewart, 2011; Stewart & Blackburn, 2015). In lecithotrophic species, embryos cannot manipulate energy allocation after ovulation, so there is a release from the mother-offspring conflict for energy. However, mothers must also control thermal conditions during pregnancy and supply a substantial amount of water to their developing embryos (Packard, 1991). Maternal water supply is essential for embryos to convert vitellus into embryonic tissues and, in addition, water demand of embryos increases with exponential somatic growth (Packard, 1991; Shine & Thompson, 2006; Lourdais *et al.*, 2015). Yet, in most squamate species from temperate regions, pregnancy occurs during summer to maximize opportunities for thermoregulation at a time when water is potentially scarce. Water restriction during pregnancy can therefore trigger intergenerational conflicts between mother and offspring in viviparous lizards and snakes (Dupoué *et al.*, 2015a, 2018a). Remarkably, water-based mother-offspring conflicts have been associated with higher offspring mortality in a viviparous lizard (Dupoué *et al.*, 2018a), suggesting that water limiting environments may challenge the benefits of prolonged egg retention.

Species with bimodal reproduction (i.e., distinct reproductive modes between populations) offer the ideal opportunity to clarify the evolution of reproductive strategies. For

instance, the bimodal European common lizard (*Zootoca vivipara*) is arguably a model species to examine costs and benefits of parity modes (Foucart *et al.*, 2014; Recknagel & Elmer, 2019), and to understand the factors leading to the transition to viviparity (Surget-Groba *et al.*, 2006; Rodríguez-Díaz & Braña, 2012). This lizard is oviparous in the southern margin of distribution range (Pyrenean Mountains, Northern Spain and locally in the Alps and Balkans) but viviparous in the rest of its Eurasian distribution (Heulin *et al.*, 2000). The two reproductive forms share similar affinities for relatively wet habitats, suggesting high water dependence for reproduction (Lorenzon *et al.*, 1999; Marquis, Massot, & Le Galliard, 2008; Le Galliard *et al.*, 2012). Two independent oviparous clades have been identified (Recknagel *et al.*, 2018): while oviparity is an ancestral trait in the Eastern oviparous populations (*Zootoca vivipara carniolica*) it likely results from reversal in Western oviparous ones (*Zootoca vivipara lousilantzi*). Females lay slightly calcified eggs at a relatively advanced stage in embryonic development [stage 30-35 *sensu* (Dufaure & Hubert, 1961)], and embryo stage at oviposition can vary with altitude (Heulin, Oseneegg-Leconte, & Michel, 1997; Rodríguez-Díaz & Braña, 2012) and reproductive effort (Foucart, Heulin, & Lourdais, 2017).

In the present study, we tested if water-based conflict between mother and offspring occurred in the Western oviparous form of the common lizard (*Zootoca vivipara lousilantzi*), as previously found in the viviparous form and using the same protocol (Dupoué *et al.*, 2018a). We compared the physiological responses (dehydration rate) of gravid and non-reproductive oviparous females exposed to a 14-day period of water restriction in early June, which occurred relatively sooner in female reproductive cycle compared to the viviparous females (Fig. 1). We characterized the two assumptions of water-based conflict by determining i) if gravid females paid an extra water cost compared to non-reproductive ones after water restriction, and ii) whether female dehydration correlated to relative clutch mass (RCM, the residuals extracted from an independent linear mixed model of clutch mass against

female body size, Fig. S1) (Dupoué *et al.*, 2015a, 2018a). We also examined the consequences of water restriction on reproductive performance including oviposition date, RCM, incubation time, hatching success and hatching traits (offspring size and mass). Water restriction may (Dauphin-Villemant & Xavier, 1986; Brusch *et al.*, 2018) or may not (Dupoué *et al.*, 2015a, 2018a) impact reproductive traits such as clutch mass at laying (oviparous species) or litter mass at parturition (viviparous species). Furthermore, a competition for water between developing siblings may exist (Bonnet, Naulleau, & Shine, 2017). These intergenerational and intrauterine conflicts may explain why hatchlings of oviparous species are generally larger than neonates of viviparous ones [see Table 1 in (Bonnet *et al.*, 2017)]. Indeed after oviposition, the physiological constraints on female water balance are released (Fig. 1). We therefore hypothesized mother-offspring conflict for water to be modest in the oviparous common lizard due to relatively low hydric investment toward the eggs. We predicted similar responses to water restriction between gravid and non-reproductive females, and that dehydration of gravid females should also be uncorrelated with RCM or treatment timing due to lower water demand for reproduction. Females were captured in the Pyrenees Mountains from six natural populations, and we further examined the effect of population altitude, water availability (permanent access in peat-bogs *versus* periodic in underwood and dry meadows) and average thermal conditions. We hypothesized females to be locally adapted to environmental conditions along altitude, as seen in a previous comparative study of thermal preferences in the same geographic area (Trochet *et al.*, 2018). In response to water restriction, we expected gravid females from low altitudes (i.e., relatively hot and dry habitats), to exhibit stronger resistance to dehydration and greater reproductive performance than those from highlands.

Material and methods

Study species, populations and husbandry

144 The European common lizard, *Zootoca vivipara*, is a small (adult snout-vent length SVL ~ 50
145 - 75 mm), widespread lacertid typically found in cold humid peat bogs and heathland habitats
146 from Western Europe to Scandinavia and Eastern Russia (Heulin *et al.*, 2000). Between the
147 15th and 31st of May 2018, we caught a total of 134 adult females (105 gravid and 29 non-
148 reproductive) from 6 populations distributed throughout the Pyrenees mountain range (Table
149 S1). The reproductive strategy of the Western oviparous form substantially changes with
150 increasing SVL across altitude (Fig. S2), and earlier and multiple clutches as well as earlier
151 age at maturation observed in warmer habitats at lowland elevations (< 300 m) compared to
152 single reproductive event at higher altitudes (Heulin *et al.*, 1997). In our study, the altitudinal
153 range (990-1580 m) was strong enough to examine altitudinal variation of reproductive
154 performance (see below), while narrow enough to avoid strong differences in life history
155 strategies.

156 Females were captured by hand and then transferred to the laboratory where they were
157 housed in individual terraria (18 x 12 x 12 cm) with sterilized soil, a shelter, and basking heat
158 until parturition. Each individual was provided a 20-35°C thermal gradient for 6 hours per day
159 (09:00-12:00 and 14:00-17:00) using a 25 W incandescent light bulb placed over one end of
160 each terrarium. They had *ad libitum* access to water in a petri dish and we further provided
161 water 3 times per day at 09:00, 13:00, and 17:00. We further provided them with 3
162 mealworms (*Tenebrio molitor*) every two days. Females were kept in these standard
163 conditions until oviposition except during the water restriction experiment (see below
164 experimental design).

165 We characterized environmental conditions for each population, with altitude (Table
166 S1), presence of permanent *versus* periodic water sources and air temperature, because these
167 measures were likely to shape local adaptations in the regulation of the water balance as
168 documented previously in the viviparous form (Dupoué *et al.*, 2017a). We recorded air

temperature using three data loggers (iButtons, Maxim Integrated Products, Sunnyvale, CA, USA, $\pm 0.5^{\circ}\text{C}$) per population placed at locations where we found most lizards within vegetation at ground level and completely shaded to avoid the effect of radiation. Air temperature was recorded every hour, and we standardized the sampling period from the June 30th to July 25th 2018 to enable population comparisons (Dupoué *et al.*, 2017a). During this sampling period, we extracted the average daily minimum and maximum temperatures (T_{\min} and T_{\max} , respectively) to assess the thermal conditions of each population (Table S1).

Experimental design

A few days following capture, we randomly assigned females within each population to two experimental treatments following the exact same protocol we previously used on viviparous females from the same species (Dupoué *et al.*, 2018a). In the water-restricted treatment, we removed the water bowl and reduced the misting frequency to once per day occurring in the morning. In the control treatment, lizards had permanent access to the water bowl and were misted three times per day. The control treatment mimics conditions in which lizards find permanent access to water (e.g., peat bog, marsh). Instead, the water-restricted treatment reflects summer conditions in dry habitats where in the absence of precipitation, morning dew is the only source of drinking water. Water restriction lasted for 14 days and occurred on a range of treatment timing from 32 to 4 days before oviposition, a time when females were between mid-late vitellogenesis to early gravidity (Fig. 1). After the period of water restriction, all females returned to the control water conditions, having permanent access to water in a water bowl and being misted three times per day. We released non-reproductive females within 2 weeks following experiments after controlling their body mass (BM) trajectories and palpation to confirm their non-reproductive status. Gravid females were released within 3 days post-laying at their capture location.

After oviposition, clutches (range = 1 to 9 eggs) were weighed (± 1 mg) and placed in individual plastic cups on water-saturated vermiculite to maintain hydric conditions and incubated at $T_{\text{set}} = 25^{\circ}\text{C}$ to optimise incubation time without risk of overheating for embryo development (Rodríguez-Díaz *et al.*, 2010; Foucart *et al.*, 2018). We used three incubators (Novital Covatutto Eco, Italy) and we randomly distributed the clutches in the three incubators ($n = 35$ per incubator) that remained within a 1°C range of observed temperatures (mean \pm SD, incubator 1: $T_{\text{obs}} = 24.38 \pm 0.26^{\circ}\text{C}$; incubator 2: $T_{\text{obs}} = 24.05 \pm 0.39^{\circ}\text{C}$; incubator 3: $T_{\text{obs}} = 24.63 \pm 0.30^{\circ}\text{C}$). Juveniles were released within 3 days post-hatching in their respective populations.

Female water balance

Females were weighed (BM, ± 1 mg) every three days throughout the water restriction period to assess effects of water restriction on short-term changes since BM is an indicator of hydration state (Lillywhite *et al.*, 2012). However, for simplicity, we only examined BM changes ($\Delta\text{BM} = \text{BM}_{\text{final}} - \text{BM}_{\text{initial}}$) from the initiation to the end of the water restriction period. We also measured absolute changes in plasma osmolality ($\Delta\text{Osmo} = \text{Osmo}_{\text{final}} - \text{Osmo}_{\text{initial}}$), which is a rigorous measure of whole-body hydration in vertebrates (Peterson, 2002). For these assessments, females were bled at the onset and at the end of the water restriction period using a standard protocol (Meylan, Dufty, & Clobert, 2003). Blood samples (ca. 40 μL whole blood) were collected from the post-orbital sinus and centrifuged for 5 min at 11,000 rpm. Plasma was then separated from the blood cells and kept frozen at -30°C in airtight tubes until analyses were performed. Plasma osmolality (± 1 mOsm.kg $^{-1}$) was determined using a vapour pressure osmometer (model 5500, Wescor, Logan, UT, USA) according to the protocol previously established in this species (Dupoué *et al.*, 2017a). Before analyses, plasma was diluted (1:1) in a physiological serum (304 mOsm.kg $^{-1}$) so that plasma

osmolality could be determined from 10 μ L duplicates (intra-individual coefficient of variation: 1.17%).

Reproductive performance

We examined the effects of water restriction on different reproductive traits. We checked females daily to compare oviposition date. For each female we subtracted the oviposition date from the last day in hydric treatment to calculate the treatment timing. As an index of reproductive effort, we estimated size-adjusted relative clutch mass (RCM) at oviposition (i.e., residuals from the linear relationship between clutch mass and body size, $CM - SVL: t_{103} = 7.2$, $p < 0.001$, Fig. S1) to determine how much females deviate from the reproductive effort predicted by their body size (Bonnet *et al.*, 2003). We used SVL as denominator in this linear regression instead of post-laying BM because i) SVL is fixed and less biased than post-laying BM (Bonnet *et al.*, 2003), ii) SVL-adjustments might better explain reproductive changes than BM-adjustments (Dupoué & Lourdais, 2014; Foucart *et al.*, 2014), and iii) because SVL was a better predictor of female clutch mass ($r^2 = 0.34$) than post-laying BM ($r^2 = 0.21$). We calculated the incubation time as the day difference between hatching and oviposition dates. We determined hatching success as the number of live juveniles within the clutch against stillborn and undeveloped eggs. All alive offspring were then counted, weighed (BM, ± 1 mg), measured (SVL, ± 1 mm), and sexed by counting ventral scales on the medioventral lines (Lecomte, Clobert, & Massot, 1992).

This method assumes a discriminant relationships between the number of ventral scales and phenotypic sex, based on sexual dimorphism in body size at birth, which has been recently shown to be independent from water restriction (Dupoué *et al.*, 2019). Given that *Zootoca vivipara* from oviparous populations differ in body size, shape, and life history from viviparous populations (Dupoué pers. obs.), we thus used the adult females sampled for this study and males with obvious secondary sexual characters ($n = 79$) captured only to count

ventral scales (released the same day) to fit a discriminant function on ventral scales and sex (mean \pm SE, left side, females: 29.61 ± 0.09 , males: 26.16 ± 0.13 , $\chi_{1,220}^2 = 31.8$, $p < 0.001$; right side, females: 29.52 ± 0.10 , males: 26.39 ± 0.14 ; $\chi_{1,221}^2 = 189.8$, $p < 0.001$) with high determination success (96.5%, Table S2). Scalation may vary across altitude (Thorpe & Baez, 1993), but here scale number differences between sexes was independent of geographic locality (interaction term between population and ventral scales, left side: $\chi_{3,168}^2 = 5.3$, $p = 0.153$, right side: $\chi_{3,171}^2 = 0.9$, $p = 0.835$).

Statistical analyses

All analyses were performed using R software (version 3.2.0, R Core Team 2016, <https://www.r-project.org/>).

First, we checked whether initial BM (BM_{ini}) and osmolality ($Osmo_{ini}$) differed between gravid and non-reproductive females according to treatment affiliation, using linear mixed models [package *lme4* (Bates *et al.*, 2015)]. Models included fixed effects of hydric treatment (control *versus* water restriction), reproductive state (gravid *versus* non-reproductive) and their first-order interaction. We set the population origin as a random effect to control for non-independence of females within populations.

ΔBM and $\Delta Osmo$ were then analysed using similar model construction, including the fixed effects of hydric treatment, reproductive state, their first-order interaction, and the random effects of population. We added the effects of initial physiological value (at the onset of experiment) as linear covariate. In gravid females, we analysed the relationships between dehydration rate (ΔBM or $\Delta Osmo$) and RCM using similar design except that we replaced the reproductive status by RCM as described in first models. Preliminary analyses showed that female SVL had no effect on dehydration rate, which was confirmed in further analyses (Table S3 & S4).

We examined whether female dehydration rate could be further related to treatment timing and environmental conditions. For each response variable (ΔBM or ΔOsmo), we used the Akaike information criterion corrected for small sample size [AICc, package AICcmodavg (Mazerolle, 2017)], to compare a set of models with different environmental measures (Table S3: all females; Table S4: gravid females only). In all models, population was set as a random factor to account for the non-independence of females within population. Our set of models included i) a *null* model with only the intercept and random factor, ii) simple models (initial values of BM, SVL, osmolality, reproductive status or hydric treatment alone), iii) additive models with initial value, SVL, reproductive status, hydric treatment and additive effects of each environmental conditions (altitude, water access, and T_{\min} and T_{\max} treated separately; see all models in Table S3), and iv) interactive models with initial value, SVL, reproductive status, hydric treatment, first and second order interactive effects between hydric treatment, reproductive status and each environmental condition treated separately (altitude, water access, T_{\min} and T_{\max} , see Table S3). In gravid females specifically, we used a similar procedure to test the effects of initial physiological state, SVL, treatment timing, hydric treatment, environmental conditions and their interaction on ΔBM and ΔOsmo (see all models in Table S4). In some models, altitude was treated as explanatory covariates in addition with SVL or treatment timing, a procedure that may induce multicollinearity given the positive correlation between those (respectively: $t_{6.1} = 3.1$, $p = 0.022$, $t_{106.0} = 6.9$, $p < 0.001$). Despite this relationship, the Pearson's correlation coefficients between SVL and altitude ($r = 0.32$) or treatment timing and altitude ($r = 0.55$) were below the threshold when multicollinearity bias may occur ($r = 0.70$) (Dormann *et al.*, 2013).

We used similar approaches to determine whether reproductive performance was correlated with treatment timing and whether it differed between hydric treatments, alone, in addition to, or in interaction with environmental conditions (altitude, water access, and T_{\min}

and T_{\max} treated separately; see all models in Table S5). In all models, population was set as a random factor. Oviposition date (Julian date), RCM and incubation time were analysed with linear mixed models, and hatching success was analysed with mixed-effect logistic regressions including a logit link and binomial error term (number of viable *versus* number of failed offspring). Offspring SVL and BM were analysed with similar linear mixed models, with offspring sex as an additive or interactive factor (see all models in Table S5) and random factors included both the mother identity and population to account for non-independence between siblings and within populations.

Results

Physiological responses to water restriction

At the onset of experiment, BM_{ini} was higher in gravid than non-gravid females ($t_{135.6} = -2.6$, $p = 0.010$), irrespective of treatment affiliation (control: 3.200 ± 0.087 , water restriction 3.192 ± 0.085 g, $t_{132.9} = -0.5$, $p = 0.632$). $Osmo_{ini}$ did not differ neither between reproductive statuses ($t_{135.0} = -0.5$, $p = 0.635$) nor between treatment affiliation (control: 319.1 ± 2.2 , water restriction 319.4 ± 2.7 mOsm.kg⁻¹, $t_{129.4} = 0.2$, $p = 0.845$).

At the end of exposure to hydric treatment, changes in body mass (ΔBM) were positively correlated with BM_{ini} ($t_{134.0} = 4.3$, $p < 0.001$) and lower in water restricted females compared to controls ($t_{134.0} = -5.5$, $p < 0.001$, Fig. 2A), irrespective of their SVL and reproductive state (Table S3). In gravid females, ΔBM was positively correlated with RCM ($t_{105.0} = 3.1$, $p = 0.003$, Fig. 2B), and negatively correlated to treatment timing ($t_{105.0} = -2.1$, $p = 0.041$, Fig. 2C), irrespective of hydric treatment (Table S4). At the same time, the changes in plasma osmolality ($\Delta Osmo$) were negatively correlated with $Osmo_{ini}$ ($t_{133.2} = -8.3$, $p < 0.001$) and significantly increased following water restriction compared to control conditions ($t_{129.2} = 6.6$, $p < 0.001$, Fig 2D) irrespective of their SVL and reproductive state (Table S3). In

315 gravid females, ΔOsmo was neither correlated with RCM ($t_{104.9} = -0.8$, $p = 0.410$, Fig. 2E),
 316 nor with treatment timing ($t_{105.0} = -0.1$, $p = 0.957$, Fig 2F), in both hydric treatments (Table
 317 S4).

318 Females from lower altitude populations exhibited higher sensitivity to water
 319 restriction since they experienced a greater loss of BM ($t_{105.0} = 2.9$, $p = 0.005$, Fig. 3A) and
 320 higher increases in plasma osmolality ($t_{105.0} = -3.2$, $p = 0.002$, Fig. 3B) than those from
 321 highlands, while no significant altitudinal variation of hydration state occurred in control
 322 females (both, $p > 0.800$, Fig 3A & 3B), irrespective of reproductive status (Table S3).

323 *Effects of water restriction on reproductive output*

324 Water restriction had no effect on reproductive performance, including oviposition date (mean
 325 \pm SE, control mothers: 29th June \pm 1 day, water-restricted mothers: 30th June \pm 1 day, $t_{100.3} =$
 326 0.8, $p = 0.415$), clutch mass (control mothers: 1.366 ± 0.059 g, water-restricted mothers:
 327 1.370 ± 0.065 g, $t_{102.7} = 0.0$, $p = 0.967$), RCM (control mothers: 0.005 ± 0.044 , water-
 328 restricted mothers: -0.005 ± 0.055 , $t_{102.6} = -0.1$, $p = 0.891$), incubation time (control mothers:
 329 19.0 ± 0.2 days, water-restricted mothers: 19.1 ± 0.2 days, $t_{73.0} = 0.7$, $p = 0.479$), hatching
 330 success (control mothers: $52.3 \pm 5.4\%$, water-restricted mothers: $59.3 \pm 5.8\%$, $z = 1.7$, $p =$
 331 0.097), nor on offspring SVL (control mothers: 20.07 ± 0.11 mm, water-restricted mothers:
 332 20.19 ± 0.10 mm, $t_{72.5} = 0.5$, $p = 0.632$) or BM (control mothers: 225.1 ± 2.7 mg, water-
 333 restricted mothers: 229.2 ± 2.7 mg, $t_{69.6} = 0.5$, $p = 0.615$). Female SVL did not influence
 334 oviposition date, RCM, hatching success, and offspring SVL and BM (Table S5) but it was
 335 negatively correlated with incubation time ($t_{78.0} = -2.1$, $p = 0.037$).

336 *Effects of environmental conditions on reproductive output*

337 Regarding the effects of environmental conditions, we found that altitude and treatment
 338 timing significantly explained variation in reproductive performance (Table S5). Gravid

339 females from lower altitude populations laid eggs earlier than those from higher altitude ($t_{106.0}$
 340 $= 8.2$, $p < 0.001$, Fig. 4A), while the incubation time decreased with altitude ($t_{78.0} = -4.3$, $p <$
 341 0.001 , Fig. 4B). RCM was negatively correlated with treatment timing ($t_{106.0} = -5.7$, $p <$
 342 0.001), so that females laying eggs sooner also had greater reproductive effort than those with
 343 late oviposition (Fig. 4C). Hatching success was negatively correlated with treatment timing
 344 ($z = -3.0$, $p = 0.002$, Fig. 4D) and interactively impacted by mother treatment and altitude ($z =$
 345 -4.1 , $p < 0.001$), since it decreased along altitude in clutches from water-restricted mothers (z
 346 $= -3.2$, $p = 0.002$, Fig. 4E), while slightly increasing in those from control mothers ($z = 2.1$, p
 347 $= 0.033$, Fig. 4E). Both morphometric measures of offspring (SVL and BM) were positively
 348 correlated with altitude (offspring SVL: $t_{7.4} = 4.0$, $p = 0.005$; offspring BM: $t_{7.1} = 3.6$, $p =$
 349 0.008), irrespective of mother treatment (Table S5). In addition, female offspring had longer
 350 SVL than males ($t_{289.3} = 6.0$, $p < 0.001$, Fig 4F), and sex differences in BM depended upon
 351 mother treatment (interaction term: $t_{269.5} = -3.1$, $p = 0.002$). That is, daughters of control
 352 mothers had lower BM than their brothers ($t_{268.6} = -2.9$, $p = 0.004$, Fig. 4G), while there was
 353 no difference between offspring of water-restricted mothers ($t_{269.3} = 1.5$, $p = 0.137$, Fig. 4G).

354 Discussion

355 Following a two-week water restriction period, both gravid and non-reproductive females
 356 responded the same way, suggesting no additional hydric cost of reproduction [*sensu*
 357 (Lourdais *et al.*, 2017)]. This was further confirmed by an absence of relationship between
 358 dehydration rate and both the relative reproductive effort and treatment timing. These results
 359 likely highlight low water requirements from embryos at early developmental stages, and
 360 contrast with recent findings in an oviparous snake, where water restriction applied during the
 361 entire gravidity period (three weeks) did affect females' hydration state and resulted in lower
 362 egg mass (Brusch *et al.*, 2018).

Interestingly, we found that independently of reproductive state, female physiological responses to water restriction were shaped by altitude, while we expected habitat water access or temperature measures of a population to better reflect phenotypic variation in water balance regulation (Guillon *et al.*, 2014; Cox & Cox, 2015; Dupoué *et al.*, 2017a). We assessed microclimatic conditions within a restricted spatiotemporal window (i.e., sensor in shade under vegetation over 3 summer weeks), following previous methodology (Dupoué *et al.*, 2017a). Due to logistical constraints, we were unable to measure other ecologically relevant components of thermal (e.g., operative temperature or thermal heterogeneity) or hydric (e.g., deficit in water vapour pressure) environments as potential determinant of local constraints for a heliothermic ectotherm. Alternatively, altitude is a fixed environmental measure that integrates many factors from macro- to microclimatic conditions, vegetation type, snow cover and may therefore represent a better descriptor of annual conditions than punctual measures of temperatures. Here, females from lower altitudes faced higher dehydration rates probably because they were exposed to water restriction when embryos were more developed with higher water needs (Lourdais *et al.*, 2015). In addition, females at high altitudes may be locally adapted and less permeable to water loss due to body shape [e.g., lower surface-to-volume ratio, (Dupoué *et al.*, 2015b)], or more prompt to initiate water-saving strategies (e.g., lower thermal preferences), to limit evaporative water loss and dehydration risk (Köhler *et al.*, 2011; Rozen-Rechels *et al.* in press). In support of this last hypothesis, we recently documented thermal preference negatively correlated with altitude in females from the exact same populations (Trochet *et al.*, 2018).

Altitude also correlated with oviposition date (sooner at lower altitudes) and incubation duration (faster at higher altitudes), consistently with expectations and previous evidence on phenology variation along elevation gradients (Heulin *et al.*, 1997; Rodríguez-Díaz & Braña, 2012; Rutschmann *et al.*, 2016). RCM and hatching success increased with

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3 388 treatment timing irrespective of hydric treatment, thus suggesting that reproduction follows a
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5 389 “sooner is better” pattern as in another lizard species (Le Henanff, Meylan, & Lourdaïs,
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7 390 2013). Once corrected by treatment timing, more unexpected was the interactive impact of
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9 391 water restriction and altitude on hatching success. In control conditions, hatching success
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11 392 slightly increased by 6% in high altitude populations whereas it increased by a strong 40% in
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13 393 lower altitude populations when females faced higher dehydration. Usually, dehydration
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15 394 during gravidity or incubation is associated with lower reproductive success (Packard, 1991)
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17 395 so that this result was surprising. Due to the orographic effects of altitude, females from low
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19 396 altitudes regularly face periods of more severe water restriction (summer droughts) compared
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21 397 to those from high altitudes with more frequent rain episodes. This contrast might have
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23 398 directly resulted in some degree of local adaptation with enhanced reproductive fitness for
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25 399 low altitude females in the drier conditions (water restriction treatment) and in high altitude
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27 400 females in the wetter conditions (control treatment). Additionally, greater hatching success in
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29 401 water-restricted females from low altitudes might have indirectly resulted from locally
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31 402 adapted thermoregulation. As stated before, females from low altitude populations have
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33 403 higher preferred body temperatures (Trochet *et al.*, 2018). In this species, small differences in
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35 404 thermoregulation during gravidity may strongly impact hatching success (Foucart *et al.*,
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37 405 2018). Surviving offspring from higher altitudes had larger body size and body mass than
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39 406 those from lower altitudes. Overall, daughters were longer than sons as classically
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41 407 documented in this species (Lecomte *et al.*, 1992; Le Galliard *et al.*, 2006; Dupoué *et al.*,
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43 408 2019), and sex differences in mass depended upon mother treatment. That is, daughters from
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45 409 control mothers had lower body mass than sons, while offspring from water-restricted
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47 410 mothers had similar mass. Altogether, our results therefore suggest multi-level trade-offs
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49 411 since females from low altitudes laid eggs sooner and despite prolonged egg incubation time
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51 412 in standard conditions, they had greater hatching success but produced smaller offspring.
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These trade-offs were relatively independent from punctual dehydration but they were rather shaped by long-term acclimation or local adaptation to altitude.

In the Western viviparous lineages of the common lizard, population extinction risk is increasing at low altitudes where lizards experience higher temperatures (Massot, Clobert, & Ferrière, 2008; Sinervo *et al.*, 2010) and associated costs (Dupoué *et al.*, 2017b, 2018b). Viviparous species are generally predicted to be more vulnerable to climate change than oviparous ones (Sinervo *et al.*, 2010, 2018). In support of this hypothesis, the oviparous common lizard remains present (in low abundance) at sea level and only in humid landscapes (peat bogs, forest marshes) that support its presence (Berroneau, 2014). Although causal factors remain elusive, we showed here that water restriction early in gravidity had relatively low physiological impacts on the oviparous form and this contrasts with previous findings in the viviparous form (Dupoué *et al.*, 2018a). In fact, our results suggest that the oviparous form at low altitudes might even gain in fitness (hatching success) when exposed to water restriction. Future work is now critically needed to experimentally manipulate both temperature and water to measure the adaptive significance and long-term response in this bimodal species.

To conclude, the evolution of reproductive strategies constitutes the core part of life-history theory (Stearns, 1992). Given their outstanding variability and flexibility in reproductive modes, squamates remain key models to investigate the causes and consequences of transitioning to viviparity (Blackburn, 2006; Laird, Thompson, & Whittington, 2019). Here, we repeated an experimental procedure in both forms of a reproductively bimodal species. Although some fitness consequences may also appear over time, the lack of changes in females physiology depending on reproductive effort suggest that they did not pay immediate water costs contrary to their viviparous relative (Dupoué *et al.*, 2018a). This implies that water demand associated with late pregnancy stages might represent

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3 438 a barrier to prolonged egg retention when evolving in water limiting environments.
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5 439 Additionally, water constraints may also favour a reverse transition from viviparity to
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7 440 oviparity, if the hydric costs of reproduction become too high (Lourdais *et al.*, 2017; Dupoué
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9 441 *et al.*, in press). In support of this innovative hypothesis, phylogenomic analyses unravelled
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11 442 that the Western lineages populations sampled here likely originated from a viviparous
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13 443 ancestor and evolved back to an oviparous reproductive mode (Recknagel *et al.*, 2018; Horreo
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15 444 *et al.*, 2020). Hence, egg-laying might have evolved during the last Pleistocene and Holocene
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17 445 as an adaptation to high habitat aridity. Our study therefore calls future work to test this
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19 446 hypothesis and include water constraints when studying the environmental drivers of
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21 447 reproductive strategies.
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Data availability

Data will be made available should the manuscript be accepted.

Authors’ contribution

AD conceived the study, captured individuals, led the experiments, performed the analyses, and draft the manuscript. MS and MR helped in capture and performed the experiments.

All authors contributed critically to the conception, the redaction and gave final approval for publication.

Ethics

This study was performed in accordance with laws relative to capture, transport and experiments on *Zootoca vivipara* (DREAL Occitanie permit #2017-s-02) and further approved by an independent ethical committee (Apafis #14651-2018041215394197 v5).

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Figure legends

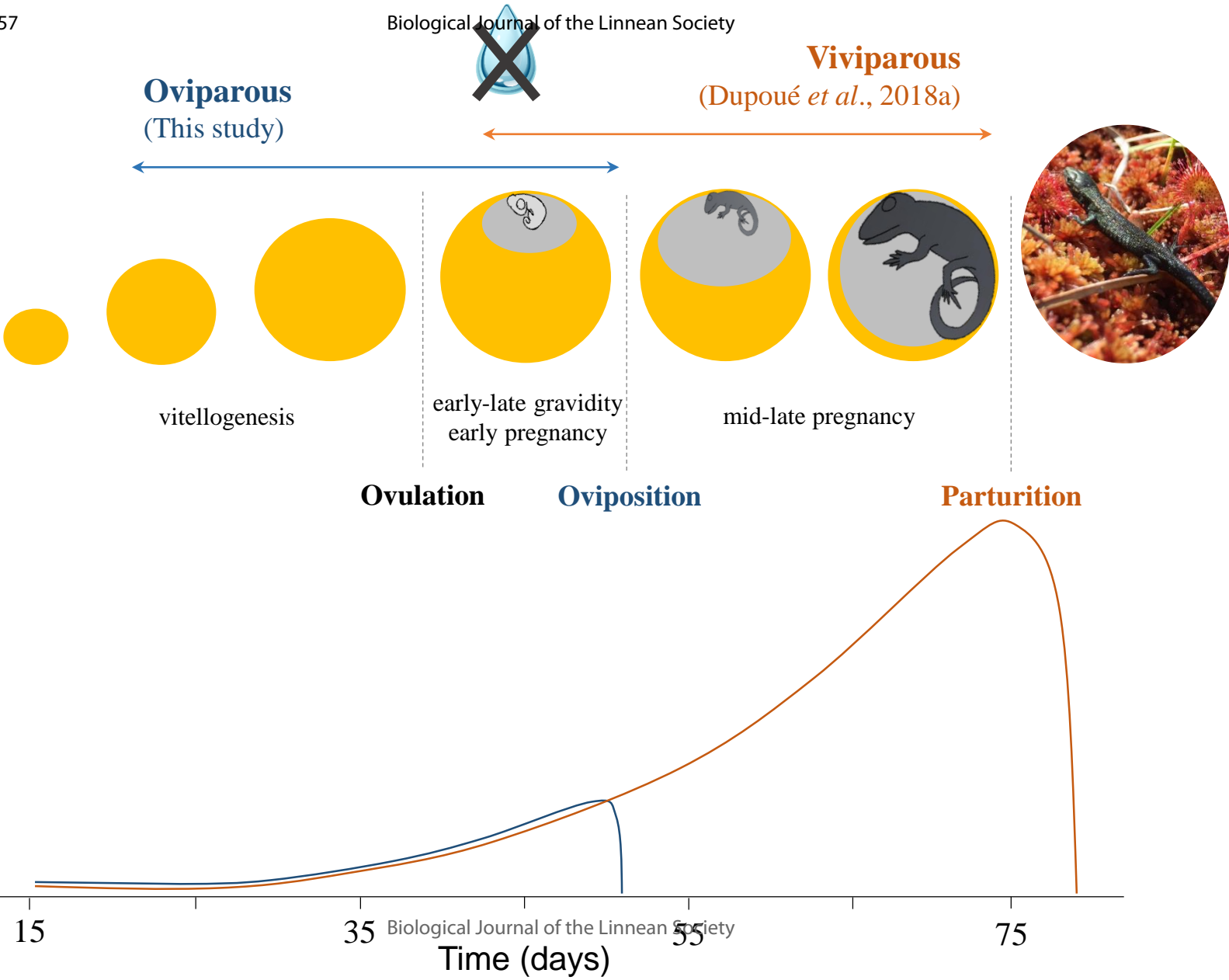
Figure 1. Representation of water restriction protocols in the oviparous form (this study) or the viviparous form (Dupoué *et al.*, 2018a) of the bimodal lizard *Zootoca vivipara*, over a standard reproductive cycle (Foucart *et al.*, 2014). In both reproductive modes, females were exposed in early June to the same experimental 14 day-period of water restriction. The associated range of treatment timing (oviparous: blue arrow; viviparous: orange arrow, scaled in the figure) covered mid-late vitellogenesis to early gravidity in oviparous females (32 to 4 days before oviposition), while water restriction occurred relatively later in the viviparous form (35 to 3 days before parturition). We hypothesized water constraints to be relatively low in oviparous females given that most of embryo water demand occurs during somatic growth (Lourdais *et al.*, 2015), once oviparous females have laid their eggs.

Figure 2. Examination of physiological responses to water restriction in gravid and non-reproductive female oviparous common lizards (n = 134). In response to a two-week period of water restriction (filled circles), A) females experienced greater loss in body mass (Δ BM) compared to control conditions (open circles), independent of their reproductive state. In addition, B) Δ BM were positively correlated with relative clutch mass (RCM), and C) negatively correlated with treatment timing (number of days between the end of hydric treatment and oviposition). Although water-restricted females were more dehydrated (higher plasma osmolality, Δ Osmo) compared to controls, D) this was independent of their reproductive state, E) independent of their RCM, and F) independent of treatment timing. Significant differences between control and water-restricted females are symbolized: (***) p < 0.001.

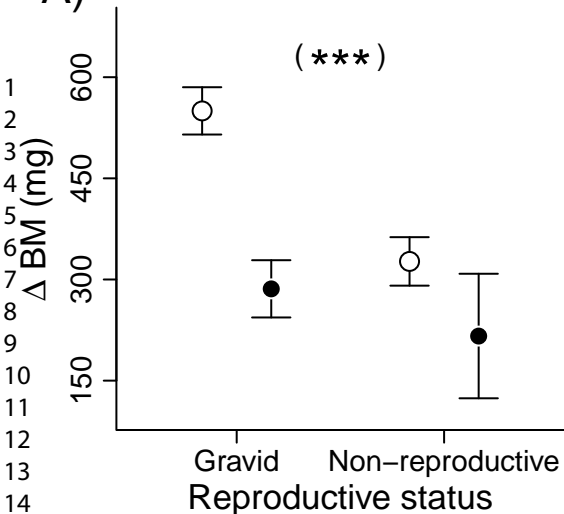
Figure 3. Relationships between physiological deviation of water balance in gravid females (n = 105) and altitude of the population. After a two-week period of water restriction (filled circles, solid lines), females from the lower altitudes experienced greater dehydration, while no-relation occurred in control females (open circles). This is illustrated by A) higher loss of BM and B) increased plasma osmolality in water-restricted females from lower altitudes. Data are represented by mean \pm SE of physiological responses within population.

Figure 4. Variation of reproductive performance in water-restricted (filled circles, solid lines) and control (open circles, dashed lines) females (n = 105) and their offspring (n = 343). A) Oviposition date was positively correlated with altitude, while altitude negatively correlated with B) incubation time. Treatment timing (number of days between the end of hydric treatment and oviposition) negatively correlated with C) relative clutch mass (RCM) and D) hatching success. E) Hatching success was also negatively correlated with altitude in water-restricted females (solid line) but not in control ones (dashed line). In offspring that survived, F) female offspring SVL was longer than males, and G) sex differences in BM between daughter and sons depended on mother treatment. Data are represented by mean \pm SE of reproductive outputs within population and significant relationships are symbolised by trend lines (predictions of final models). Significant effects of interaction terms between offspring sex and mother treatments are symbolized: {n.s.} non-significant and {**} $p < 0.01$.

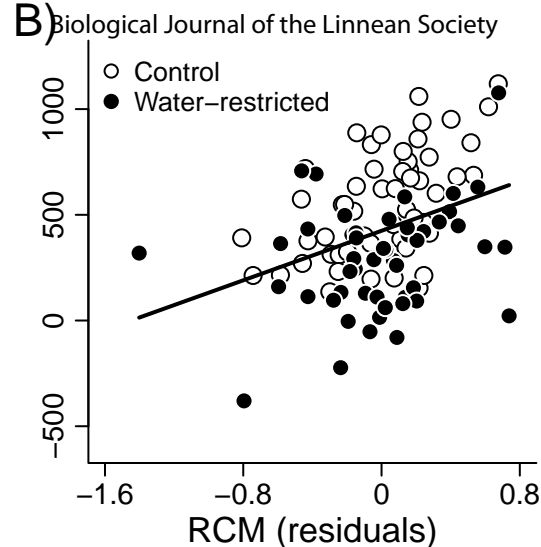
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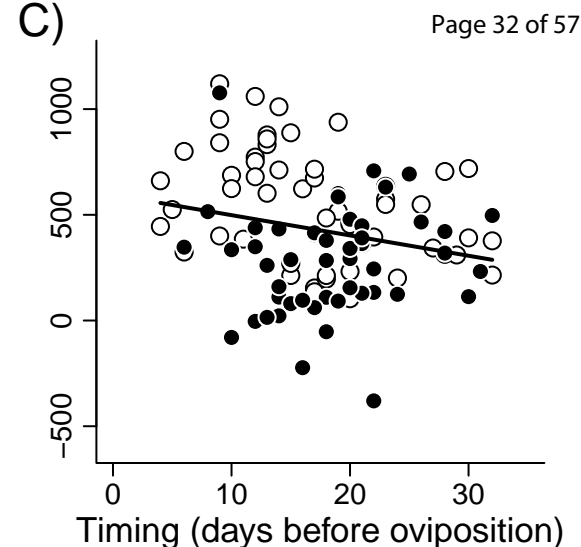
A)



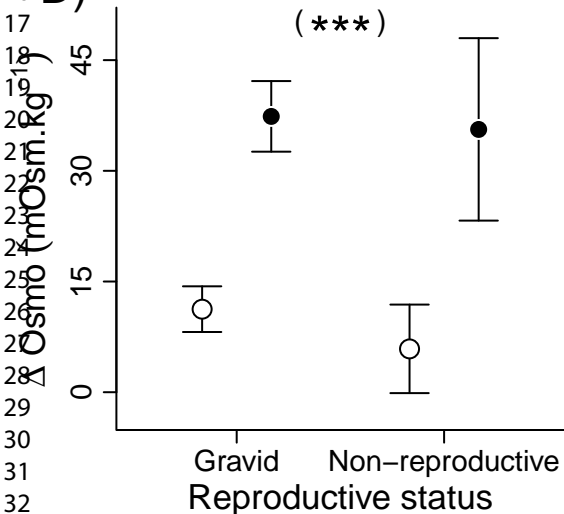
B)



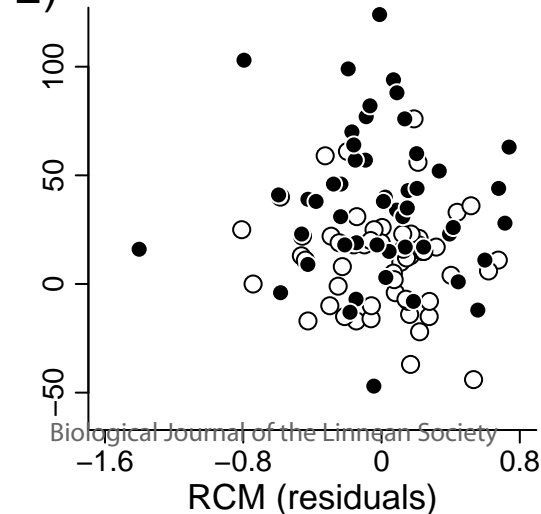
C)



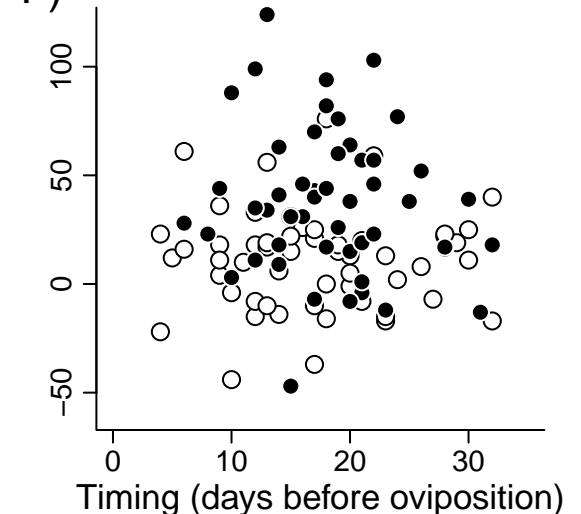
D)



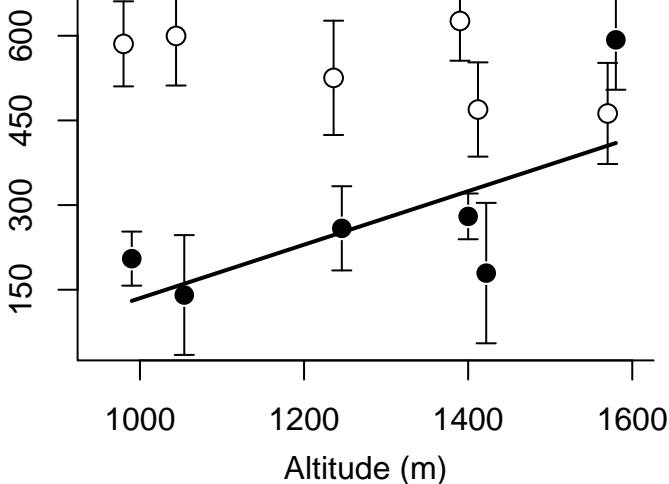
E)



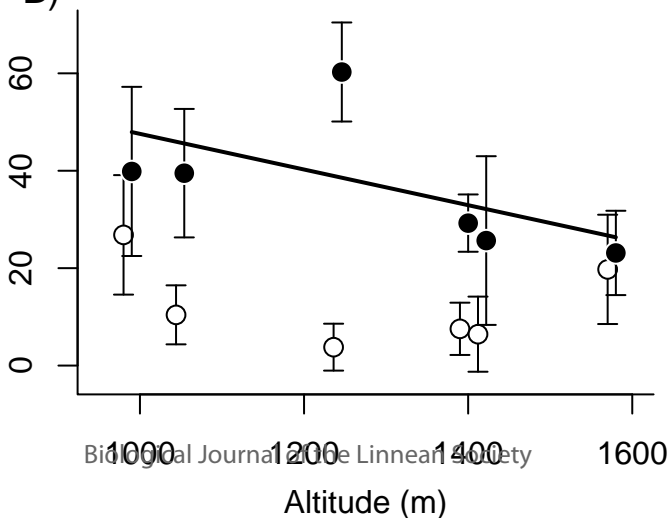
F)

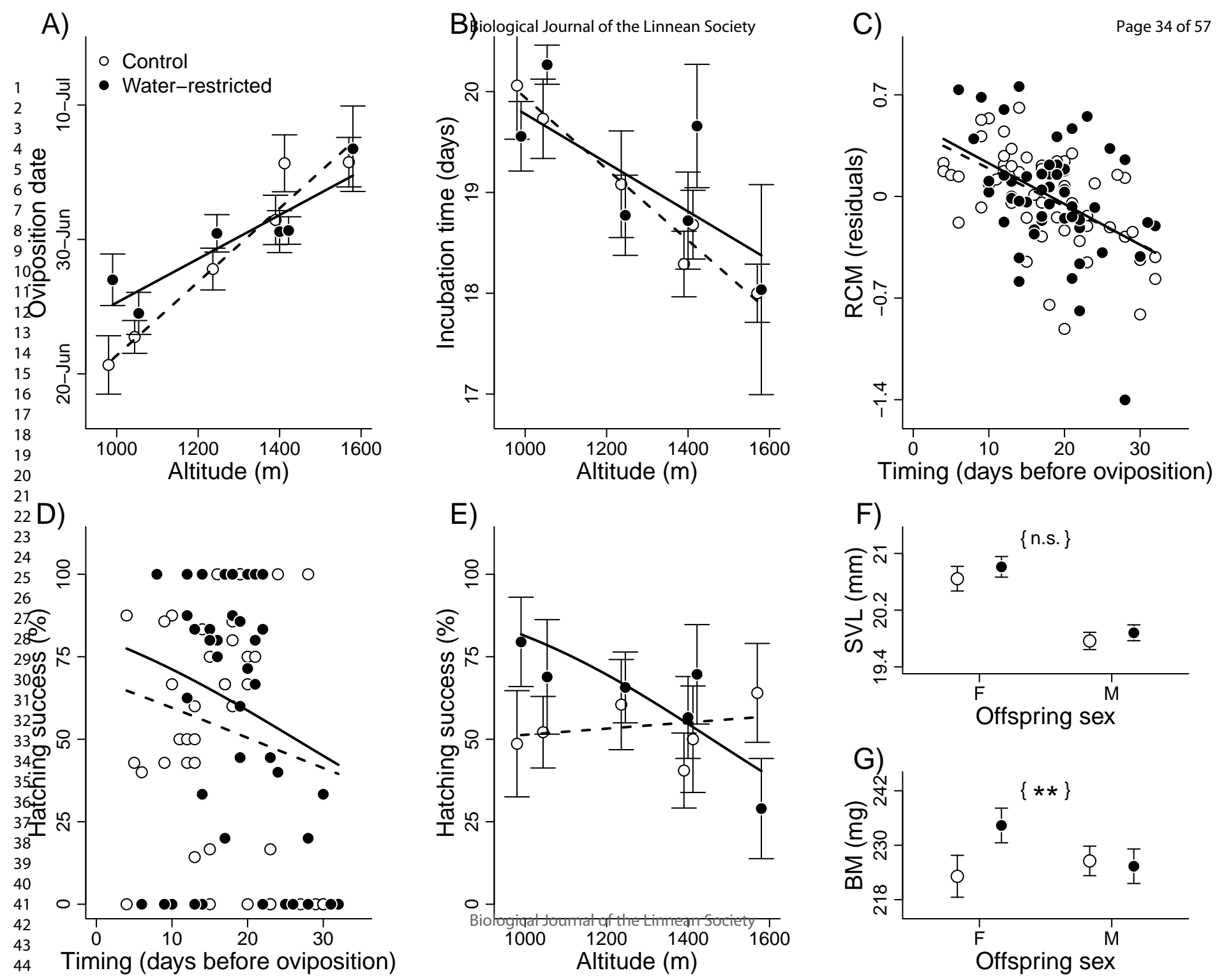


A)



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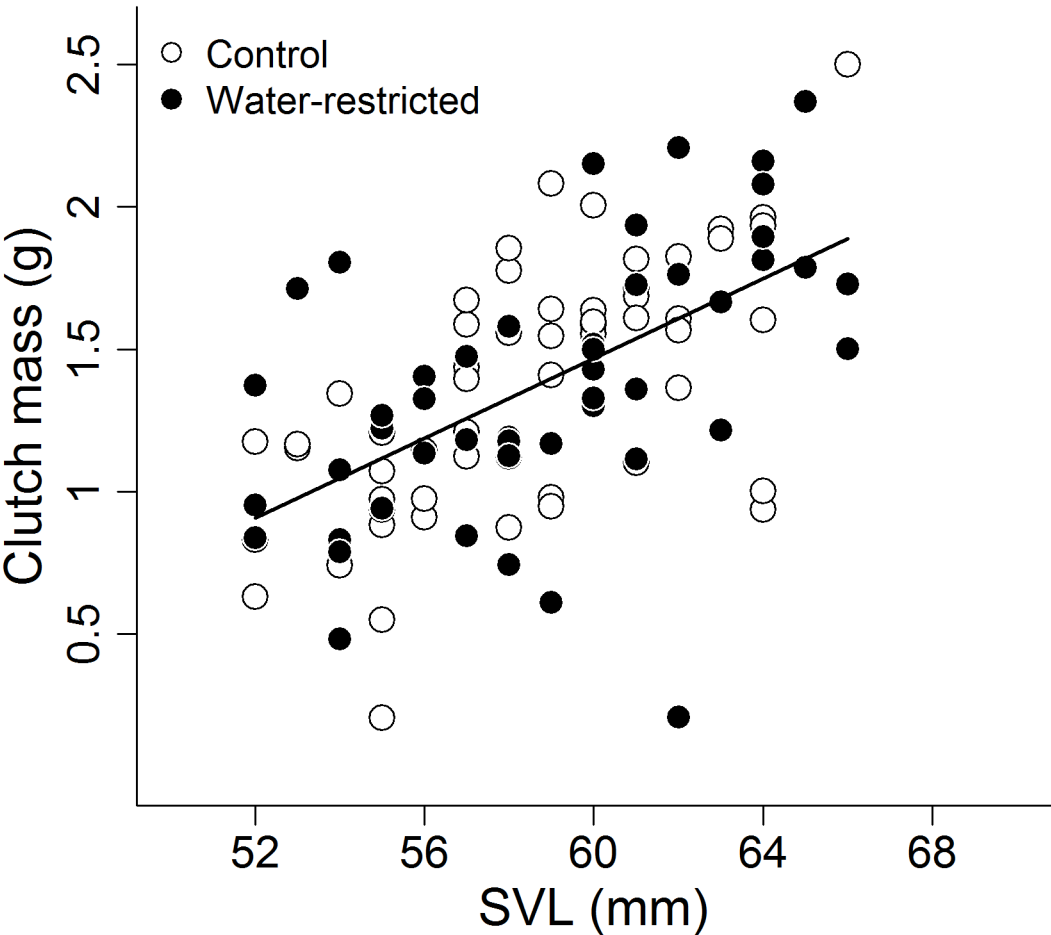


Mother-offspring conflict for water varies across altitude but is mitigated in the oviparous form of the bimodal lizard *Zootoca vivipara*

Andréaz Dupoué, Mahaut Sorlin, Murielle Richard, Jean-François Le Galliard, Olivier Lourdais, Jean Clobert, Fabien Aubret

Supplementary materials

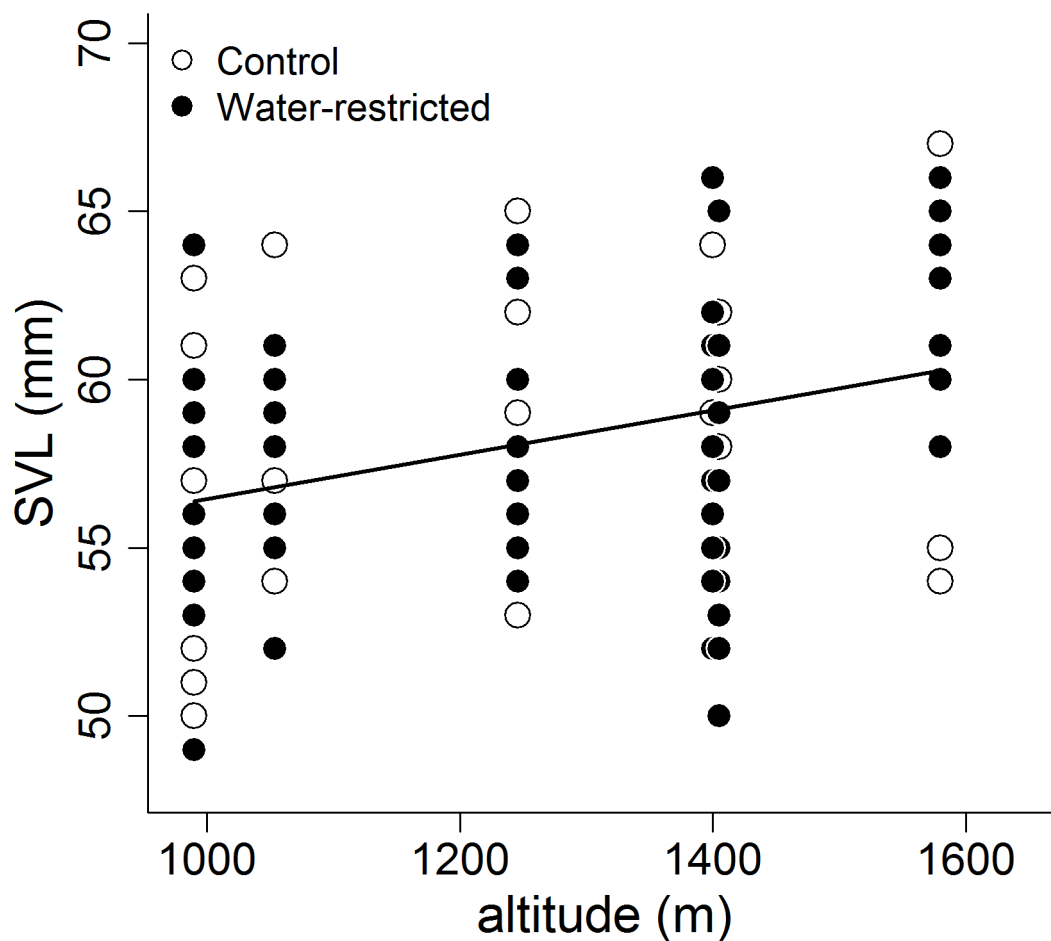
Figure S1. Positive relationship between reproductive effort (clutch mass) and female body size (snout-vent length – SVL). We used the residuals of this linear relationship ($t_{104.0} = 7.3$, $p < 0.001$, $r^2 = 0.34$) to calculate relative clutch mass (RCM). There was no difference between water-restricted (filled circles) and control females (open circles), neither in raw clutch mass ($t_{102.6} = 0.0$, $p = 0.967$), nor in size-adjusted clutch mass ($t_{102.6} = -0.1$, $p = 0.891$).



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Figure S2. Positive relationship between female body size (snout-vent length – SVL) and altitude ($t_{6,4} = 3.1$, $p = 0.022$). Females had similar SVL between the affiliation to water-restriction (filled circles) or control conditions (open circles) ($t_{129,4} = -0.1$, $p = 0.908$), irrespective of the altitude of the population of origin ($t_{129,3} = 0.1$, $p = 0.929$).



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Andréaz Dupoué, Mahaut Sorlin, Murielle Richard, Jean-François Le Galliard, Olivier Lourdaïs, Jean Clobert, Fabien Aubret

Table S1. Localizations, altitude, climatic conditions and water access (permanent in peatbog type habitat, periodic in dry meadow) in the 6 natural populations of the oviparous form of common lizard (*Z. vivipara*) from the Pyrenees Mountain range. Table shows the mean \pm SE of environmental temperatures (minimal: T_{\min} and maximal: T_{\max}) recorded between June 30th and July 25th, 2018. See text for details.

Population	GPS localization	Altitude	Water access	T_{\min}	T_{\max}
Col des Marrous	42°57'44.26"N ; 1°26'40.36"E	990	Periodic	14.75 \pm 0.20	17.50 \pm 0.22
Lac de Bethmale	42°51'43.62"N ; 1°05'03.77"E	1054	Permanent	13.06 \pm 0.19	16.77 \pm 0.31
Col de la Core	42°51'33.37"N ; 1°06'20.12"E	1405	Periodic	11.56 \pm 0.30	19.82 \pm 0.65
Etang de Lers	42°48'32.06"N ; 1°22'32.56"E	1246	Permanent	13.75 \pm 0.20	17.21 \pm 0.30
Aulus	42°46'57.47"N ; 1°23'11.68"E	1400	Permanent	14.50 \pm 0.21	19.81 \pm 0.39
Col d'Agnes	42°47'39.69"N ; 1°22'27.63"E	1580	Periodic	12.33 \pm 0.19	17.91 \pm 0.47

Mother-offspring conflict for water varies across altitude but is mitigated in the oviparous form of the bimodal lizard *Zootoca vivipara*

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Table S2. Sex determination table using scale counting along medioventral (left and right side) as previously described (Lecomte et al., 1992).

Left table reports the number of ventral scales in reproductive adults (147 females and 79 males) with obvious secondary sexual traits phenotypes. Right table illustrates that scale counting matched phenotypic sex with high determination success (96.5%).

Sex determination using number of ventral scales												N individuals with sex determined		
left \ right	23	24	25	26	27	28	29	30	31	32		scales \ phenotypic	F	M
23	M	M	M	M	M	M	-	-	-	-		F	143	4
24	M	M	M	M	M	M	-	-	-	-		M	4	75
25	M	M	M	M	M	M	-	-	-	-				
26	M	M	M	M	M	M	-	-	-	-				
27	M	M	M	M	M	M	F	F	F	F				
28	M	M	M	M	M	F	F	F	F	F				
29	-	-	-	-	F	F	F	F	F	F				
30	-	-	-	-	F	F	F	F	F	F				
31	-	-	-	-	F	F	F	F	F	F				
32	-	-	-	-	F	F	F	F	F	F				

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Table S3. AICc based model selection in all females (gravid and non-reproductive) comparing a null model (intercept only) to models testing relationships between female dehydration indexes (changes in body mass ΔBM and changes in plasma osmolality $\Delta Osmo$) and reproductive status, hydric treatment and environmental conditions. Models included the initial physiological value (BM_{ini} or $Osmo_{ini}$), SVL, altitude and temperature indexes (T_{min} and T_{max}) treated as linear co-variables, while reproductive status (gravid *versus* non-reproductive) hydric treatment (control *versus* water restriction) and water access (permanent *versus* periodic) were treated as fixed factors. Population was set as a random factor in all models to account for intra-population variation and non-independence. Highlighted models (bolded characters) are those explaining the greatest variation in response variables.

Physiological responses	Models	k	AICc	$\Delta AICc$	w_i	LogLike
ΔBM	$BM_{ini} + status + treatment + status * treatment$	7	8.64	0.00	0.13	3.13
	$BM_{ini} + status + treatment + altitude + treatment * altitude$	8	9.28	0.64	0.10	3.94
	$BM_{ini} + status + treatment$	6	9.64	1.00	0.08	1.51
	$BM_{ini} + treatment + status + altitude + treatment * status + treatment * altitude + status * altitude$	10	9.73	1.09	0.08	6.03
	$BM_{ini} + status + treatment + water access + treatment * water access$	8	10.20	1.57	0.06	3.48
	$BM_{ini} + treatment + status + altitude + treatment * status$	8	10.51	1.87	0.05	3.32
	$BM_{ini} + treatment + status + T_{max} + treatment * status$	8	10.53	1.90	0.05	3.31
	$BM_{ini} + treatment + status + water access + treatment * status$	8	10.77	2.14	0.05	3.19
	$BM_{ini} + treatment$	5	10.80	2.17	0.05	-0.17
	$BM_{ini} + treatment + status + T_{min} + treatment * status$	8	10.85	2.22	0.04	3.15
	$SVL + BM_{ini} + status + treatment + status * treatment$	8	10.89	2.26	0.03	3.13
	$BM_{ini} + treatment + status + altitude + treatment * status + treatment * altitude + status * altitude + treatment * status * altitude$	11	11.03	2.39	0.04	6.57
	$BM_{ini} + status + treatment + T_{max}$	7	11.31	2.67	0.04	1.79
	$BM_{ini} + status + treatment + altitude$	7	11.37	2.73	0.03	1.76
	$BM_{ini} + status + treatment + T_{min} + treatment * T_{min}$	8	11.53	2.89	0.03	2.81
	$SVL + BM_{ini} + status + treatment + altitude + treatment * altitude$	9	11.56	2.92	0.02	3.95

Mother-offspring conflict for water varies across altitude but is mitigated in the oviparous form of the bimodal lizard *Zootoca vivipara*

Andréaz Dupoué, Mahaut Sorlin, Murielle Richard, Jean-François Le Galliard, Olivier Lourdais, Jean Clobert, Fabien Aubret

BM _{ini} + status + treatment + water access	7	11.78	3.14	0.03	1.55
SVL + BM _{ini} + status + treatment	7	11.86	3.22	0.02	1.52
BM _{ini} + status + treatment + Tmin	7	11.86	3.23	0.03	1.51
SVL + BM _{ini} + treatment + status + altitude + treatment * status + treatment * altitude + status * altitude	11	12.06	3.43	0.02	6.05
SVL + BM _{ini} + status + treatment + water access + treatment * water access	9	12.48	3.84	0.01	3.49
BM _{ini} + treatment + status + water access + treatment * status + treatment * water access + status * water access	10	12.61	3.98	0.02	4.59
SVL + BM _{ini} + treatment + status + altitude + treatment * status	9	12.80	4.16	0.01	3.33
SVL + BM _{ini} + treatment + status + Tmax + treatment * status	9	12.83	4.19	0.01	3.31
SVL + BM _{ini} + treatment	6	12.99	4.36	0.01	-0.17
BM _{ini} + treatment + status + Tmin + treatment * status + treatment * Tmin + status * Tmin	10	13.00	4.36	0.02	4.40
BM _{ini} + treatment + status + Tmax + status * Tmax	8	13.01	4.37	0.02	2.07
SVL + BM _{ini} + treatment + status + water access + treatment * status	9	13.07	4.43	0.01	3.19
SVL + treatment + status + Tmin + treatment * status	9	13.14	4.50	0.01	3.16
SVL + BM _{ini} + treatment + status + altitude + treatment * status + treatment * altitude + status * altitude + treatment * status * altitude	12	13.44	4.81	0.01	6.57
SVL + BM _{ini} + status + treatment + Tmax	8	13.57	4.94	0.01	1.79
BM _{ini} + status + treatment + Tmax + treatment * Tmax	8	13.57	4.94	0.01	1.79
SVL + BM _{ini} + status + treatment + altitude	8	13.62	4.99	0.01	1.76
BM _{ini} + treatment + status + altitude + status * altitude	8	13.63	4.99	0.01	1.76
SVL + BM _{ini} + status + treatment + Tmin + treatment * Tmin	9	13.78	5.15	0.01	2.83
BM _{ini} + treatment + status + Tmin + status * Tmin	8	13.80	5.17	0.01	1.67
BM _{ini} + treatment + status + water access + status * water access	8	13.92	5.28	0.01	1.62
SVL + BM _{ini} + status + treatment + water access	8	14.04	5.40	0.01	1.56
SVL + BM _{ini} + status + treatment + Tmin	8	14.12	5.48	0.01	1.52
BM _{ini} + treatment + status + water access + treatment * status + treatment * water access + status * water access + treatment * status * water access	11	14.82	6.19	0.01	4.67

Mother-offspring conflict for water varies across altitude but is mitigated in the oviparous form of the bimodal lizard *Zootoca vivipara*

Andréaz Dupoué, Mahaut Sorlin, Murielle Richard, Jean-François Le Galliard, Olivier Lourdais, Jean Clobert, Fabien Aubret

	BM _{ini} + treatment + status + Tmax + treatment * status + treatment * Tmax + status * Tmax	10	14.89	6.25	0.01	3.45
	SVL + BM _{ini} + treatment + status + water access + treatment * status + treatment * water access + status * water access	11	14.97	6.33	0.00	4.60
	SVL + BM _{ini} + treatment + status + Tmax + status * Tmax	9	15.29	6.66	0.00	2.08
	SVL + BM _{ini} + treatment + status + Tmin + treatment * status + treatment * Tmin + status * Tmin	11	15.33	6.69	0.00	4.42
	BM _{ini} + treatment + status + Tmin + treatment * status + treatment * Tmin + status * Tmin + treatment * status * Tmin	11	15.35	6.72	0.00	4.41
	SVL + BM _{ini} + status + treatment + Tmax + treatment * Tmax	9	15.87	7.23	0.00	1.79
	SVL + BM _{ini} + treatment + status + altitude + status * altitude	9	15.92	7.28	0.00	1.77
	SVL + BM _{ini} + treatment + status + Tmin + status * Tmin	9	16.10	7.47	0.00	1.67
	SVL + BM _{ini} + treatment + status + water access + status * water access	9	16.20	7.57	0.00	1.62
	BM _{ini} + treatment + status + Tmax + treatment * status + treatment * Tmax + status * Tmax + treatment * status * Tmax	11	16.34	7.71	0.00	3.91
	SVL + BM _{ini} + treatment + status + water access + treatment * status + treatment * water access + status * water access + treatment * status * water access	12	17.22	8.58	0.00	4.68
	SVL + BM _{ini} + treatment + status + Tmax + treatment * status + treatment * Tmax + status * Tmax	11	17.26	8.62	0.00	3.45
	SVL + BM _{ini} + treatment + status + Tmin + treatment * status + treatment * Tmin + status * Tmin + treatment * status * Tmin	12	17.71	9.08	0.00	4.43
	SVL + BM _{ini} + treatment + status + Tmax + treatment * status + treatment * Tmax + status * Tmax + treatment * status * Tmax	12	18.76	10.12	0.00	3.91
	BM _{ini} + status	5	34.61	25.97	0.00	-12.07
	BM _{ini}	4	34.77	26.13	0.00	-13.23
	SVL + BM _{ini} + status	6	36.80	28.16	0.00	-12.07
	SVL + BM _{ini}	5	36.92	28.28	0.00	-13.22
	SVL	4	40.93	32.29	0.00	-16.31
	Null	3	51.26	42.63	0.00	-22.54
ΔOsmo	Osmo _{ini} + status + treatment + altitude + treatment * altitude	8	1239.24	0.00	0.45	-611.04
	SVL + Osmo _{ini} + status + treatment + altitude + treatment * altitude	9	1241.52	2.29	0.11	-611.04
	Osmo _{ini} + status + treatment + altitude	7	1242.15	2.91	0.11	-613.63

Mother-offspring conflict for water varies across altitude but is mitigated in the oviparous form of the bimodal lizard *Zootoca vivipara*

Andréaz Dupoué, Mahaut Sorlin, Murielle Richard, Jean-François Le Galliard, Olivier Lourdais, Jean Clobert, Fabien Aubret

Osmo _{ini} + treatment + status + altitude + treatment * status + treatment * altitude + status * altitude	10	1243.16	3.92	0.06	-610.69
Osmo _{ini} + treatment + status + altitude + status * altitude	8	1243.73	4.49	0.05	-613.29
Osmo _{ini} + treatment	5	1243.76	4.52	0.05	-616.65
Osmo _{ini} + status + treatment + Tmax + treatment * Tmax	8	1243.82	4.59	0.05	-613.34
Osmo _{ini} + status + treatment + Tmax	7	1244.27	5.03	0.04	-614.69
SVL + Osmo _{ini} + status + treatment + altitude	8	1244.38	5.15	0.03	-613.62
Osmo _{ini} + treatment + status + altitude + treatment * status	8	1244.40	5.17	0.03	-613.63
Osmo _{ini} + status + treatment	6	1244.56	5.33	0.03	-615.95
Osmo _{ini} + treatment + status + altitude + treatment * status + treatment * altitude + status * altitude + treatment * status * altitude	11	1245.43	6.19	0.02	-610.63
SVL + Osmo _{ini} + treatment + status + altitude + treatment * status + treatment * altitude + status * altitude	11	1245.47	6.24	0.01	-610.66
SVL + Osmo _{ini} + status + treatment + Tmax + treatment * Tmax	9	1245.51	6.27	0.01	-613.03
SVL + Osmo _{ini} + treatment	6	1245.70	6.46	0.01	-616.52
SVL + Osmo _{ini} + status + treatment + Tmax	8	1245.92	6.68	0.01	-614.38
SVL + Osmo _{ini} + treatment + status + altitude + treatment * status	9	1245.95	6.71	0.01	-613.25
Osmo _{ini} + status + treatment + water access + treatment * water access	8	1246.11	6.87	0.01	-614.48
SVL + Osmo _{ini} + status + treatment	7	1246.33	7.10	0.01	-615.72
Osmo _{ini} + treatment + status + Tmax + treatment * status	8	1246.50	7.26	0.01	-614.67
Osmo _{ini} + treatment + status + Tmax + status * Tmax	8	1246.50	7.27	0.01	-614.68
SVL + Osmo _{ini} + treatment + status + altitude + treatment * status	9	1246.68	7.44	0.01	-613.61
Osmo _{ini} + status + treatment + Tmin	7	1246.71	7.47	0.01	-615.91
Osmo _{ini} + status + treatment + water access	7	1246.77	7.53	0.01	-615.94
Osmo _{ini} + status + treatment + status * treatment	7	1246.79	7.55	0.01	-615.95
Osmo _{ini} + treatment + status + water access + status * water access	8	1246.94	7.70	0.01	-614.89
SVL + Osmo _{ini} + treatment + status + altitude + treatment * status + treatment * altitude + status * altitude + treatment * status * altitude	12	1247.81	8.57	0.00	-610.61
Osmo _{ini} + treatment + status + Tmin + status * Tmin	8	1247.89	8.65	0.01	-615.37

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Andréaz Dupoué, Mahaut Sorlin, Murielle Richard, Jean-François Le Galliard, Olivier Lourdais, Jean Clobert, Fabien Aubret

Osmo _{ini} + treatment + status + water access + treatment * status + treatment * water access + status * water access + treatment * status * water access	11	1247.99	8.75	0.01	-611.91
SVL + Osmo _{ini} + status + treatment + water access + treatment * water access	9	1248.07	8.84	0.00	-614.31
SVL + Osmo _{ini} + status + Tmax + status * treatment	9	1248.20	8.96	0.00	-614.37
SVL + Osmo _{ini} + treatment + status + Tmax + status * Tmax	9	1248.21	8.97	0.00	-614.38
Osmo _{ini} + treatment + status + Tmax + treatment * status + treatment * Tmax + status * Tmax + treatment * status * Tmax	11	1248.33	9.10	0.00	-612.09
Osmo _{ini} + treatment + status + Tmax + treatment * status + treatment * Tmax + status * Tmax	10	1248.38	9.15	0.00	-613.30
SVL + Osmo _{ini} + status + treatment + Tmin	8	1248.44	9.21	0.00	-615.65
SVL + Osmo _{ini} + status + treatment + water access	8	1248.56	9.33	0.00	-615.71
SVL + Osmo _{ini} + status + treatment + status * treatment	8	1248.59	9.36	0.00	-615.72
Osmo _{ini} + treatment + status + water access + treatment * status + treatment * water access + status * water access	10	1248.66	9.42	0.00	-613.43
Osmo _{ini} + treatment + status + Tmin + treatment * status	8	1248.97	9.73	0.00	-615.91
Osmo _{ini} + status + treatment + Tmin + treatment * Tmin	8	1248.97	9.73	0.00	-615.91
SVL + Osmo _{ini} + treatment + status + water access + status * water access	9	1249.01	9.78	0.00	-614.78
Osmo _{ini} + treatment + status + water access + treatment * status	8	1249.03	9.79	0.00	-615.94
SVL + Osmo _{ini} + treatment + status + Tmin + status * Tmin	9	1249.58	10.34	0.00	-615.06
SVL + Osmo _{ini} + treatment + status + Tmax + status * Tmax	12	1249.82	10.59	0.00	-611.62
SVL + Osmo _{ini} + treatment + status + Tmax + treatment * status + treatment * Tmax + status * Tmax	11	1250.19	10.95	0.00	-613.01
SVL + Osmo _{ini} + treatment + status + water access + treatment * status + treatment * water access + status * water access + treatment * status * water access	12	1250.36	11.12	0.00	-611.89
SVL + Osmo _{ini} + treatment + status + Tmin + treatment * status	9	1250.73	11.49	0.00	-615.64
SVL + Osmo _{ini} + status + treatment + Tmin + treatment * Tmin	9	1250.74	11.51	0.00	-615.65
SVL + Osmo _{ini} + treatment + status + water access + treatment * status	9	1250.86	11.62	0.00	-615.70
SVL + Osmo _{ini} + treatment + status + water access + treatment * status + treatment * water access + status * water access	11	1250.90	11.66	0.00	-613.37
Osmo _{ini} + treatment + status + Tmin + treatment * status + treatment * Tmin + status * Tmin	10	1252.45	13.21	0.00	-615.33

Mother-offspring conflict for water varies across altitude but is mitigated in the oviparous form of the bimodal lizard *Zootoca vivipara*

Andréaz Dupoué, Mahaut Sorlin, Murielle Richard, Jean-François Le Galliard, Olivier Lourdais, Jean Clobert, Fabien Aubret

SVL + Osmo _{ini} + treatment + status + Tmin + treatment * status + treatment * Tmin + status * Tmin	11	1254.19	14.95	0.00	-615.01
Osmo _{ini} + treatment + status + Tmin + treatment * status + treatment * Tmin + status * Tmin + treatment * status * Tmin	11	1254.83	15.59	0.00	-615.33
SVL + Osmo _{ini} + treatment + status + Tmin + treatment * status + treatment * Tmin + status * Tmin + treatment * status * Tmin	12	1256.57	17.33	0.00	-615.00
Osmo _{ini}	4	1278.83	39.59	0.00	-635.26
Osmo _{ini} + status	5	1279.89	40.65	0.00	-634.71
SVL + Osmo _{ini}	5	1280.71	41.47	0.00	-635.12
SVL + Osmo _{ini} + status	6	1281.50	42.26	0.00	-634.42
<i>Null</i>	3	1319.57	80.33	0.00	-656.69
SVL	4	1321.67	82.43	0.00	-656.68

Mother-offspring conflict for water varies across altitude but is mitigated in the oviparous form of the bimodal lizard *Zootoca vivipara*

Andréaz Dupoué, Mahaut Sorlin, Murielle Richard, Jean-François Le Galliard, Olivier Lourdais, Jean Clobert, Fabien Aubret

Table S4. AICc based model selection in gravid female only comparing a null model (intercept only) to models testing relationships between female dehydration indexes (changes in body mass ΔBM and changes in plasma osmolality $\Delta Osmo$) and environmental conditions. Models included the initial physiological value (BM_{ini} or $Osmo_{ini}$), SVL, treatment timing (number of days between laying date and the end of water restriction), altitudes and temperature indexes (T_{min} and T_{max}) treated as linear co-variates, while hydric treatment (control *versus* water restriction) and water access (permanent *versus* periodic) were treated as fixed factors. Population was set as a random factor in all models to account for intra-population variation and non-independence. Highlighted models (bolded characters) are those explaining the greatest variation in response variables.

Physiological responses	Models	k	AICc	$\Delta AICc$	w_i	LogLike
ΔBM	BM_{ini} + timing + treatment + altitude + treatment * altitude	8	-2.94	0.00	0.38	10.22
	BM_{ini} + treatment + altitude + treatment * altitude	7	-1.09	1.85	0.15	8.12
	SVL + BM_{ini} + timing + treatment + altitude + treatment * altitude	9	-0.55	2.38	0.09	10.22
	BM_{ini} + timing + treatment + altitude	7	-0.40	2.54	0.11	7.78
	BM_{ini} + timing + treatment	6	0.67	3.61	0.06	6.09
	BM_{ini} + treatment	5	0.81	3.75	0.06	4.90
	SVL + BM_{ini} + treatment + altitude + treatment * altitude	8	0.82	3.76	0.04	8.34
	BM_{ini} + timing + treatment + Tmax	7	1.94	4.88	0.03	6.61
	SVL + BM_{ini} + timing + treatment + altitude	8	1.95	4.88	0.02	7.78
	BM_{ini} + treatment + water access + treatment * water access	7	2.44	5.38	0.03	6.36
	BM_{ini} + treatment + water access	6	2.78	5.71	0.02	5.04
	BM_{ini} + treatment + altitude	6	2.80	5.74	0.02	5.03
	SVL + BM_{ini} + treatment	6	2.80	5.74	0.02	5.03
	BM_{ini} + timing + treatment + water access + treatment * water access	8	2.84	5.78	0.02	7.33
	BM_{ini} + timing + treatment + water access	7	2.93	5.86	0.02	6.11
	BM_{ini} + treatment + Tmax	6	2.95	5.89	0.02	4.95
	BM_{ini} + timing + treatment + Tmin	7	2.96	5.89	0.02	6.10
	BM_{ini} + treatment + Tmin	6	2.96	5.90	0.02	4.95

Mother-offspring conflict for water varies across altitude but is mitigated in the oviparous form of the bimodal lizard *Zootoca vivipara*

Andréaz Dupoué, Mahaut Sorlin, Murielle Richard, Jean-François Le Galliard, Olivier Lourdais, Jean Clobert, Fabien Aubret

SVL + BM _{ini} + timing + treatment	7	2.97	5.91	0.01	6.09
BM _{ini} + timing + treatment + Tmax + treatment * Tmax	8	3.36	6.29	0.02	7.07
BM _{ini} + treatment + Tmin + treatment * Tmin	7	3.92	6.86	0.01	5.62
BM _{ini} + timing + treatment + Tmin + treatment * Tmin	8	4.28	7.22	0.01	6.61
SVL + BM _{ini} + timing + treatment + Tmax	8	4.29	7.23	0.01	6.61
SVL + BM _{ini} + treatment + water access + treatment * water access	8	4.56	7.50	0.01	6.47
SVL + BM _{ini} + treatment + altitude	7	4.71	7.65	0.01	5.22
SVL + BM _{ini} + treatment + water access	7	4.81	7.75	0.01	5.17
SVL + BM _{ini} + treatment + Tmax	7	4.94	7.87	0.01	5.11
BM _{ini} + treatment + Tmax + treatment * Tmax	7	5.00	7.94	0.01	5.08
SVL + BM _{ini} + treatment + Tmin	7	5.03	7.96	0.01	5.06
SVL + BM _{ini} + timing + treatment + water access + treatment * water access	9	5.23	8.17	0.00	7.33
SVL + BM _{ini} + timing + treatment + water access	8	5.27	8.21	0.00	6.11
SVL + BM _{ini} + timing + treatment + Tmin	8	5.30	8.24	0.00	6.10
SVL + BM _{ini} + timing + treatment + Tmax + treatment * Tmax	9	5.75	8.69	0.00	7.07
SVL + BM _{ini} + treatment + Tmin + treatment * Tmin	8	6.01	8.94	0.00	5.75
SVL + BM _{ini} + timing + treatment + Tmin + treatment * Tmin	9	6.67	9.61	0.00	6.61
SVL + BM _{ini} + treatment + Tmax + treatment * Tmax	8	7.02	9.96	0.00	5.24
BM _{ini} + timing	5	27.49	30.42	0.00	-8.44
BM _{ini}	4	28.70	31.64	0.00	-10.15
SVL + BM _{ini} + timing	6	29.73	32.67	0.00	-8.44
SVL + BM _{ini}	5	30.59	33.53	0.00	-9.99
SVL	4	35.52	38.46	0.00	-13.56
<i>Null</i>	3	42.03	44.96	0.00	-17.89
Osmo_{ini} + treatment + altitude + treatment * altitude	7	961.79	0.00	0.49	-473.32
SVL + Osmo _{ini} + treatment + altitude + treatment * altitude	8	964.11	2.32	0.12	-473.30
Osmo _{ini} + timing + treatment + altitude + treatment * altitude	8	964.13	2.34	0.15	-473.32
Osmo _{ini} + treatment + altitude	6	964.33	2.54	0.14	-475.74

Mother-offspring conflict for water varies across altitude but is mitigated in the oviparous form of the bimodal lizard *Zootoca vivipara*

Andréaz Dupoué, Mahaut Sorlin, Murielle Richard, Jean-François Le Galliard, Olivier Lourdais, Jean Clobert, Fabien Aubret

Osmo _{ini} + timing + treatment + altitude	7	966.50	4.71	0.05	-475.67
SVL + Osmo _{ini} + timing + treatment + altitude + treatment * altitude	9	966.50	4.71	0.04	-473.30
SVL + Osmo _{ini} + treatment + altitude	7	966.61	4.83	0.03	-475.73
Osmo _{ini} + treatment + water access + treatment * water access	7	966.66	4.87	0.04	-475.75
Osmo _{ini} + treatment + Tmax	6	967.74	5.95	0.02	-477.44
Osmo _{ini} + treatment	5	967.89	6.10	0.02	-478.64
Osmo _{ini} + timing + treatment + water access + treatment * water access	8	967.96	6.17	0.02	-475.23
SVL + Osmo _{ini} + timing + treatment + altitude	8	968.84	7.05	0.01	-475.67
SVL + Osmo _{ini} + treatment + water access + treatment * water access	8	968.90	7.11	0.01	-475.70
Osmo _{ini} + timing + treatment	6	969.16	7.37	0.01	-478.15
Osmo _{ini} + treatment + Tmax + treatment * Tmax	7	969.51	7.72	0.01	-477.18
SVL + Osmo _{ini} + treatment + Tmax	7	969.54	7.75	0.01	-477.19
SVL + Osmo _{ini} + treatment	6	969.74	7.95	0.01	-478.44
Osmo _{ini} + timing + treatment + Tmax	7	969.83	8.04	0.01	-477.34
Osmo _{ini} + treatment + water access	6	969.95	8.17	0.01	-478.55
Osmo _{ini} + treatment + Tmin	6	970.07	8.28	0.01	-478.61
SVL + Osmo _{ini} + timing + treatment + water access + treatment * water access	9	970.13	8.34	0.01	-475.12
SVL + Osmo _{ini} + timing + treatment	7	971.00	9.22	0.00	-477.92
Osmo _{ini} + timing + treatment + water access	7	971.38	9.60	0.00	-478.11
Osmo _{ini} + timing + treatment + Tmax + treatment * Tmax	8	971.42	9.63	0.00	-476.96
SVL + Osmo _{ini} + treatment + Tmax + treatment * Tmax	8	971.43	9.64	0.00	-476.96
Osmo _{ini} + timing + treatment + Tmin	7	971.45	9.66	0.00	-478.15
SVL + Osmo _{ini} + timing + treatment + Tmax	8	971.70	9.91	0.00	-477.10
SVL + Osmo _{ini} + treatment + water access	7	971.88	10.10	0.00	-478.36
SVL + Osmo _{ini} + treatment + Tmin	7	971.99	10.20	0.00	-478.42
Osmo _{ini} + treatment + Tmin + treatment * Tmin	7	972.35	10.56	0.00	-478.60
SVL + Osmo _{ini} + timing + treatment + water access	8	973.31	11.52	0.00	-477.90
SVL + Osmo _{ini} + timing + treatment + Tmin	8	973.35	11.56	0.00	-477.92

Mother-offspring conflict for water varies across altitude but is mitigated in the oviparous form of the bimodal lizard *Zootoca vivipara*

Andréaz Dupoué, Mahaut Sorlin, Murielle Richard, Jean-François Le Galliard, Olivier Lourdais, Jean Clobert, Fabien Aubret

SVL + Osmo _{ini} + timing + treatment + Tmax + treatment * Tmax	9	973.44	11.65	0.00	-476.77
Osmo _{ini} + timing + treatment + Tmin + treatment * Tmin	8	973.73	11.94	0.00	-478.11
SVL + Osmo _{ini} + treatment + Tmin + treatment * Tmin	8	974.33	12.54	0.00	-478.42
SVL + Osmo _{ini} + timing + treatment + Tmin + treatment * Tmin	9	975.72	13.93	0.00	-477.91
Osmo _{ini}	4	996.64	34.85	0.00	-494.12
SVL + Osmo _{ini}	5	998.62	36.83	0.00	-494.01
Osmo _{ini} + timing	5	998.69	36.90	0.00	-494.04
SVL + Osmo _{ini} + timing	6	1000.73	38.94	0.00	-493.94
<i>Null</i>	3	1026.90	65.11	0.00	-510.33
SVL	4	1029.04	67.26	0.00	-510.32

Mother-offspring conflict for water varies across altitude but is mitigated in the oviparous form of the bimodal lizard *Zootoca vivipara*

Andréaz Dupoué, Mahaut Sorlin, Murielle Richard, Jean-François Le Galliard, Olivier Lourdais, Jean Clobert, Fabien Aubret

Table S5. AICc based model selection comparing a null model (intercept only) to models testing relationships between female reproductive performance and environmental conditions. Models included the treatment timing (number of days between laying date and the end of water restriction), altitude and temperature indexes (T_{\min} and T_{\max}) treated as linear co-variates, while and hydric treatment and water access were treated as fixed factors. Population was set as a random factor in all models to account for intra-population variation and non-independence. In analyses on offspring traits (SVL and BM), models also included mother treatment timing as linear co-variate, the juvenile sexes as fixed factor and mother identity as additional random factor to account for sibling non-independence. Preliminary investigations showed that female SVL did not explain variation in reproductive traits except for incubation time so this parameter was discarded from analyses on laying date, RCM, hatching success and offspring morphology to simplify model averaging. Highlighted models (bolded characters) are those explaining the greatest variation in response variables.

Reproductive performance	Models	k	AICc	Δ AICc	w_i	LogLike
Laying date	treatment + altitude + treatment * altitude	6	669.06	0.00	0.46	-328.11
	altitude	4	669.54	0.48	0.36	-330.57
	treatment + altitude	5	671.03	1.97	0.17	-330.21
	treatment + Tmax + treatment * Tmax	6	681.78	12.72	0.00	-334.46
	Tmax	4	684.99	15.93	0.00	-338.30
	Tmin	4	685.02	15.96	0.00	-338.31
	<i>Null</i>	3	685.21	16.15	0.00	-339.49
	treatment + Tmin + treatment * Tmin	6	685.72	16.66	0.00	-336.44
	treatment + Tmin	5	686.44	17.38	0.00	-337.92
	water access	4	686.45	17.39	0.00	-339.03
	treatment + Tmax	5	686.49	17.43	0.00	-337.94
	treatment	4	686.70	17.64	0.00	-339.15
	treatment + water access	5	687.99	18.93	0.00	-338.69
	treatment + water access + treatment * water access	6	690.15	21.09	0.00	-338.65

Mother-offspring conflict for water varies across altitude but is mitigated in the oviparous form of the bimodal lizard *Zootoca vivipara*

Andréaz Dupoué, Mahaut Sorlin, Murielle Richard, Jean-François Le Galliard, Olivier Lourdaïs, Jean Clobert, Fabien Aubret

Incubation time	SVL + timing + altitude	6	242.90	0.00	0.30	-114.86
	SVL + timing + treatment + altitude	7	243.40	0.50	0.23	-113.90
	SVL + timing + treatment + altitude + treatment * altitude	8	245.31	2.41	0.09	-113.61
	SVL + altitude	5	246.06	3.16	0.06	-117.61
	SVL + timing + treatment	6	246.82	3.92	0.04	-116.82
	SVL + timing	5	247.66	4.75	0.03	-118.41
	SVL + timing + treatment + Tmax	7	247.73	4.82	0.03	-116.06
	timing + altitude	5	247.81	4.90	0.03	-118.49
	altitude	4	248.16	5.25	0.02	-119.80
	SVL + treatment + altitude	6	248.16	5.26	0.02	-117.49
	SVL + timing + Tmax	6	248.20	5.30	0.02	-117.51
	SVL + timing + treatment + Tmax + treatment * Tmax	8	248.51	5.61	0.02	-115.21
	timing + treatment + altitude	6	248.85	5.95	0.02	-117.83
	SVL + timing + treatment + water access	7	249.09	6.19	0.01	-116.75
	SVL + timing + treatment + Tmin	7	249.24	6.33	0.01	-116.82
	SVL + treatment + altitude + treatment * altitude	7	249.30	6.39	0.01	-116.85
	SVL + timing + water access	6	249.93	7.03	0.01	-118.37
	SVL + timing + Tmin	6	249.96	7.06	0.01	-118.39
	treatment + altitude	5	250.15	7.25	0.01	-119.66
	SVL + timing + treatment + Tmin + treatment * Tmin	8	250.44	7.54	0.01	-116.18
	SVL + timing + treatment + water access + treatment * water access	8	250.81	7.90	0.01	-116.36
	timing + treatment + altitude + treatment * altitude	7	251.01	8.10	0.01	-117.70
	treatment + altitude + treatment * altitude	6	251.79	8.89	0.00	-119.31
	timing	4	254.67	11.77	0.00	-123.06
	timing + treatment	5	254.85	11.95	0.00	-122.01
	SVL	4	255.00	12.10	0.00	-123.23

Mother-offspring conflict for water varies across altitude but is mitigated in the oviparous form of the bimodal lizard *Zootoca vivipara*

Andréaz Dupoué, Mahaut Sorlin, Murielle Richard, Jean-François Le Galliard, Olivier Lourdais, Jean Clobert, Fabien Aubret

SVL + Tmax	5	255.45	12.54	0.00	-122.31
timing + Tmax	5	256.16	13.26	0.00	-122.66
timing + treatment + Tmax	6	256.47	13.57	0.00	-121.64
SVL + treatment + Tmax + treatment * Tmax	7	256.75	13.84	0.00	-120.57
SVL + treatment	5	256.81	13.90	0.00	-122.99
timing + Tmin	5	256.88	13.98	0.00	-123.02
Null	3	256.93	14.03	0.00	-125.31
timing + water access	5	256.96	14.05	0.00	-123.06
SVL + Tmin	5	257.00	14.09	0.00	-123.08
timing + treatment + Tmin	6	257.19	14.28	0.00	-122.00
timing + treatment + water access	6	257.20	14.30	0.00	-122.01
SVL + water access	5	257.26	14.36	0.00	-123.21
SVL + treatment + Tmax	6	257.33	14.42	0.00	-122.07
timing + treatment + Tmax + treatment * Tmax	7	257.70	14.80	0.00	-121.05
Tmax	4	258.04	15.14	0.00	-124.75
treatment	4	258.65	15.75	0.00	-125.05
SVL + treatment + Tmin + treatment * Tmin	7	258.66	15.76	0.00	-121.53
SVL + treatment + Tmin	6	258.91	16.00	0.00	-122.86
Tmin	4	258.97	16.06	0.00	-125.21
timing + treatment + Tmin + treatment * Tmin	7	259.10	16.19	0.00	-121.75
water access	4	259.13	16.22	0.00	-125.29
SVL + treatment + water access	6	259.14	16.23	0.00	-122.98
timing + treatment + water access + treatment * water access	7	259.57	16.67	0.00	-121.98
treatment + Tmax	5	259.81	16.91	0.00	-124.49
treatment + Tmax + treatment * Tmax	6	259.98	17.07	0.00	-123.40
treatment + Tmin	5	260.78	17.87	0.00	-124.97
treatment + water access	5	260.91	18.01	0.00	-125.04

Mother-offspring conflict for water varies across altitude but is mitigated in the oviparous form of the bimodal lizard *Zootoca vivipara*

Andréaz Dupoué, Mahaut Sorlin, Murielle Richard, Jean-François Le Galliard, Olivier Lourdais, Jean Clobert, Fabien Aubret

	SVL + treatment + water access + treatment * water access	7	261.28	18.38	0.00	-122.84
	treatment + Tmin + treatment * Tmin	6	261.78	18.87	0.00	-124.30
	treatment + water access + treatment * water access	6	263.24	20.33	0.00	-125.03
RCM	timing + water access	5	66.14	0.00	0.22	-27.77
	timing	4	66.33	0.19	0.20	-28.97
	timing + Tmin	5	67.99	1.85	0.09	-28.70
	timing + treatment + water access + treatment * water access	7	68.20	2.06	0.08	-26.53
	timing + Tmax	5	68.21	2.07	0.08	-28.80
	timing + treatment + water access	6	68.27	2.13	0.07	-27.71
	timing + treatment	5	68.43	2.29	0.07	-28.92
	timing + altitude	5	68.44	2.30	0.07	-28.92
	timing + treatment + Tmax + treatment * Tmax	7	69.52	3.37	0.04	-27.19
	timing + treatment + Tmin	6	70.07	3.93	0.03	-28.61
	timing + treatment + Tmax	6	70.37	4.23	0.03	-28.76
	timing + treatment + altitude	6	70.58	4.44	0.02	-28.87
	timing + treatment + Tmin + treatment * Tmin	7	71.93	5.79	0.01	-28.39
	timing + treatment + altitude + treatment * altitude	7	72.85	6.71	0.01	-28.85
	altitude	4	88.13	21.99	0.00	-39.87
	Tmax	4	89.12	22.98	0.00	-40.36
	treatment + altitude	5	90.33	24.19	0.00	-39.86
	treatment + Tmax	5	91.28	25.14	0.00	-40.34
	treatment + altitude + treatment * altitude	6	91.61	25.47	0.00	-39.38
	<i>Null</i>	3	92.27	26.13	0.00	-43.02
	treatment + Tmax + treatment * Tmax	6	93.33	27.19	0.00	-40.24
	Tmin	4	93.96	27.81	0.00	-42.78
	water access	4	94.35	28.21	0.00	-42.98
	treatment	4	94.41	28.27	0.00	-43.01

Mother-offspring conflict for water varies across altitude but is mitigated in the oviparous form of the bimodal lizard *Zootoca vivipara*

Andréaz Dupoué, Mahaut Sorlin, Murielle Richard, Jean-François Le Galliard, Olivier Lourdais, Jean Clobert, Fabien Aubret

	treatment + Tmin	5	96.13	29.98	0.00	-42.76
	treatment + water access + treatment * water access	6	96.18	30.03	0.00	-41.66
	treatment + water access	5	96.53	30.39	0.00	-42.97
	treatment + Tmin + treatment * Tmin	6	98.37	32.22	0.00	-42.76
Hatching success	timing + treatment + altitude + treatment * altitude	6	551.77	0.00	0.95	-269.47
	treatment + altitude + treatment * altitude	5	559.10	7.33	0.02	-274.25
	timing + treatment + Tmin + treatment * Tmin	6	559.80	8.02	0.02	-273.48
	timing + treatment	4	565.66	13.89	0.00	-278.63
	timing	3	567.34	15.57	0.00	-280.55
	timing + treatment + altitude	5	567.48	15.71	0.00	-278.44
	timing + treatment + Tmax	5	567.79	16.02	0.00	-278.60
	timing + treatment + Tmin	5	567.80	16.03	0.00	-278.60
	timing + treatment + water access	5	567.82	16.04	0.00	-278.61
	timing + treatment + water access + treatment * water access	6	568.04	16.27	0.00	-277.60
	treatment + Tmin + treatment * Tmin	5	569.14	17.37	0.00	-279.27
	timing + altitude	4	569.19	17.41	0.00	-280.40
	timing + Tmax	4	569.38	17.60	0.00	-280.49
	timing + water access	4	569.40	17.63	0.00	-280.51
	timing + Tmin	4	569.49	17.71	0.00	-280.55
	timing + treatment + Tmax + treatment * Tmax	6	569.56	17.79	0.00	-278.36
	treatment + altitude	4	570.61	18.84	0.00	-281.11
	altitude	3	571.80	20.03	0.00	-282.78
	treatment	3	572.54	20.77	0.00	-283.15
	<i>Null</i>	2	573.19	21.42	0.00	-284.54
	treatment + Tmax	4	573.38	21.61	0.00	-282.49
	treatment + Tmax + treatment * Tmax	5	573.60	21.82	0.00	-281.50
	Tmax	3	573.90	22.13	0.00	-283.84

Mother-offspring conflict for water varies across altitude but is mitigated in the oviparous form of the bimodal lizard *Zootoca vivipara*

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	treatment + Tmin	4	574.47	22.70	0.00	-283.04
	treatment + water access	4	574.63	22.85	0.00	-283.12
	treatment + water access + treatment * water access	5	574.94	23.17	0.00	-282.17
	Tmin	3	575.03	23.26	0.00	-284.40
	water access	3	575.29	23.51	0.00	-284.53
Offspring SVL	sex + altitude	6	960.54	0.00	0.29	-474.14
	sex + treatment + altitude	7	962.07	1.53	0.14	-473.86
	sex + treatment + altitude + treatment * altitude	8	962.08	1.55	0.13	-472.82
	timing + sex + altitude	7	962.42	1.88	0.11	-474.04
	treatment + sex + altitude + sex * altitude	8	963.96	3.42	0.05	-473.76
	timing + sex + treatment + altitude	8	964.10	3.56	0.05	-473.83
	timing + sex + treatment + altitude + treatment * altitude	9	964.19	3.66	0.05	-472.82
	sex + Tmax	6	965.04	4.50	0.03	-476.39
	timing + treatment + treatment + altitude + sex * altitude	9	966.00	5.46	0.02	-473.72
	sex	5	966.23	5.69	0.02	-478.02
	timing + sex + Tmax	7	966.66	6.12	0.01	-476.16
	sex + treatment + Tmax	7	966.86	6.32	0.01	-476.26
	sex + treatment + sex * treatment	7	967.40	6.87	0.01	-476.53
	timing + sex	6	967.80	7.26	0.01	-477.77
	sex + treatment	6	968.05	7.51	0.01	-477.89
	sex + Tmin	6	968.12	7.58	0.01	-477.93
	sex + water access	6	968.14	7.60	0.01	-477.94
	sex + treatment + Tmax + treatment * Tmax	8	968.27	7.74	0.01	-475.91
	timing + sex + treatment + Tmax	8	968.63	8.10	0.01	-476.09
	treatment + sex + Tmax + sex * Tmax	8	968.82	8.28	0.00	-476.19
	timing + sex + treatment + sex * treatment	8	969.09	8.56	0.00	-476.32
	timing + sex + water access	7	969.64	9.11	0.00	-477.65

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timing + sex + Tmin	7	969.73	9.19	0.00	-477.69
timing + sex + treatment	7	969.78	9.24	0.00	-477.71
sex + treatment + Tmin	7	969.92	9.39	0.00	-477.79
sex + treatment + water access	7	969.96	9.43	0.00	-477.81
treatment + sex + water access + sex * water access	8	970.03	9.49	0.00	-476.79
timing + sex + treatment + Tmax + treatment * Tmax	9	970.21	9.67	0.00	-475.83
timing + treatment + sex + Tmax + sex * Tmax	9	970.61	10.08	0.00	-476.03
timing + treatment + sex + water access + sex * water access	9	971.60	11.06	0.00	-476.52
timing + sex + treatment + water access	8	971.64	11.10	0.00	-477.60
timing + sex + treatment + Tmin	8	971.70	11.16	0.00	-477.63
treatment + sex + Tmin + sex * Tmin	8	971.82	11.28	0.00	-477.69
sex + treatment + water access + treatment * water access	8	971.98	11.45	0.00	-477.77
sex + treatment + Tmin + treatment * Tmin	8	972.02	11.49	0.00	-477.79
timing + treatment + treatment + Tmin + sex * Tmin	9	973.62	13.08	0.00	-477.53
timing + sex + treatment + water access + treatment * water access	9	973.66	13.12	0.00	-477.55
timing + sex + treatment + Tmin + treatment * Tmin	9	973.78	13.24	0.00	-477.61
altitude	5	992.06	31.53	0.00	-490.94
timing + altitude	6	993.84	33.30	0.00	-490.79
Tmax	5	997.55	37.01	0.00	-493.68
Null	4	998.25	37.71	0.00	-495.06
timing + Tmax	6	999.06	38.52	0.00	-493.40
timing	5	999.69	39.15	0.00	-494.75
treatment	5	1000.08	39.54	0.00	-494.95
Tmin	5	1000.12	39.58	0.00	-494.97
water access	5	1000.18	39.64	0.00	-495.00
timing + water access	6	1001.57	41.03	0.00	-494.66

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	timing + Tmin	6	1001.61	41.07	0.00	-494.67
	timing + treatment	6	1001.68	41.15	0.00	-494.71
Offspring BM	altitude	5	3062.26	0.00	0.21	-1526.04
	sex + treatment + sex * treatment	7	3062.87	0.61	0.15	-1524.26
	sex + altitude	6	3063.27	1.01	0.13	-1525.51
	timing + altitude	6	3064.27	2.01	0.08	-1526.01
	sex + treatment + altitude	7	3064.90	2.64	0.06	-1525.28
	timing + sex + treatment + sex * treatment	8	3064.97	2.71	0.05	-1524.26
	timing + sex + altitude	7	3065.30	3.04	0.05	-1525.48
	Tmax	5	3065.81	3.54	0.04	-1527.81
	sex + treatment + altitude + treatment * altitude	8	3066.77	4.51	0.02	-1525.16
	timing + sex + treatment + altitude	8	3066.79	4.53	0.02	-1525.17
	treatment + sex + altitude + sex * altitude	8	3066.93	4.66	0.02	-1525.24
	sex + Tmax	6	3066.94	4.68	0.02	-1527.34
	<i>Null</i>	4	3067.16	4.89	0.02	-1529.52
	timing + Tmax	6	3067.88	5.62	0.01	-1527.81
	sex	5	3068.22	5.95	0.01	-1529.02
	timing + sex + treatment + altitude + treatment * altitude	9	3068.56	6.29	0.01	-1525.00
	water access	5	3068.72	6.45	0.01	-1529.27
	sex + treatment + Tmax	7	3068.77	6.51	0.01	-1527.21
	treatment + sex + Tmax + sex * Tmax	8	3068.82	6.55	0.01	-1526.19
	timing + treatment + sex + altitude + sex * altitude	9	3068.83	6.57	0.01	-1525.14
	treatment	5	3068.97	6.70	0.01	-1529.39
	timing + sex + Tmax	7	3069.03	6.77	0.01	-1527.34
	Tmin	5	3069.12	6.85	0.01	-1529.47
	timing	5	3069.22	6.95	0.01	-1529.52
	sex + water access	6	3069.80	7.54	0.00	-1528.77
	sex + treatment	6	3070.04	7.78	0.00	-1528.89

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sex + Tmin	6	3070.19	7.92	0.00	-1528.96
timing + sex	6	3070.29	8.02	0.00	-1529.01
sex + treatment + Tmax + treatment * Tmax	8	3070.35	8.08	0.00	-1526.95
timing + water access	6	3070.77	8.50	0.00	-1529.26
timing + sex + treatment + Tmax	8	3070.86	8.59	0.00	-1527.21
timing + treatment + sex + Tmax + sex * Tmax	9	3070.92	8.66	0.00	-1526.18
timing + treatment	6	3071.03	8.77	0.00	-1529.39
timing + Tmin	6	3071.19	8.93	0.00	-1529.47
sex + treatment + water access	7	3071.64	9.37	0.00	-1528.65
timing + sex + water access	7	3071.86	9.60	0.00	-1528.76
sex + treatment + Tmin	7	3072.01	9.74	0.00	-1528.83
timing + sex + treatment	7	3072.12	9.86	0.00	-1528.89
timing + sex + Tmin	7	3072.27	10.01	0.00	-1528.96
timing + sex + treatment + Tmax + treatment * Tmax	9	3072.40	10.13	0.00	-1526.92
sex + treatment + water access + treatment * water access	8	3073.12	10.85	0.00	-1528.34
treatment + sex + water access + sex * water access	8	3073.17	10.91	0.00	-1528.36
sex + treatment + Tmin + treatment * Tmin	8	3073.59	11.32	0.00	-1528.57
treatment + sex + Tmin + sex * Tmin	8	3073.65	11.38	0.00	-1528.60
timing + sex + treatment + water access	8	3073.74	11.47	0.00	-1528.65
timing + sex + treatment + Tmin	8	3074.10	11.83	0.00	-1528.83
timing + sex + treatment + water access + treatment * water access	9	3075.23	12.97	0.00	-1528.34
timing + treatment + sex + water access + sex * water access	9	3075.29	13.02	0.00	-1528.36
timing + sex + treatment + Tmin + treatment * Tmin	9	3075.70	13.43	0.00	-1528.57
timing + treatment + sex + Tmin + sex * Tmin	9	3075.75	13.48	0.00	-1528.59