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

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Parent-offspring conflicts are widespread given that resources are often limited. Recent evidence has shown that availability of 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 a protocol previously used on the viviparous form. Females were captured in early gravidity from six populations along a 600 m altitudinal gradient to investigate whether environmental conditions (altitude, water access and temperature) exacerbate responses to water restriction. Females were significantly dehydrated after water restriction, irrespective of their reproductive status (gravid vs. non-reproductive), relative reproductive effort (relative clutch mass), and treatment timing (embryonic development stage). Female dehydration, together with reproductive performance, varied with altitude, probably due to long term acclimation or local adaptation. This moderate water-based intergenerational conflict in gravid females contrasts sharply with previous findings for the viviparous form, with implications to the evolutionary reversion from viviparity to oviparity. It is likely that oviparity constitutes a water-saving reproductive mode which might help mitigate intensive temperature-driven population extinctions at low altitudes.

ADDITIONAL KEYWORDS: altitude – dehydration – ectotherm – mother-offspring conflicts – parity mode – reproduction.

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

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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 *et al.*, 2014). The different selective forces involved in the evolution of viviparity in squamates remain under debate, as shown by recent phylogenetic and comparative studies (Pyron & 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; Lorioux *et al.*, 2013a, b; Foucart *et al.*, 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 *et al.*, 2018; Gao *et al.*, 2019; Horreo *et al.*, 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). Embryos then rely on this store of nutrients for their growth and development (Blackburn & Stewart, 2011). 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 (*Z. 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 *et al.*, 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 (*Z. vivipara carniolica)* it likely results from reversal in Western oviparous ones (*Z. vivipara louislantzi*). 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 *et al.*, 1997; Rodríguez-Díaz & Braña, 2012) and reproductive effort (Foucart *et al.*, 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 (*Z. vivipara louislantzi*), 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. Treatment exposure occurred in early June, relatively soon 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

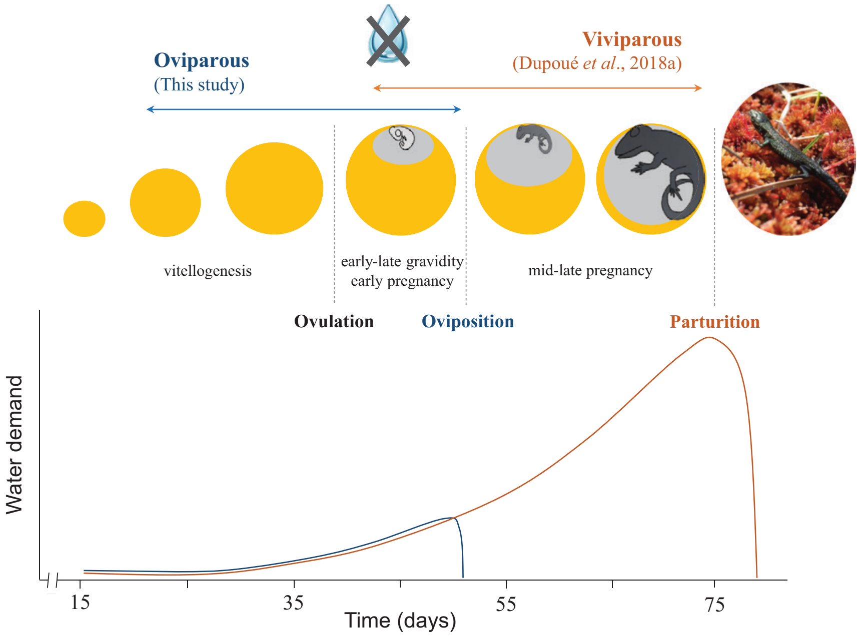

Figure 1. Representation of water restriction protocols in the oviparous form (this study) or the viviparous form (Dupoué *et al.*, 2018a) of the bimodal lizard *Z. vivipara*, over a standard reproductive cycle (Foucart *et al.*, 2014). In both reproductive modes, females were exposed in early June to 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.

clutch mass (RCM, the residuals extracted from an independent linear mixed model of clutch mass against female body size) (Supporting Information, 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 *et al.*, 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 Pyrenean Mountains from six natural populations, and we further examined the effect of population altitude, water availability (permanent access in peat-bogs vs. periodic in underwood and dry meadows) and average thermal conditions. We hypothesized that females would be locally adapted to the environmental conditions associated with 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 compared with those from high altitudes.

MATERIAL AND METHODS

Study species, populations and husbandry

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

Females were captured by hand and then transferred to the laboratory where they were housed in individual terraria (18 x 12 x 12 cm) with sterilized soil, a shelter, and basking heat until parturition. Each individual was provided a 20–35 °C thermal gradient for 6 h per day (09:00-12:00 and 14:00-17:00) using a 25 W incandescent light bulb placed over one end of each terrarium. They had *ad libitum* access to water in a petri dish and we further provided water three times per day at 09:00, 13:00 and 17:00. We further provided them with three mealworms (*Tenebrio molitor*) every 2 days. Females were kept in these standard conditions until oviposition except during the water restriction experiment (see *Experimental Design*).

We characterized environmental conditions for each population, with altitude (Supporting Information, Table S1), presence of permanent vs. periodic water sources and air temperature, because these measures were likely to shape local adaptations in the regulation of the water balance as 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, ± 0.5 °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 (Supporting Information, 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_{set} = 25 °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 ± SD, incubator 1: T_{obs} = 24.38 ± 0.26 °C; incubator 2: T_{obs} = 24.05 ± 0.39 °C; incubator 3: T_{obs} = 24.63 ± 0.30 °C). Juveniles were released within 3 days post-hatching in their respective populations.

FEMALE WATER BALANCE

Females were weighed (BM, ± 1 mg) every 3 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 ($\Delta BM = BM_{final} - BM_{initial}$) from the initiation to the end of the water restriction period. We also measured absolute changes in plasma osmolality ($\Delta Osmo = Osmo_{final} - Osmo_{initial}$), 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 *et al.*, 2003). Blood samples (*c*. 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 µL 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: $t_{103} = 7.2$, $P < 0.001$) (Supporting Information, 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 the 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 *et al.*, 1992).

This method assumes a discriminant relationship 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). *Z. vivipara* from oviparous populations differ in body size, shape and life history from viviparous populations (A. Dupoué, pers. obs.). Thus, we 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 ± SE, left side, females: 29.61 ± 0.09, males: 26.16 ± 0.13, $\chi_{1,220} = 31.8$, $P < 0.001$; right side, females: 29.52 ± 0.10, males: 26.39 ± 0.14; $\chi_{1,221} = 189.8$, $P < 0.001$) with high determination success (96.5%) (Supporting Information, 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: $\chi_{3,168} = 5.3$, $P = 0.153$, right side: $\chi_{3,171} = 0.9$, $P = 0.835$).

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 vs. water restriction), reproductive state (gravid vs. 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 ΔOsmo 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 ΔOsmo) 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 (Supporting Information, Tables 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, 2019)], to compare a set of models with different environmental measures (Supporting Information, Table S3: all females; Supporting Information, Table S4: gravid females only). In all models, population was set as a random factor to account for the non-independence of females within a 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 Supporting Information, 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 Supporting Information, 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 Supporting Information, 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 Supporting information, 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 vs. 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 Supporting information, 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 either between reproductive statuses ($t_{135.0} = -0.5$, $P = 0.635$) or 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 (Supporting information, 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 (Supporting Information, Table S4). At the same time, the changes in plasma osmolality (ΔOsmo) 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 (Supporting Information, Table S3). In gravid females, ΔOsmo was neither correlated with RCM ($t_{104.9} = -0.8$, $P = 0.410$) (Fig. 2E), nor with treatment timing ($t_{105.0} = -0.1$, $P = 0.957$) (Fig. 2F), in both hydric treatments (Supporting Information, Table S4).

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

EFFECTS OF WATER RESTRICTION ON REPRODUCTIVE OUTPUT

Water restriction had no effect on reproductive performance, including oviposition date (mean ± SE, control mothers: 29th June ± 1 day, water-restricted mothers: 30th June ± 1 day, $t_{100.3} = 0.8$, $P = 0.415$), clutch mass (control mothers: 1.366 ± 0.059 g, water-restricted mothers: 1.370 ± 0.065 g, $t_{102.7} = 0.0$, $P = 0.967$), RCM (control mothers: 0.005 ± 0.044, water-restricted mothers: -0.005 ± 0.055, $t_{102.6} = -0.1$, $P = 0.891$), incubation time (control mothers: 19.0 ± 0.2 days, water-restricted mothers: 19.1 ± 0.2 days, $t_{73.0} = 0.7$, $P = 0.479$), hatching success (control mothers: 52.3 ± 5.4%, water-restricted mothers: 59.3 ± 5.8%, $z = 1.7$, $P = 0.097$), or on offspring SVL (control mothers: 20.07 ± 0.11 mm, water-restricted mothers: 20.19 ± 0.10 mm, $t_{72.5} = 0.5$, $P = 0.632$) or BM (control mothers: 225.1 ± 2.7 mg, water-restricted mothers: 229.2 ± 2.7 mg, $t_{69.6} = 0.5$, $P = 0.615$). Female SVL did

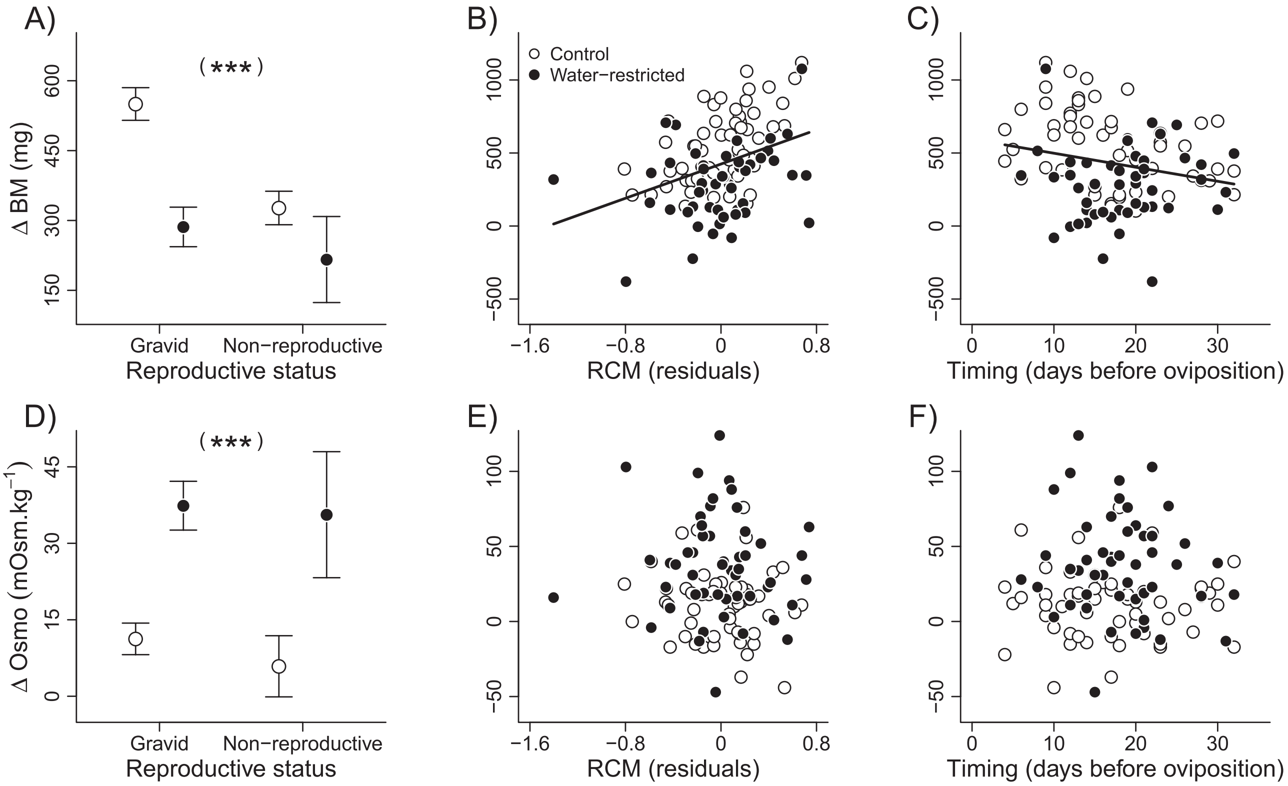

Figure 2. Examination of physiological responses to water restriction in gravid and non-reproductive female oviparous common lizards (*N* = 134). In response to a 2-week period of water restriction (filled circles), (A) females experienced greater loss in body mass (ΔBM) compared to control conditions (open circles), independent of their reproductive state. In addition, (B) ΔBM were positively correlated with 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, ΔOsmo) compared to controls, this was independent of (D) reproductive state, (E) RCM, and (F) treatment timing. Significant differences between control and water-restricted females are symbolized: (***) = *P* < 0.001.

not influence oviposition date, RCM, hatching success, and offspring SVL and BM (Supporting information, Table S5); however, it was negatively correlated with incubation time ($t_{78.0}$ = -2.1, *P* = 0.037).

EFFECTS OF ENVIRONMENTAL CONDITIONS ON REPRODUCTIVE OUTPUT

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

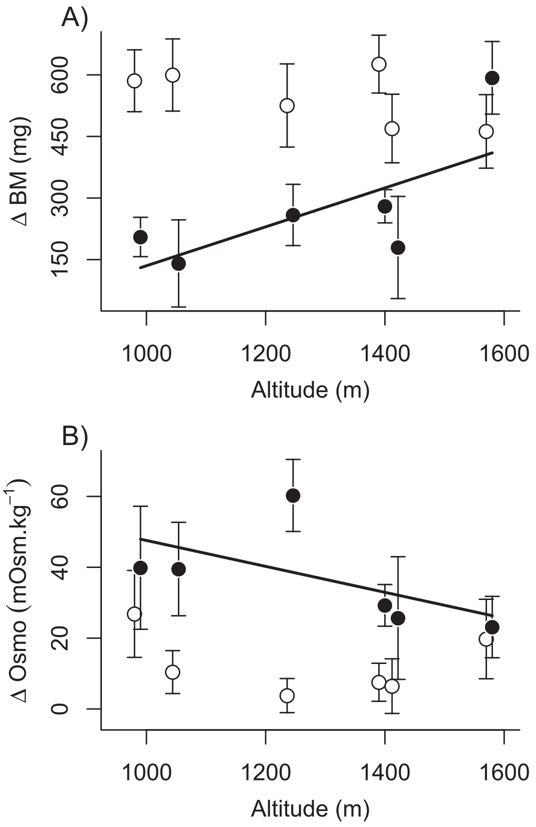

Figure 3. Relationships between physiological deviation of water balance in gravid females ($N = 105$) and altitude of the population. After a 2-week period of water restriction (filled circles, solid lines), females from the lower altitudes experienced greater dehydration, whereas no-relation between changes in hydration state and altitude 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 ± SE of body mass changes (Δ BM) and osmolality changes (Δ Osmo) within population.

DISCUSSION

Following a 2-week water restriction period, both gravid and non-reproductive females responded the same way, suggesting no additional hydric cost of reproduction [*sensu* Lourdais *et al.* (2017)]. This was further confirmed by an absence of a relationship between dehydration rate and both relative reproductive effort and treatment timing. These results probably reflect the low water requirements of embryos at early developmental stages, and contrast with recent findings in an oviparous snake, where water restriction applied during the entire gravidity period (3 weeks) did affect females' hydration state and resulted in lower egg mass (Brusch *et al.*, 2018).

Interestingly, we found that independently of reproductive state, female physiological responses to water restriction were shaped by altitude. We had expected habitat water access or temperature 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 determinants 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, and 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 and 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.*, 2019). 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). This is consistent 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 treatment timing irrespective of hydric treatment, thus suggesting that reproduction follows a "sooner is better" pattern as found in another lizard species (Le Henanff *et al.*, 2013). Once corrected for treatment timing, more unexpected was the interactive impact of water restriction and altitude on hatching success. In control conditions, hatching success increased by 6% in high altitude populations whereas it increased by a strong 40% in lower altitude populations when females faced higher dehydration. This result is surprising, because dehydration during gravidity or incubation is usually associated with lower reproductive success (Packard, 1991). Due to the orographic effects of altitude, females

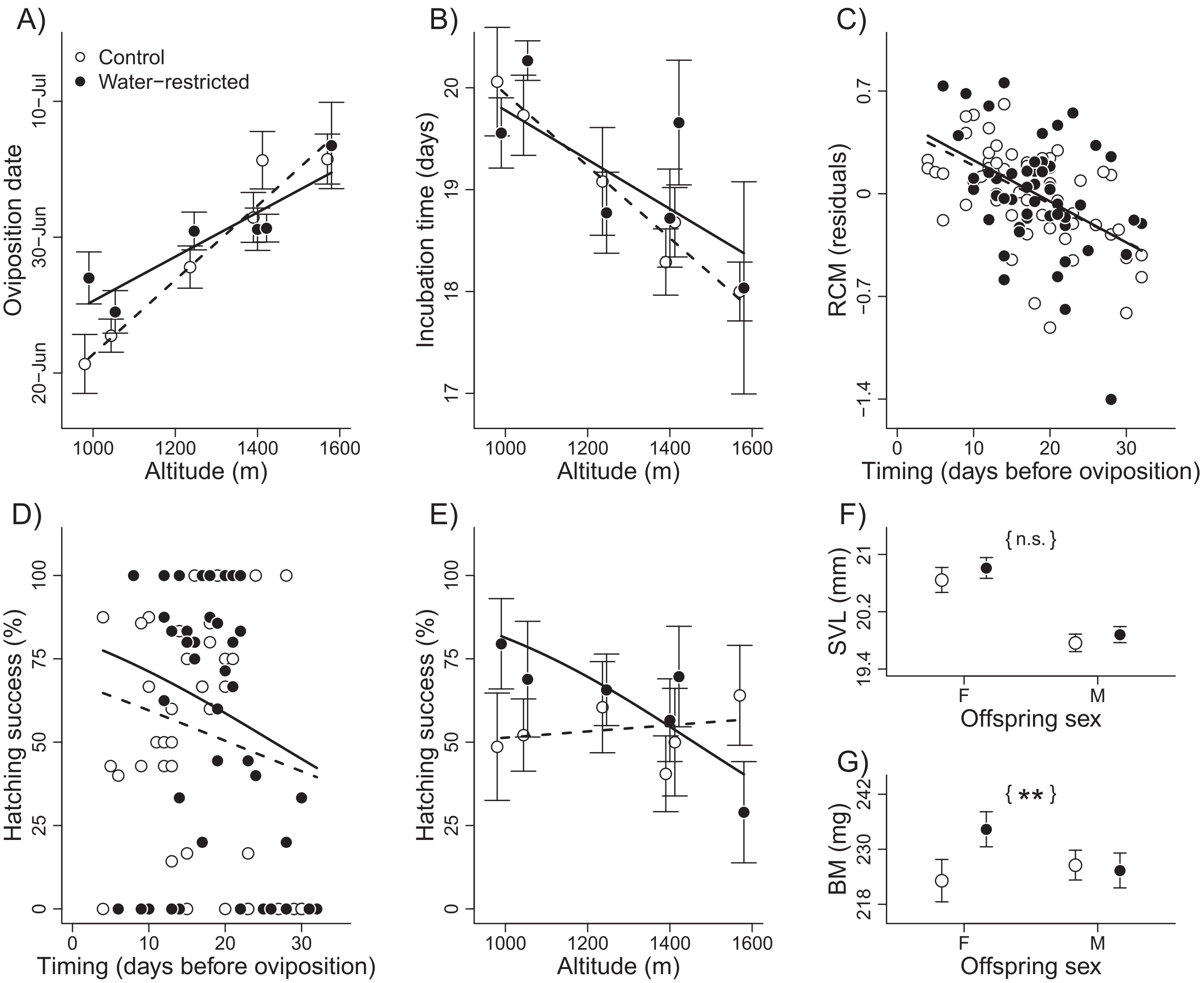

Figure 4. Variation of reproductive performance in water-restricted (filled circles, solid lines) and control (open circles, dashed lines) females ($N = 105$) and their offspring ($N = 343$). (A) oviposition date was positively correlated with altitude, while altitude negatively correlated with (B) incubation 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 ± 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 {**} = $P < 0.01$.

from low altitudes regularly face periods of more severe water restriction (summer droughts) compared to those from high altitudes with more frequent rain episodes. This contrast might have resulted in some degree of local adaptation with enhanced reproductive fitness for low altitude females in the drier conditions (water restriction treatment) and in high altitude females in the wetter conditions (control treatment). Additionally, greater hatching success in water-restricted females from low altitudes might have indirectly resulted from locally adapted thermoregulation. As stated before, females from low altitude populations have higher preferred body temperatures (Trochet *et al.*, 2018). In this species, small differences in thermoregulation during gravidity may strongly impact hatching success (Foucart *et al.*, 2018). Surviving offspring from higher altitudes had larger body size and body mass than those from lower altitudes. Overall, daughters were longer than sons as classically documented in this species (Lecomte *et al.*, 1992; Le Galliard *et al.*, 2006; Dupoué *et al.*, 2019), and sex differences in mass depended upon mother treatment. That is, daughters from control mothers had lower body mass than sons, whereas offspring from water-restricted mothers had similar mass. Altogether, our results therefore suggest multi-level trade-offs since females from low altitudes laid eggs sooner and despite prolonged egg incubation time in standard conditions, they had greater hatching success but produced smaller offspring. These trade-offs were relatively independent of punctual dehydration but they were 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 are exposed to higher temperatures (Massot *et al.*, 2008; Sinervo *et al.*, 2010) and their 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 those 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 impact 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 *et al.*, 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 a barrier to prolonged egg retention when evolving in water limiting environments. Additionally, water constraints may also favour a reverse transition from viviparity to oviparity, if the hydric costs of reproduction become too high (Lourdais *et al.*, 2017; Dupoué *et al.*, 2019a). In support of this innovative hypothesis, phylogenomic analyses unravelled that the Western lineages populations sampled here likely originated from a viviparous ancestor and evolved back to an oviparous reproductive mode (Recknagel *et al.*, 2018; Horreo *et al.*, 2020). Hence, egg-laying might have evolved during the last Pleistocene and Holocene as an adaptation to high habitat aridity. Our study therefore calls for future work to test this hypothesis and include water constraints when studying the environmental drivers of reproductive strategies.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Figure S1. Positive relationship between reproductive effort (clutch mass) and female body size (SVL).
Figure S2. Positive relationship between female body size (SVL) and altitude ($t_{6.4\,=}$ 3.1, $P = 0.022$).
Table S1. Localizations, altitude, climatic conditions and water access (permanent in peatbog type habitat, periodic in dry meadow) in the six natural populations of the oviparous form of common lizard (*Z. vivipara*) from the Pyrenees Mountain range.
Table S2. Sex determination table using scale counting along the medioventral (left and right side) as previously described (Lecomte *et al.*, 1992).
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 ΔOsmo) and reproductive status, hydric treatment and environmental conditions.
Table S4. AICc based model selection in gravid females 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 ΔOsmo) and environmental conditions.
Table S5. AICc based model selection comparing a null model (intercept only) to models testing relationships between female reproductive performance and environmental conditions.