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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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6 2 **Mother-offspring conflict for water varies across altitude and is mitigated**
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9 3 **in the oviparous form of the bimodal lizard *Zootoca vivipara***
10

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1
2
3 **23 Abstract**
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6 **24** Parent-offspring conflicts are widespread in nature given that resources are often limited.
7
8 **25** Recent evidence has shown that water can trigger such conflict during pregnancy in
9
10 **26** viviparous squamate species (lizards and snakes) and thus questions the role of water in the
11
12 **27** evolution of reproductive modes. Here, we examined the impact of water restriction during
13
14 **28** gravidity in the oviparous form of the bimodal common lizard (*Zootoca vivipara*), using the
15
16 **29** same protocol previously used in the viviparous form. Females were captured in early
17
18 **30** gravidity from six populations across a 600 m altitudinal gradient to investigate if
19
20 **31** environmental conditions (altitude, water access and temperature) may exacerbate responses
21
22 **32** to water restriction. Females were significantly dehydrated after water restriction, irrespective
23
24 **33** of their reproductive status (gravid *versus* non-reproductive), relative reproductive effort
25
26 **34** (relative clutch mass), and treatment timing (embryonic development stage). Female
27
28 **35** dehydration together with reproductive performance varied along altitude, likely due to long
29
30 **36** term acclimation or local adaptation. This moderate water-based intergenerational conflict in
31
32 **37** gravid females sharply contrasts to previous findings in the viviparous form, suggesting a
33
34 **38** potential implication in the reversion from viviparity to oviparity. Therefore, oviparity may
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36 **39** constitute a water-saving reproductive mode which might help mitigate intensive temperature-
37
38 **40** driven population extinctions at low altitudes.
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48 **42 Keywords.** Altitude, mother-offspring conflicts, dehydration, ectotherm, parity mode,
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50 **43** reproduction
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44 Introduction

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

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

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3 69 from oviparity to viviparity and explain intermediate stages of retention as observed in many
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5 70 oviparous squamates (Andrews, 2004; Blackburn, 2015). Additionally, pregnancy costs may
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7 71 explain reverse transitions from viviparity to oviparity as recently hypothesized (Recknagel,
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9 72 Kamenos, & Elmer, 2018; Gao *et al.*, 2019; Horreo, Suarez, & Fitze, 2020). That said, how
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11 73 water shapes the evolution of reproductive strategies remains an open question, and our
12
13 74 objective was to determine whether a mother-offspring conflict for water would differ
14
15 75 between reproductive modes.
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20 76 The vast majority of reptile species are lecithotrophic, meaning that mothers invest
21
22 77 nutrients into the yolk prior to ovulation (Fig. 1) and embryos rely on this store of nutrients
23
24 78 for their growth and development (Blackburn & Stewart, 2011; Stewart & Blackburn, 2015).
25
26 79 In lecithotrophic species, embryos cannot manipulate energy allocation after ovulation, so
27
28 80 there is a release from the mother-offspring conflict for energy. However, mothers must also
29
30 81 control thermal conditions during pregnancy and supply a substantial amount of water to their
31
32 82 developing embryos (Packard, 1991). Maternal water supply is essential for embryos to
33
34 83 convert vitellus into embryonic tissues and, in addition, water demand of embryos increases
35
36 84 with exponential somatic growth (Packard, 1991; Shine & Thompson, 2006; Lourdais *et al.*,
37
38 85 2015). Yet, in most squamate species from temperate regions, pregnancy occurs during
39
40 86 summer to maximize opportunities for thermoregulation at a time when water is potentially
41
42 87 scarce. Water restriction during pregnancy can therefore trigger intergenerational conflicts
43
44 88 between mother and offspring in viviparous lizards and snakes (Dupoué *et al.*, 2015a, 2018a).
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46 89 Remarkably, water-based mother-offspring conflicts have been associated with higher
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48 90 offspring mortality in a viviparous lizard (Dupoué *et al.*, 2018a), suggesting that water
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50 91 limiting environments may challenge the benefits of prolonged egg retention.
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57 92 Species with bimodal reproduction (i.e., distinct reproductive modes between
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59 93 populations) offer the ideal opportunity to clarify the evolution of reproductive strategies. For
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3 94 instance, the bimodal European common lizard (*Zootoca vivipara*) is arguably a model
4
5 95 species to examine costs and benefits of parity modes (Foucart *et al.*, 2014; Recknagel &
6
7 96 Elmer, 2019), and to understand the factors leading to the transition to viviparity (Surget-
8
9 97 Groba *et al.*, 2006; Rodríguez-Díaz & Braña, 2012). This lizard is oviparous in the southern
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11 98 margin of distribution range (Pyrenean Mountains, Northern Spain and locally in the Alps and
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13 99 Balkans) but viviparous in the rest of its Eurasian distribution (Heulin *et al.*, 2000). The two
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15 100 reproductive forms share similar affinities for relatively wet habitats, suggesting high water
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17 101 dependence for reproduction (Lorenzon *et al.*, 1999; Marquis, Massot, & Le Galliard, 2008;
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19 102 Le Galliard *et al.*, 2012). Two independent oviparous clades have been identified (Recknagel
20
21 103 *et al.*, 2018): while oviparity is an ancestral trait in the Eastern oviparous populations
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23 104 (*Zootoca vivipara carniolica*) it likely results from reversal in Western oviparous ones
24
25 105 (*Zootoca vivipara louislantzi*). Females lay slightly calcified eggs at a relatively advanced
26
27 106 stage in embryonic development [stage 30-35 *sensu* (Dufaure & Hubert, 1961)], and embryo
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29 107 stage at oviposition can vary with altitude (Heulin, Oseneegg-Leconte, & Michel, 1997;
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31 108 Rodríguez-Díaz & Braña, 2012) and reproductive effort (Foucart, Heulin, & Lourdais, 2017).
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38 109 In the present study, we tested if water-based conflict between mother and offspring
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40 110 occurred in the Western oviparous form of the common lizard (*Zootoca vivipara louislantzi*),
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42 111 as previously found in the viviparous form and using the same protocol (Dupoué *et al.*,
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44 112 2018a). We compared the physiological responses (dehydration rate) of gravid and non-
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46 113 reproductive oviparous females exposed to a 14-day period of water restriction in early June,
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48 114 which occurred relatively sooner in female reproductive cycle compared to the viviparous
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50 115 females (Fig. 1). We characterized the two assumptions of water-based conflict by
51
52 116 determining i) if gravid females paid an extra water cost compared to non-reproductive ones
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54 117 after water restriction, and ii) whether female dehydration correlated to relative clutch mass
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56 118 (RCM, the residuals extracted from an independent linear mixed model of clutch mass against
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3 119 female body size, Fig. S1) (Dupoué *et al.*, 2015a, 2018a). We also examined the
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5 120 consequences of water restriction on reproductive performance including oviposition date,
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7 121 RCM, incubation time, hatching success and hatching traits (offspring size and mass). Water
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9 122 restriction may (Dauphin-Villemant & Xavier, 1986; Bruschi *et al.*, 2018) or may not (Dupoué
10
11 123 *et al.*, 2015a, 2018a) impact reproductive traits such as clutch mass at laying (oviparous
12
13 124 species) or litter mass at parturition (viviparous species). Furthermore, a competition for water
14
15 125 between developing siblings may exist (Bonnet, Naulleau, & Shine, 2017). These
16
17 126 intergenerational and intrauterine conflicts may explain why hatchlings of oviparous species
18
19 127 are generally larger than neonates of viviparous ones [see Table 1 in (Bonnet *et al.*, 2017)].
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21 128 Indeed after oviposition, the physiological constraints on female water balance are released
22
23 129 (Fig. 1). We therefore hypothesized mother-offspring conflict for water to be modest in the
24
25 130 oviparous common lizard due to relatively low hydric investment toward the eggs. We
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27 131 predicted similar responses to water restriction between gravid and non-reproductive females,
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29 132 and that dehydration of gravid females should also be uncorrelated with RCM or treatment
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31 133 timing due to lower water demand for reproduction. Females were captured in the Pyrenees
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33 134 Mountains from six natural populations, and we further examined the effect of population
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35 135 altitude, water availability (permanent access in peat-bogs *versus* periodic in underwood and
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37 136 dry meadows) and average thermal conditions. We hypothesized females to be locally adapted
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39 137 to environmental conditions along altitude, as seen in a previous comparative study of thermal
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41 138 preferences in the same geographic area (Trochet *et al.*, 2018). In response to water
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43 139 restriction, we expected gravid females from low altitudes (i.e., relatively hot and dry
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45 140 habitats), to exhibit stronger resistance to dehydration and greater reproductive performance
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47 141 than those from highlands.

142 **Material and methods**

143 *Study species, populations and husbandry*

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3 144 The European common lizard, *Zootoca vivipara*, is a small (adult snout-vent length SVL ~ 50
4
5 145 - 75 mm), widespread lacertid typically found in cold humid peat bogs and heathland habitats
6
7 146 from Western Europe to Scandinavia and Eastern Russia (Heulin *et al.*, 2000). Between the
8
9 147 15th and 31st of May 2018, we caught a total of 134 adult females (105 gravid and 29 non-
10
11 148 reproductive) from 6 populations distributed throughout the Pyrenees mountain range (Table
12
13 149 S1). The reproductive strategy of the Western oviparous form substantially changes with
14
15 150 increasing SVL across altitude (Fig. S2), and earlier and multiple clutches as well as earlier
16
17 151 age at maturation observed in warmer habitats at lowland elevations (< 300 m) compared to
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19 152 single reproductive event at higher altitudes (Heulin *et al.*, 1997). In our study, the altitudinal
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21 153 range (990-1580 m) was strong enough to examine altitudinal variation of reproductive
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23 154 performance (see below), while narrow enough to avoid strong differences in life history
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25 155 strategies.

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31 156 Females were captured by hand and then transferred to the laboratory where they were
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33 157 housed in individual terraria (18 x 12 x 12 cm) with sterilized soil, a shelter, and basking heat
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35 158 until parturition. Each individual was provided a 20-35°C thermal gradient for 6 hours per day
36
37 159 (09:00-12:00 and 14:00-17:00) using a 25 W incandescent light bulb placed over one end of
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39 160 each terrarium. They had *ad libitum* access to water in a petri dish and we further provided
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41 161 water 3 times per day at 09:00, 13:00, and 17:00. We further provided them with 3
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43 162 mealworms (*Tenebrio molitor*) every two days. Females were kept in these standard
44
45 163 conditions until oviposition except during the water restriction experiment (see below
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47 164 experimental design).

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52 165 We characterized environmental conditions for each population, with altitude (Table
53
54 166 S1), presence of permanent *versus* periodic water sources and air temperature, because these
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56 167 measures were likely to shape local adaptations in the regulation of the water balance as
57
58 168 documented previously in the viviparous form (Dupoué *et al.*, 2017a). We recorded air
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3 169 temperature using three data loggers (iButtons, Maxim Integrated Products, Sunnyvale, CA,
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5 170 USA, $\pm 0.5^{\circ}\text{C}$) per population placed at locations where we found most lizards within
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7 171 vegetation at ground level and completely shaded to avoid the effect of radiation. Air
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10 172 temperature was recorded every hour, and we standardized the sampling period from the June
11
12 173 30th to July 25th 2018 to enable population comparisons (Dupoué *et al.*, 2017a). During this
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14 174 sampling period, we extracted the average daily minimum and maximum temperatures (T_{\min}
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16 and T_{\max} , respectively) to assess the thermal conditions of each population (Table S1).
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19 176 *Experimental design*

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22 177 A few days following capture, we randomly assigned females within each population to two
23
24 178 experimental treatments following the exact same protocol we previously used on viviparous
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26 179 females from the same species (Dupoué *et al.*, 2018a). In the water-restricted treatment, we
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28 180 removed the water bowl and reduced the misting frequency to once per day occurring in the
29
30 181 morning. In the control treatment, lizards had permanent access to the water bowl and were
31
32 182 misted three times per day. The control treatment mimics conditions in which lizards find
33
34 183 permanent access to water (e.g., peat bog, marsh). Instead, the water-restricted treatment
35
36 184 reflects summer conditions in dry habitats where in the absence of precipitation, morning dew
37
38 185 is the only source of drinking water. Water restriction lasted for 14 days and occurred on a
39
40 186 range of treatment timing from 32 to 4 days before oviposition, a time when females were
41
42 187 between mid-late vitellogenesis to early gravidity (Fig. 1). After the period of water
43
44 188 restriction, all females returned to the control water conditions, having permanent access to
45
46 189 water in a water bowl and being misted three times per day. We released non-reproductive
47
48 190 females within 2 weeks following experiments after controlling their body mass (BM)
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50 191 trajectories and palpation to confirm their non-reproductive status. Gravid females were
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52 192 released within 3 days post-laying at their capture location.
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3 193 After oviposition, clutches (range = 1 to 9 eggs) were weighed (± 1 mg) and placed in
4
5 194 individual plastic cups on water-saturated vermiculite to maintain hydric conditions and
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8 195 incubated at $T_{\text{set}} = 25^{\circ}\text{C}$ to optimise incubation time without risk of overheating for embryo
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10 196 development (Rodríguez-Díaz *et al.*, 2010; Foucart *et al.*, 2018). We used three incubators
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12 197 (Novital Covatutto Eco, Italy) and we randomly distributed the clutches in the three
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14 198 incubators ($n = 35$ per incubator) that remained within a 1°C range of observed temperatures
15
16 199 (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
17
18 200 3: $T_{\text{obs}} = 24.63 \pm 0.30^{\circ}\text{C}$). Juveniles were released within 3 days post-hatching in their
19
20 201 respective populations.
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23 24 202 *Female water balance*

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27 203 Females were weighed (BM, ± 1 mg) every three days throughout the water restriction period
28
29 204 to assess effects of water restriction on short-term changes since BM is an indicator of
30
31 205 hydration state (Lillywhite *et al.*, 2012). However, for simplicity, we only examined BM
32
33 206 changes ($\Delta\text{BM} = \text{BM}_{\text{final}} - \text{BM}_{\text{initial}}$) from the initiation to the end of the water restriction
34
35 207 period. We also measured absolute changes in plasma osmolality ($\Delta\text{Osmo} = \text{Osmo}_{\text{final}} -$
36
37 208 $\text{Osmo}_{\text{initial}}$), which is a rigorous measure of whole-body hydration in vertebrates (Peterson,
38
39 209 2002). For these assessments, females were bled at the onset and at the end of the water
40
41 210 restriction period using a standard protocol (Meylan, Dufty, & Clobert, 2003). Blood samples
42
43 211 (ca. 40 μL whole blood) were collected from the post-orbital sinus and centrifuged for 5 min
44
45 212 at 11,000 rpm. Plasma was then separated from the blood cells and kept frozen at -30°C in
46
47 213 airtight tubes until analyses were performed. Plasma osmolality (± 1 mOsm.kg $^{-1}$) was
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49 214 determined using a vapour pressure osmometer (model 5500, Wescor, Logan, UT, USA)
50
51 215 according to the protocol previously established in this species (Dupoué *et al.*, 2017a). Before
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53 216 analyses, plasma was diluted (1:1) in a physiological serum (304 mOsm.kg $^{-1}$) so that plasma
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3 217 osmolality could be determined from 10 μ L duplicates (intra-individual coefficient of
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5 218 variation: 1.17%).
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8 219 *Reproductive performance*
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11 220 We examined the effects of water restriction on different reproductive traits. We checked
12
13 221 females daily to compare oviposition date. For each female we subtracted the oviposition date
14
15 222 from the last day in hydric treatment to calculate the treatment timing. As an index of
16
17 223 reproductive effort, we estimated size-adjusted relative clutch mass (RCM) at oviposition
18
19 224 (i.e., residuals from the linear relationship between clutch mass and body size, $CM - SVL: t_{103}$
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21
22 225 = 7.2, $p < 0.001$, Fig. S1) to determine how much females deviate from the reproductive effort
23
24 226 predicted by their body size (Bonnet *et al.*, 2003). We used SVL as denominator in this linear
25
26 227 regression instead of post-laying BM because i) SVL is fixed and less biased than post-laying
27
28 228 BM (Bonnet *et al.*, 2003), ii) SVL-adjustments might better explain reproductive changes
29
30 229 than BM-adjustments (Dupoué & Lourdais, 2014; Foucart *et al.*, 2014), and iii) because SVL
31
32 230 was a better predictor of female clutch mass ($r^2 = 0.34$) than post-laying BM ($r^2 = 0.21$). We
33
34 231 calculated the incubation time as the day difference between hatching and oviposition dates.
35
36 232 We determined hatching success as the number of live juveniles within the clutch against
37
38 233 stillborn and undeveloped eggs. All alive offspring were then counted, weighed (BM, ± 1
39
40 234 mg), measured (SVL, ± 1 mm), and sexed by counting ventral scales on the medioventral
41
42 235 lines (Lecomte, Clobert, & Massot, 1992).
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48 236 This method assumes a discriminant relationships between the number of ventral
49
50 237 scales and phenotypic sex, based on sexual dimorphism in body size at birth, which has been
51
52 238 recently shown to be independent from water restriction (Dupoué *et al.*, 2019). Given that
53
54 239 *Zootoca vivipara* from oviparous populations differ in body size, shape, and life history from
55
56 240 viviparous populations (Dupoué pers. obs.), we thus used the adult females sampled for this
57
58 241 study and males with obvious secondary sexual characters ($n = 79$) captured only to count
59
60

242 ventral scales (released the same day) to fit a discriminant function on ventral scales and sex
243 (mean \pm SE, left side, females: 29.61 ± 0.09 , males: 26.16 ± 0.13 , $\chi_{1,220} = 31.8$, $p < 0.001$;
244 right side, females: 29.52 ± 0.10 , males: 26.39 ± 0.14 ; $\chi_{1,221} = 189.8$, $p < 0.001$) with high
245 determination success (96.5%, Table S2). Scalation may vary across altitude (Thorpe & Baez,
246 1993), but here scale number differences between sexes was independent of geographic
247 locality (interaction term between population and ventral scales, left side: $\chi_{3,168} = 5.3$, $p =$
248 0.153 , right side: $\chi_{3,171} = 0.9$, $p = 0.835$).

249 *Statistical analyses*

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

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

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

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2
3 266 We examined whether female dehydration rate could be further related to treatment
4
5 267 timing and environmental conditions. For each response variable (ΔBM or ΔOsmo), we used
6
7 268 the Akaike information criterion corrected for small sample size [AICc, package
8
9
10 269 AICcmodavg (Mazerolle, 2017)], to compare a set of models with different environmental
11
12 270 measures (Table S3: all females; Table S4: gravid females only). In all models, population
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14 271 was set as a random factor to account for the non-independence of females within population.
15
16 272 Our set of models included i) a *null* model with only the intercept and random factor, ii)
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18 273 simple models (initial values of BM, SVL, osmolality, reproductive status or hydric treatment
19
20 274 alone), iii) additive models with initial value, SVL, reproductive status, hydric treatment and
21
22 275 additive effects of each environmental conditions (altitude, water access, and T_{\min} and T_{\max}
23
24 276 treated separately; see all models in Table S3), and iv) interactive models with initial value,
25
26 277 SVL, reproductive status, hydric treatment, first and second order interactive effects between
27
28 278 hydric treatment, reproductive status and each environmental condition treated separately
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30 279 (altitude, water access, T_{\min} and T_{\max} , see Table S3). In gravid females specifically, we used a
31
32 280 similar procedure to test the effects of initial physiological state, SVL, treatment timing,
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34 281 hydric treatment, environmental conditions and their interaction on ΔBM and ΔOsmo (see all
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36 282 models in Table S4). In some models, altitude was treated as explanatory covariates in
37
38 283 addition with SVL or treatment timing, a procedure that may induce multicollinearity given
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40 284 the positive correlation between those (respectively: $t_{6.1} = 3.1$, $p = 0.022$, $t_{106.0} = 6.9$, $p <$
41
42 285 0.001). Despite this relationship, the Pearson's correlation coefficients between SVL and
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44 286 altitude ($r = 0.32$) or treatment timing and altitude ($r = 0.55$) were below the threshold when
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46 287 multicollinearity bias may occur ($r = 0.70$) (Dormann *et al.*, 2013).

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49 288 We used similar approaches to determine whether reproductive performance was
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51 289 correlated with treatment timing and whether it differed between hydric treatments, alone, in
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53 290 addition to, or in interaction with environmental conditions (altitude, water access, and T_{\min}
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3 291 and T_{\max} treated separately; see all models in Table S5). In all models, population was set as a
4
5 292 random factor. Oviposition date (Julian date), RCM and incubation time were analysed with
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7 293 linear mixed models, and hatching success was analysed with mixed-effect logistic
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9 294 regressions including a logit link and binomial error term (number of viable *versus* number of
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11 295 failed offspring). Offspring SVL and BM were analysed with similar linear mixed models,
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13 296 with offspring sex as an additive or interactive factor (see all models in Table S5) and random
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15 297 factors included both the mother identity and population to account for non-independence
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17 298 between siblings and within populations.

22 299 **Results**

25 300 *Physiological responses to water restriction*

27 301 At the onset of experiment, BM_{ini} was higher in gravid than non-gravid females ($t_{135.6} = -2.6$,
28
29 302 $p = 0.010$), irrespective of treatment affiliation (control: 3.200 ± 0.087 , water restriction 3.192
30
31 ± 0.085 g, $t_{132.9} = -0.5$, $p = 0.632$). $Osmo_{\text{ini}}$ did not differ neither between reproductive statuses
32
33 303 ($t_{135.0} = -0.5$, $p = 0.635$) nor between treatment affiliation (control: 319.1 ± 2.2 , water
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35 304 restriction 319.4 ± 2.7 mOsm.kg⁻¹, $t_{129.4} = 0.2$, $p = 0.845$).

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37 305
38
39 306 At the end of exposure to hydric treatment, changes in body mass (ΔBM) were
40
41 307 positively correlated with BM_{ini} ($t_{134.0} = 4.3$, $p < 0.001$) and lower in water restricted females
42
43 308 compared to controls ($t_{134.0} = -5.5$, $p < 0.001$, Fig. 2A), irrespective of their SVL and
44
45 309 reproductive state (Table S3). In gravid females, ΔBM was positively correlated with RCM
46
47 310 ($t_{105.0} = 3.1$, $p = 0.003$, Fig. 2B), and negatively correlated to treatment timing ($t_{105.0} = -2.1$, p
48
49 311 $= 0.041$, Fig. 2C), irrespective of hydric treatment (Table S4). At the same time, the changes
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51 312 in plasma osmolality ($\Delta Osmo$) were negatively correlated with $Osmo_{\text{ini}}$ ($t_{133.2} = -8.3$, $p <$
52
53 313 0.001) and significantly increased following water restriction compared to control conditions
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55 314 ($t_{129.2} = 6.6$, $p < 0.001$, Fig 2D) irrespective of their SVL and reproductive state (Table S3). In
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3 315 gravid females, ΔOsmo was neither correlated with RCM ($t_{104.9} = -0.8$, $p = 0.410$, Fig. 2E),
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5 316 nor with treatment timing ($t_{105.0} = -0.1$, $p = 0.957$, Fig 2F), in both hydric treatments (Table
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7 317 S4).

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9
10 318 Females from lower altitude populations exhibited higher sensitivity to water
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12 319 restriction since they experienced a greater loss of BM ($t_{105.0} = 2.9$, $p = 0.005$, Fig. 3A) and
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14 320 higher increases in plasma osmolality ($t_{105.0} = -3.2$, $p = 0.002$, Fig. 3B) than those from
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16 321 highlands, while no significant altitudinal variation of hydration state occurred in control
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18 322 females (both, $p > 0.800$, Fig 3A & 3B), irrespective of reproductive status (Table S3).

21 22 323 *Effects of water restriction on reproductive output*

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25 324 Water restriction had no effect on reproductive performance, including oviposition date (mean
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27 325 \pm SE, control mothers: 29th June \pm 1 day, water-restricted mothers: 30th June \pm 1 day, $t_{100.3} =$
28
29 326 0.8, $p = 0.415$), clutch mass (control mothers: 1.366 ± 0.059 g, water-restricted mothers:
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31 327 1.370 ± 0.065 g, $t_{102.7} = 0.0$, $p = 0.967$), RCM (control mothers: 0.005 ± 0.044 , water-
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33 328 restricted mothers: -0.005 ± 0.055 , $t_{102.6} = -0.1$, $p = 0.891$), incubation time (control mothers:
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35 329 19.0 ± 0.2 days, water-restricted mothers: 19.1 ± 0.2 days, $t_{73.0} = 0.7$, $p = 0.479$), hatching
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37 330 success (control mothers: $52.3 \pm 5.4\%$, water-restricted mothers: $59.3 \pm 5.8\%$, $z = 1.7$, $p =$
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39 331 0.097), nor on offspring SVL (control mothers: 20.07 ± 0.11 mm, water-restricted mothers:
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41 332 20.19 ± 0.10 mm, $t_{72.5} = 0.5$, $p = 0.632$) or BM (control mothers: 225.1 ± 2.7 mg, water-
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43 333 restricted mothers: 229.2 ± 2.7 mg, $t_{69.6} = 0.5$, $p = 0.615$). Female SVL did not influence
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45 334 oviposition date, RCM, hatching success, and offspring SVL and BM (Table S5) but it was
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47 335 negatively correlated with incubation time ($t_{78.0} = -2.1$, $p = 0.037$).

48 49 336 *Effects of environmental conditions on reproductive output*

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51 337 Regarding the effects of environmental conditions, we found that altitude and treatment
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53 338 timing significantly explained variation in reproductive performance (Table S5). Gravid
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3 339 females from lower altitude populations laid eggs earlier than those from higher altitude ($t_{106.0}$
4 = 8.2, $p < 0.001$, Fig. 4A), while the incubation time decreased with altitude ($t_{78.0} = -4.3$, $p <$
5 340 0.001, Fig. 4B). RCM was negatively correlated with treatment timing ($t_{106.0} = -5.7$, $p <$
6 341 0.001), so that females laying eggs sooner also had greater reproductive effort than those with
7 342 late oviposition (Fig. 4C). Hatching success was negatively correlated with treatment timing
8 343 ($z = -3.0$, $p = 0.002$, Fig. 4D) and interactively impacted by mother treatment and altitude ($z =$
9 344 -4.1 , $p < 0.001$), since it decreased along altitude in clutches from water-restricted mothers (z
10 345 = -3.2 , $p = 0.002$, Fig. 4E), while slightly increasing in those from control mothers ($z = 2.1$, p
11 346 = 0.033 , Fig. 4E). Both morphometric measures of offspring (SVL and BM) were positively
12 347 correlated with altitude (offspring SVL: $t_{7.4} = 4.0$, $p = 0.005$; offspring BM: $t_{7.1} = 3.6$, $p =$
13 348 0.008), irrespective of mother treatment (Table S5). In addition, female offspring had longer
14 349 SVL than males ($t_{289.3} = 6.0$, $p < 0.001$, Fig 4F), and sex differences in BM depended upon
15 350 mother treatment (interaction term: $t_{269.5} = -3.1$, $p = 0.002$). That is, daughters of control
16 351 mothers had lower BM than their brothers ($t_{268.6} = -2.9$, $p = 0.004$, Fig. 4G), while there was
17 352 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).

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3 363 Interestingly, we found that independently of reproductive state, female physiological
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5 364 responses to water restriction were shaped by altitude, while we expected habitat water access
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8 365 or temperature measures of a population to better reflect phenotypic variation in water balance
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10 366 regulation (Guillon *et al.*, 2014; Cox & Cox, 2015; Dupoué *et al.*, 2017a). We assessed
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12 367 microclimatic conditions within a restricted spatiotemporal window (i.e., sensor in shade
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14 368 under vegetation over 3 summer weeks), following previous methodology (Dupoué *et al.*,
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16 369 2017a). Due to logistical constraints, we were unable to measure other ecologically relevant
17
18 370 components of thermal (e.g., operative temperature or thermal heterogeneity) or hydric (e.g.,
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20 371 deficit in water vapour pressure) environments as potential determinant of local constraints
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22 372 for a heliothermic ectotherm. Alternatively, altitude is a fixed environmental measure that
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24 373 integrates many factors from macro- to microclimatic conditions, vegetation type, snow cover
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26 374 and may therefore represent a better descriptor of annual conditions than punctual measures of
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28 375 temperatures. Here, females from lower altitudes faced higher dehydration rates probably
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30 376 because they were exposed to water restriction when embryos were more developed with
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32 377 higher water needs (Lourdais *et al.*, 2015). In addition, females at high altitudes may be
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34 378 locally adapted and less permeable to water loss due to body shape [e.g., lower surface-to-
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36 379 volume ratio, (Dupoué *et al.*, 2015b)], or more prompt to initiate water-saving strategies (e.g.,
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38 380 lower thermal preferences), to limit evaporative water loss and dehydration risk (Köhler *et al.*,
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40 381 2011; Rozen-Rechels *et al.* in press). In support of this last hypothesis, we recently
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42 382 documented thermal preference negatively correlated with altitude in females from the exact
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44 383 same populations (Trochet *et al.*, 2018).

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52 384 Altitude also correlated with oviposition date (sooner at lower altitudes) and
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54 385 incubation duration (faster at higher altitudes), consistently with expectations and previous
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56 386 evidence on phenology variation along elevation gradients (Heulin *et al.*, 1997; Rodríguez-
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58 387 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, & Lourdaï,
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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)
16
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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3 413 These trade-offs were relatively independent from punctual dehydration but they were rather
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5 414 shaped by long-term acclimation or local adaptation to altitude.
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8 415 In the Western viviparous lineages of the common lizard, population extinction risk is
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10 416 increasing at low altitudes where lizards experience higher temperatures (Massot, Clobert, &
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12 417 Ferrière, 2008; Sinervo *et al.*, 2010) and associated costs (Dupoué *et al.*, 2017b, 2018b).
13
14 418 Viviparous species are generally predicted to be more vulnerable to climate change than
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16 419 oviparous ones (Sinervo *et al.*, 2010, 2018). In support of this hypothesis, the oviparous
17
18 420 common lizard remains present (in low abundance) at sea level and only in humid landscapes
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20 421 (peat bogs, forest marshes) that support its presence (Berroneau, 2014). Although causal
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22 422 factors remain elusive, we showed here that water restriction early in gravidity had relatively
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24 423 low physiological impacts on the oviparous form and this contrasts with previous findings in
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26 424 the viviparous form (Dupoué *et al.*, 2018a). In fact, our results suggest that the oviparous
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28 425 form at low altitudes might even gain in fitness (hatching success) when exposed to water
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30 426 restriction. Future work is now critically needed to experimentally manipulate both
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32 427 temperature and water to measure the adaptive significance and long-term response in this
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34 428 bimodal species.
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41 429 To conclude, the evolution of reproductive strategies constitutes the core part of life-
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43 430 history theory (Stearns, 1992). Given their outstanding variability and flexibility in
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45 431 reproductive modes, squamates remain key models to investigate the causes and
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47 432 consequences of transitioning to viviparity (Blackburn, 2006; Laird, Thompson, &
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49 433 Whittington, 2019). Here, we repeated an experimental procedure in both forms of a
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51 434 reproductively bimodal species. Although some fitness consequences may also appear over
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53 435 time, the lack of changes in females physiology depending on reproductive effort suggest that
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55 436 they did not pay immediate water costs contrary to their viviparous relative (Dupoué *et al.*,
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57 437 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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41 454 **Competing interest**

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43
44 455 The authors declare no conflicts of interest.
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46

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8 463 **Data availability**

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11 464 Data will be made available should the manuscript be accepted.
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14 465 **Authors’ contribution**

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17 466 AD conceived the study, captured individuals, led the experiments, performed the analyses,
18
19 467 and draft the manuscript. MS and MR helped in capture and performed the experiments.
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21 468 All authors contributed critically to the conception, the redaction and gave final approval for
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23 469 publication.
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25 470 **Ethics**

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29 471 This study was performed in accordance with laws relative to capture, transport and
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31 472 experiments on *Zootoca vivipara* (DREAL Occitanie permit #2017-s-02) and further
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33 473 approved by an independent ethical committee (Apafis #14651-2018041215394197 v5).
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3 669 **Figure legends**
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6 670 **Figure 1.** Representation of water restriction protocols in the oviparous form (this study) or
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8 671 the viviparous form (Dupoué *et al.*, 2018a) of the bimodal lizard *Zootoca vivipara*, over a
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10 672 standard reproductive cycle (Foucart *et al.*, 2014). In both reproductive modes, females were
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12 673 exposed in early June to the same experimental 14 day-period of water restriction. The
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14 674 associated range of treatment timing (oviparous: blue arrow; viviparous: orange arrow, scaled
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16 675 in the figure) covered mid-late vitellogenesis to early gravidity in oviparous females (32 to 4
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18 676 days before oviposition), while water restriction occurred relatively later in the viviparous
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20 677 form (35 to 3 days before parturition). We hypothesized water constraints to be relatively low
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22 678 in oviparous females given that most of embryo water demand occurs during somatic growth
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24 679 (Lourdais *et al.*, 2015), once oviparous females have laid their eggs.
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32 681 **Figure 2.** Examination of physiological responses to water restriction in gravid and non-
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34 682 reproductive female oviparous common lizards (n = 134). In response to a two-week period of
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36 683 water restriction (filled circles), A) females experienced greater loss in body mass (Δ BM)
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38 684 compared to control conditions (open circles), independent of their reproductive state. In
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40 685 addition, B) Δ BM were positively correlated with relative clutch mass (RCM), and C)
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42 686 negatively correlated with treatment timing (number of days between the end of hydric
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44 687 treatment and oviposition). Although water-restricted females were more dehydrated (higher
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46 688 plasma osmolality, Δ Osmo) compared to controls, D) this was independent of their
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48 689 reproductive state, E) independent of their RCM, and F) independent of treatment timing.
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51 690 Significant differences between control and water-restricted females are symbolized: (***) p
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53 691 < 0.001.
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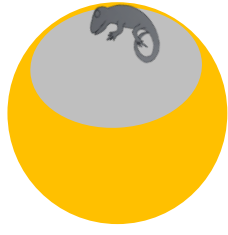
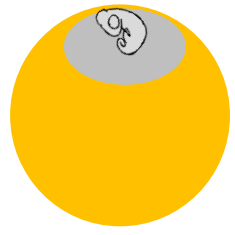
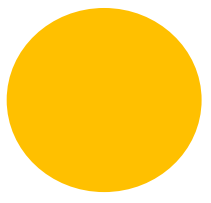
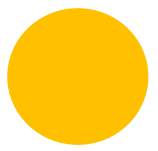
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3 693 **Figure 3.** Relationships between physiological deviation of water balance in gravid females
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5 694 (n = 105) and altitude of the population. After a two-week period of water restriction (filled
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7 695 circles, solid lines), females from the lower altitudes experienced greater dehydration, while
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9 696 no-relation occurred in control females (open circles). This is illustrated by A) higher loss of
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11 697 BM and B) increased plasma osmolality in water-restricted females from lower altitudes. Data
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13 698 are represented by mean \pm SE of physiological responses within population.
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20 700 **Figure 4.** Variation of reproductive performance in water-restricted (filled circles, solid lines)
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22 701 and control (open circles, dashed lines) females (n = 105) and their offspring (n = 343). A)
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24 702 Oviposition date was positively correlated with altitude, while altitude negatively correlated
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26 703 with B) incubation time. Treatment timing (number of days between the end of hydric
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28 704 treatment and oviposition) negatively correlated with C) relative clutch mass (RCM) and D)
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30 705 hatching success. E) Hatching success was also negatively correlated with altitude in water-
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32 706 restricted females (solid line) but not in control ones (dashed line). In offspring that survived,
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34 707 F) female offspring SVL was longer than males, and G) sex differences in BM between
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36 708 daughter and sons depended on mother treatment. Data are represented by mean \pm SE of
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38 709 reproductive outputs within population and significant relationships are symbolised by trend
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40 710 lines (predictions of final models). Significant effects of interaction terms between offspring
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42 711 sex and mother treatments are symbolized: {n.s.} non-significant and {**} $p < 0.01$.
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Oviparous
(This study)

Viviparous
(Dupoué *et al.*, 2018a)



vitellogenesis

early-late gravidity
early pregnancy

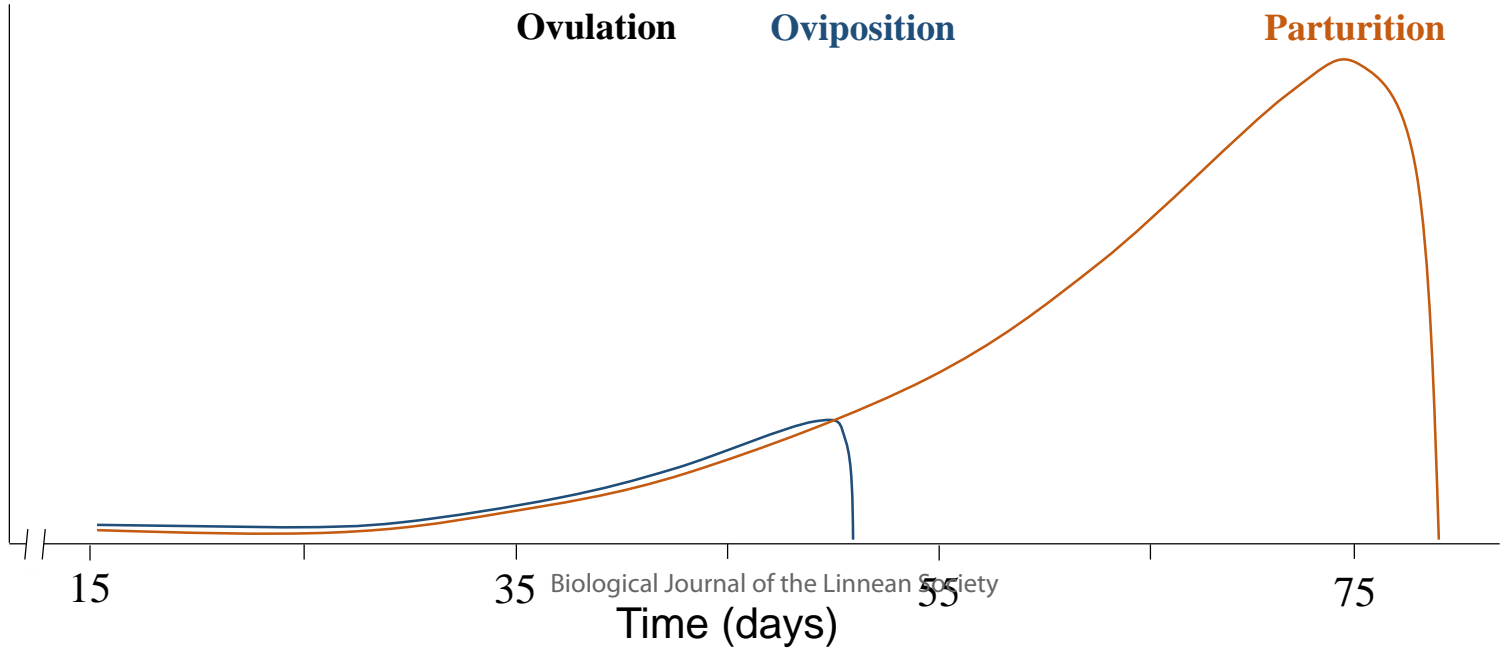
mid-late pregnancy

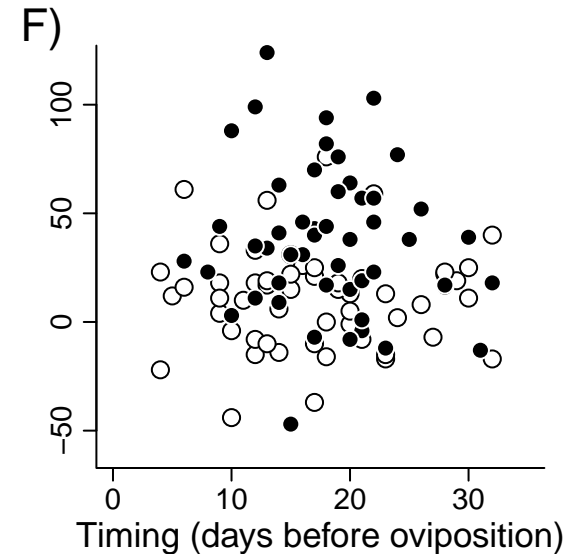
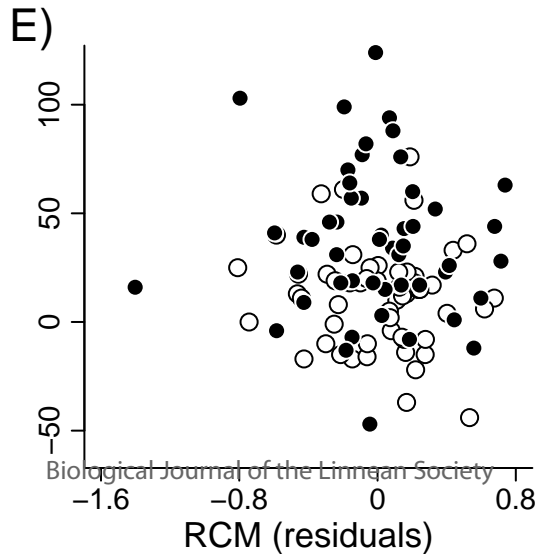
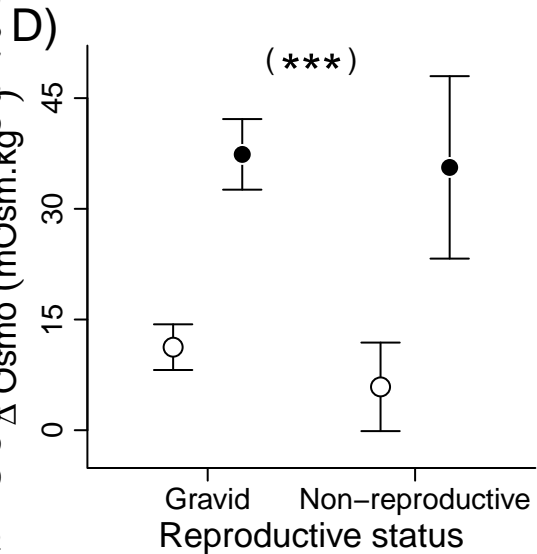
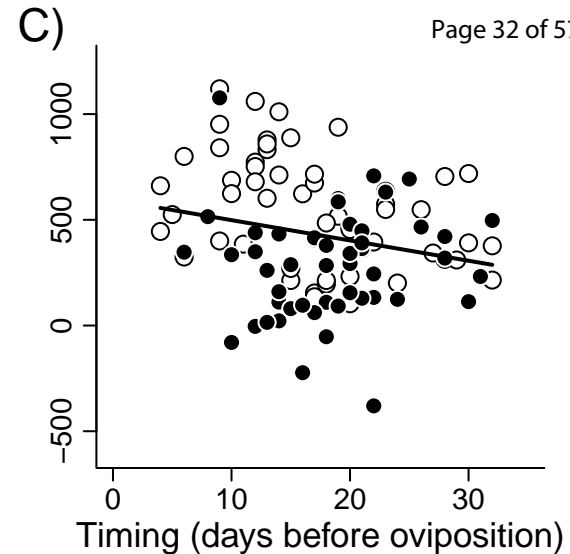
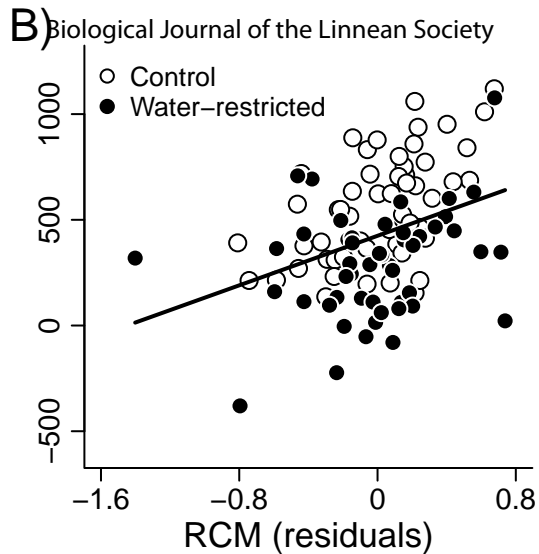
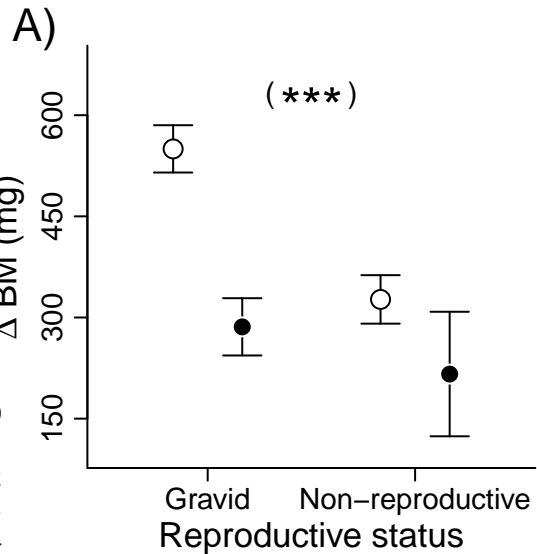
Ovulation

Oviposition

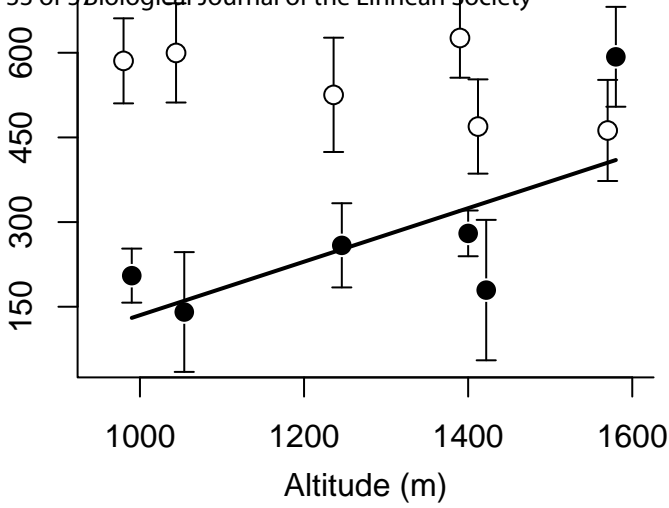
Parturition

Water demand

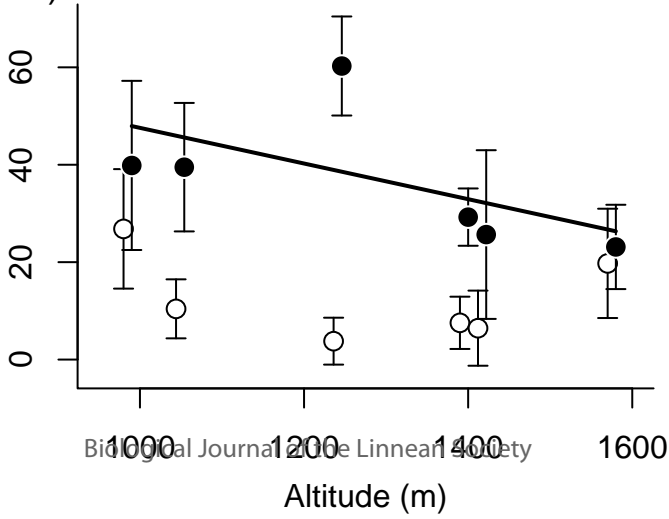




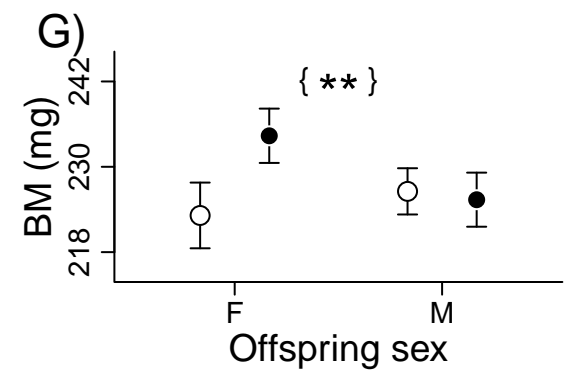
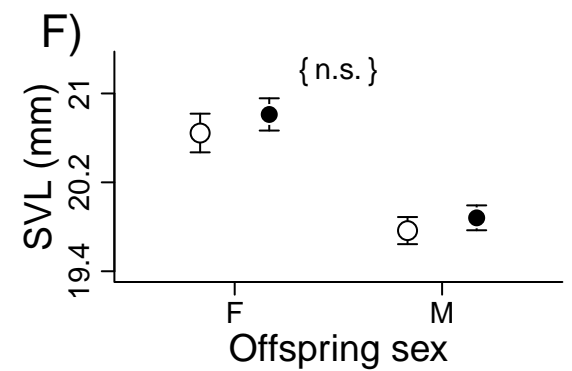
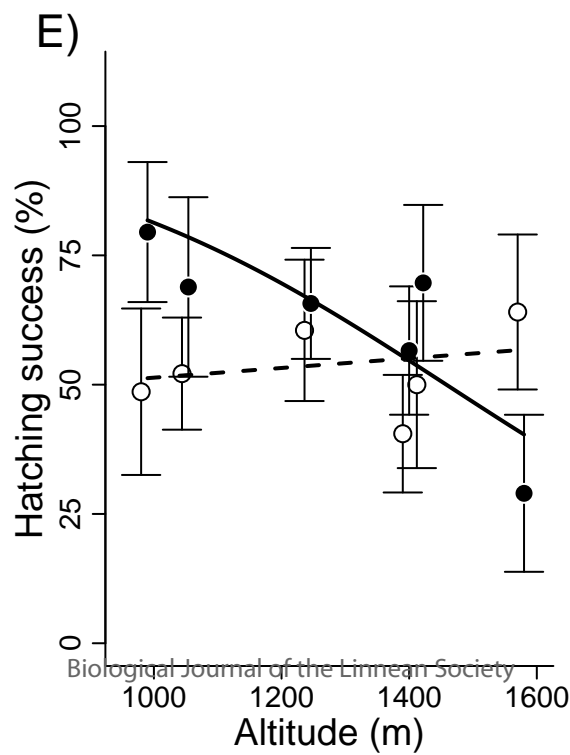
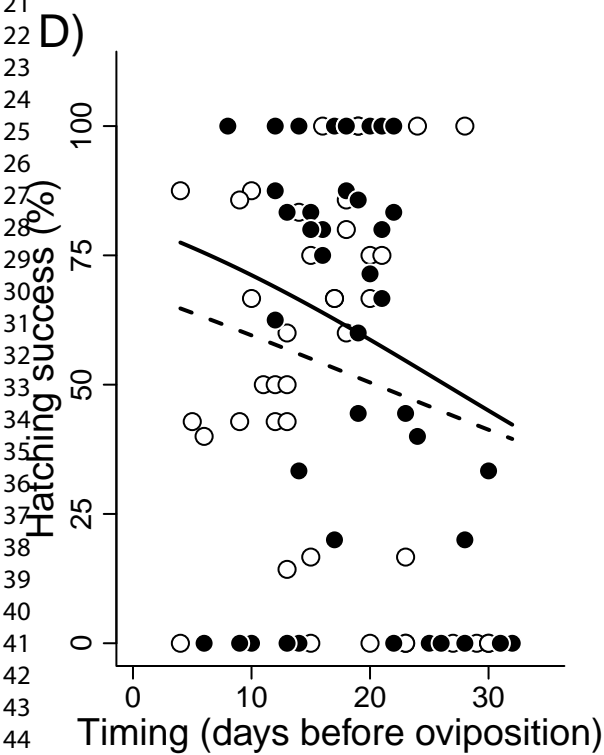
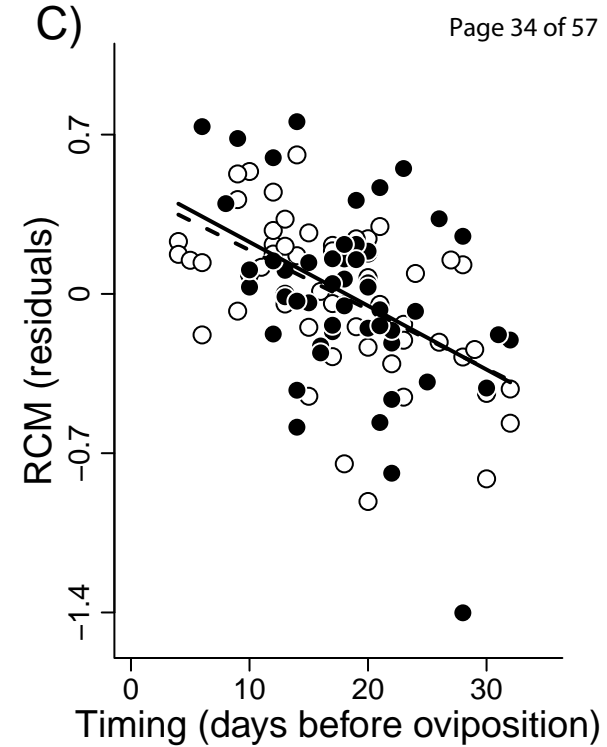
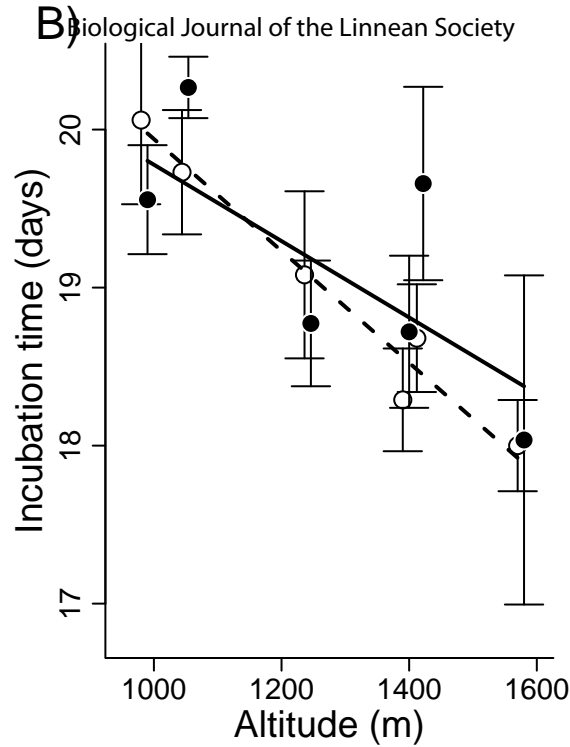
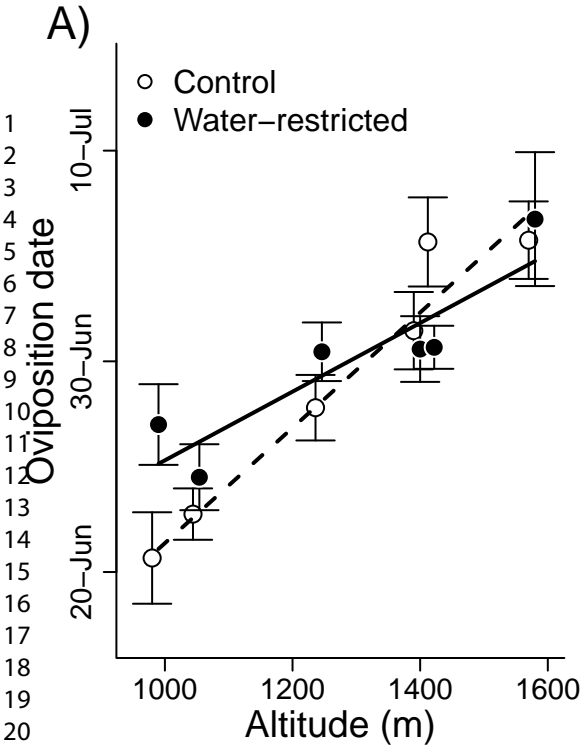
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B)



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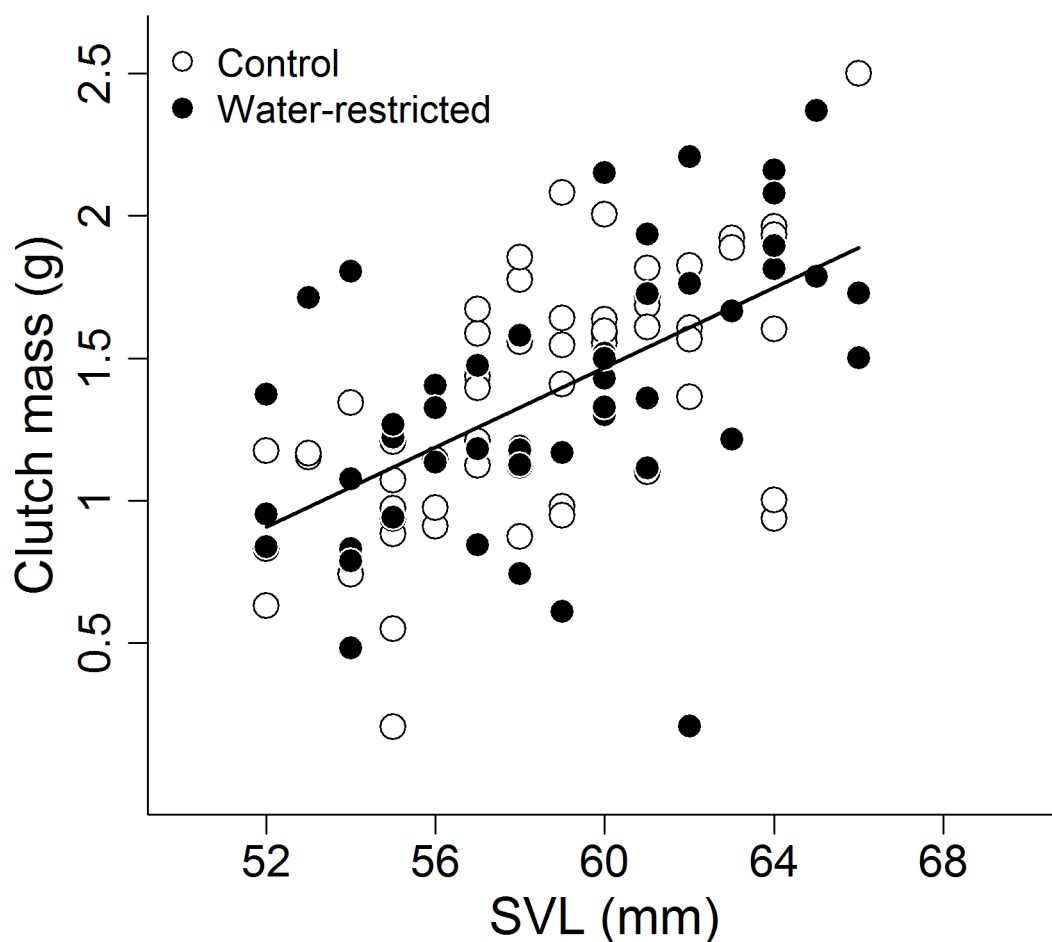


Mother-offspring conflict for water varies across altitude but is mitigated in the oviparous form of the bimodal lizard *Zootoca vivipara*

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

Supplementary materials

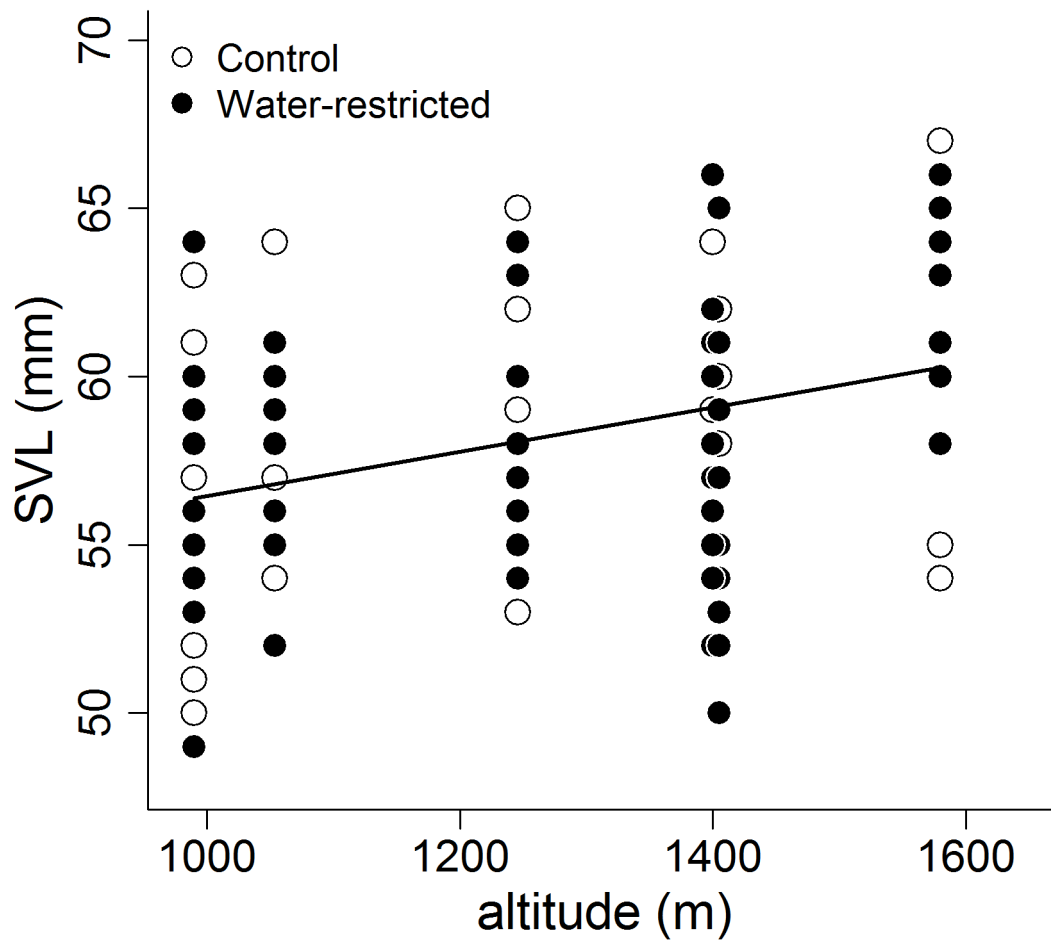
Figure S1. Positive relationship between reproductive effort (clutch mass) and female body size (snout-vent length – SVL). We used the residuals of this linear relationship ($t_{104.0} = 7.3$, $p < 0.001$, $r^2 = 0.34$) to calculate relative clutch mass (RCM). There was no difference between water-restricted (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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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	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				

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 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. 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-variates, 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	ΔAICc	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
	<i>Null</i>	3	51.26	42.63	0.00	-22.54
Δ Osmo	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

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 + 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 Δ BM and changes in plasma osmolality Δ 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	Δ AICc	w_i	LogLike
Δ BM	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	
Δ Osmo	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 Lourdais, 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
<i>Null</i>	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*

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

	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

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

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
<i>Null</i>	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

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

	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

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

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