



Water restriction in viviparous lizards causes transgenerational effects on behavioral anxiety and immediate effects on exploration behavior

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Abstract

Behavioral plasticity induced by maternal effects is crucial in adjusting offspring phenotype to match the environment. In particular, changes in water availability during development may initiate a range of behavioral responses, such as natal dispersal, but the contribution of maternal effects from water stress in explaining behavioral variation has been overlooked so far. In this study, we examined behavioral plasticity of juvenile common lizards (*Zootoca vivipara*) in response to changes in pre-natal and post-natal hydric conditions. We exposed pregnant mothers either to a moderate water restriction or to ad libitum access to water. We used neutral arena tests to measure repeatedly activity and space use behaviors of their offspring, either in dry or wet soil conditions, at two distinct life stages (juveniles and yearlings) in order to quantify behavioral flexibility, age differences, and personalities (consistent inter-individual differences). Juveniles and yearlings had greater exploration scores in dry than wet conditions regardless of the pre-natal conditions. Pre-natal water restriction and dry post-natal conditions enhanced thigmotaxis (i.e., a behavior related to anxiety) in juveniles. Maternal environment did not influence behavioral flexibility nor the behavior of yearlings. Behaviors were barely repeatable in juveniles and inconsistent through early life. Assuming that dry conditions may initiate flight responses, these results suggest complex relationships between the developmental timing of water stress, exploration and anxiety behaviors, and dispersal syndromes.

Significance statement

Water restriction should initiate a range of behaviors related to a flight response. However, there is little evidence that changes in water availability across development influence offspring behavior in wild animals. Experiments with lizards demonstrate that maternal water restriction increased the anxiety of their juveniles, whereas their exploration was higher in dry environments. Thus, water availability may be a critical determinant of space use behavior and dispersal syndromes.

Keywords Maternal effects · Exploration · Thigmotaxis · Stress · Reptiles · Water availability

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Introduction

Water availability and ambient humidity (i.e., hydric conditions) are critical determinants of general ecological patterns as they influence dehydration risk (e.g., Seebacher and Alford 2002; Shochat et al. 2004; Rozen-Rechels et al. 2015; Dupoué et al. 2016, 2017). When water becomes limited, animals may alter a range of behavioral traits including changes in drinking behavior (Rautenberg et al. 1980), changes in posture or decreased locomotor activity to limit water loss (Pough et al. 1983; Lorenzon et al. 1999; Davies and DeNardo 2009; Pintor et al. 2016), and/or shifts in micro-habitat use (Chown et al. 2011; Rozen-Rechels et al. 2015). Dry conditions may also elicit flight responses since limited water availability drives dispersal behaviors (e.g., Massot et al. 2002). Collectively, these behaviors may contribute to regulate the water balance and can influence the fitness of animals in their natural environments (Kearney et al. 2013). Yet, sources of variation in behavioral hydroregulation (i.e., behaviors involved in the regulation of water intake and water loss) among individuals remain poorly investigated so far.

One of the main sources of variation of hydroregulation behaviors, as well as other behaviors, is likely to be intra-individual behavioral flexibility. Behavioral flexibility (also often called behavioral plasticity) is a crucial component of individual responses to changes in environmental conditions that can determine the capacity of organisms to match their environment (Lima and Dill 1990; Dingemanse et al. 2010). In the short term, behavioral flexibility involves fast and reversible changes in response to the environment. Another source of variation of hydration behaviors could be transgenerational effects. Phenotypic traits of mothers and/or environmental conditions encountered by mothers during early development can indeed influence the phenotype of their offspring at birth or later in life (i.e., maternal effects, Mousseau and Fox 1998). Examples of maternal effects include not only adaptive effects that enhance the offspring fitness (e.g., transgenerational induction of defenses against predators, Agrawal et al. 1999) but also non-adaptive responses that decrease the offspring fitness (e.g., overcrowding effects on offspring size, McCormick 2006). Maternal effects can strongly influence mean behavior as well as behavioral flexibility given the influence of maternal environment on fetal neural development (Forstmeier et al. 2004). Yet, maternal effects on offspring behavior induced by water restriction have not been investigated so far. A range of studies in insects and amphibians have shown that these animals are able to adjust flexibly their behavior to control their rates of desiccation and water intake (e.g., Chown et al. 2011; Köhler et al. 2011). In addition, animals exposed to desiccating conditions tend to acclimate both their behavior and their physiology in order to reduce their water loss rates (e.g., Hertz et al. 1979; Chown et al. 2011). Still, whether these functional responses

in adults carry over to influence offspring behavior remains an open question.

Another potential source of variation in behavioral responses to water availability is intra-individual change with age, although age-dependent sensitivity of behavior to water availability has still not been investigated. Differences in behavioral flexibility with age could be due to an age-dependent physiological sensitivity to desiccation or may be related to the size scaling of water loss and dehydration tolerance. Evaporative water loss seems to be independent from age in birds (Versteegh et al. 2008); on the contrary, small individuals are more sensitive to water loss than adults in toads (e.g., Newman and Dunham 1994), in insects (Chown and Gaston 1999), and in plants and animals in general (Woods and Smith 2010). Thus, the behavior of juvenile lizards might be more sensitive to changes in their water environment because they are smaller than adults on average. In addition, dispersal and habitat selection abilities vary through life, and behavioral responses to water availability may thus involve either flight or acclimation responses depending on the age of individuals. Because common lizards disperse mainly at the juvenile life stage (e.g., Massot et al. 2002; Meylan et al. 2002), we expect stronger flight responses to water restriction in this age class than in yearlings or more than 2-year-old adults. Recently, it has also been emphasized that individuals of the same age can be highly variable in their behavioral flexibility because individuals vary in their “personalities” (e.g., Dall et al. 2004; Sih et al. 2004; Le Galliard et al. 2013). Personalities imply a low intra-individual and a high inter-individual behavioral flexibility (Dingemanse et al. 2010). Thus, studies of behavioral plasticity should account for both intra-individual and inter-individual responses (Dingemanse et al. 2010).

We addressed these three issues (i.e., maternal effects, age dependence, and personality) by examining the effects of maternal water restriction and post-natal habitat humidity on the space use behavior of offspring at two distinct life stages in the European common lizard, *Zootoca vivipara* (Lichtenstein, 1823), a small Lacertid widely distributed in Eurasia. Populations of this species are dependent on permanent access to free standing water and humid conditions for their long-term persistence (Lorenzon et al. 2001). Limited water availability can impair reproduction and has also direct effects on behavioral activity and natal dispersal behavior; that is, juveniles from dry habitats disperse more, but yearlings are less active when chronically exposed to water restriction (Lorenzon et al. 1999; Massot et al. 2002). In juveniles, behavioral responses to water restriction may thus be explained by their relationship with natal dispersal, whereas behavioral flexibility in yearlings and more than 2-year-old adults may be related to tactics to reduce energy expenditure and water loss or to increase water intake, but not dispersal which is 10 times less on average after the juvenile life stage. However, effects of maternal water restriction on offspring behavior from

juvenile to the yearling stage have not been examined so far. Here, we compared the space use behavior of offspring from mothers exposed to a water restriction period for 2 weeks in mid pregnancy with those from mothers with water ad libitum, hereafter called the “maternal treatment.” Behavior was scored 1 day after birth (juveniles) and at the age of 10–11 months (yearlings) by the use of the neutral arena test (Réale et al. 2007). In order to quantify behavioral flexibility, post-natal conditions were manipulated in the neutral arena test by changing the soil moisture (dry or wet), hereafter called the “soil moisture treatment.” Individuals were tested two times in each post-natal condition at each life stage to assess their personalities (Dingemanse and Dochtermann 2013).

We predicted that exposure to a mild water restriction during pregnancy would enhance exploration behavior of offspring (e.g., Greenberg 2002), especially at the juvenile life stage when lizards should be more sensitive to desiccation and are more prone to disperse than yearlings (Newman and Dunham 1994; Massot et al. 2002; Meylan et al. 2002). Lizards should also invest more in exploration behavior in dry post-natal environments (e.g., Lorenzon et al. 1999; Massot et al. 2002), and juveniles from water-restricted mothers should have a stronger behavioral response in dry environments due to an interaction between pre- and post-natal environments. In addition, we expected significant and consistent inter-individual variation in exploration behaviors (Le Galliard et al. 2013) and in behavioral flexibility (Dingemanse et al. 2010).

Material and methods

Data availability statement The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

Study species

Common lizard studied individuals were captured from captive populations maintained in 24 outdoor enclosures (10 × 10 m) in the Centre de Recherche en Écologie Expérimentale et Prédictive (CEREEP), France (48° 17' N, 2° 41' E). Enclosures have a permanent vegetation layer (mainly grass), and individuals have permanent access to free water in ponds, and access to refuges and basking sites made of pile of rocks. Both ground and avian predation are avoided with plastic polyvinyl chloride (PVC) walls and with nets. As in the wild, main pressures on survival in the enclosures are thus social interactions, energy depletion, or parasites (Massot et al. 1992; Le Galliard et al. 2004). Hibernation usually lasts from October to February–March. Mating season usually begins upon emergence of females in March–April and lasts between

2 to 4 weeks. Gestation lasts usually 2 months but is highly sensitive to climatic conditions. This species is lecithotrophic implying that most of the energy supply is provided with yolk produced during vitellogenesis (Bleu et al. 2012). During pregnancy, there is no evidence of nutrient sharing between the mother and the embryo, and maternal effort is therefore oriented through mineral exchanges such as water and oxygen. Litter size ranges from 1 up to 12 juveniles (5 on average). There is no post-natal parental care. Body growth is continuous though life and decelerates with age. In our study populations, age at maturation varies from sometimes 1 (yearlings) to most of the time 2 years old (adults). Yearling individuals are distinguishable from older lizards by smaller body size, the majority not being sexually mature and not being as brightly colored as older lizards.

Study sample and rearing conditions

In May 2015, animals were captured in outdoor enclosures and identified by their unique “toe clip.” The day of capture, each lizard was measured for snout-vent length (SVL ± 1 mm) and body mass (BM ± 1 mg). Lizards were then sorted in individual terraria with sterilized peat soil and kept under natural day-night light and temperature conditions in a temperature-controlled room (16 h of night at 16 °C and 8 h of day at 23 °C). Each terrarium provided lizards with a thermal gradient (23 to 35 °C) 6 h a day (09:00 to 12:00 and 14:00 to 17:00) with a light bulb (25 W) at one end of the terrarium. Animals were fed with house crickets three times per week (*Acheta domestica*, 300 ± 10 mg for yearlings; 400 ± 20 mg for more than 2-year-old adults). In this study, we used 171 pregnant females (151 adults, mean ± SD: SVL = 65.8 ± 3.6 mm, BM = 5.83 ± 1.05 g; 20 yearlings: SVL = 56.6 ± 1.8 mm, BM = 3.36 ± 0.31 g). Water was available ad libitum in a bowl (petri dish) and misted three times a day (09:00, 13:00, 17:00).

Experimental manipulation of the pre-natal environment

We randomly selected and exposed 87 females (more than 2-year-old adults, $n = 77$, yearlings, $n = 10$) to a mild water restriction period between 01 and 15 June 2015 whatever their stage in gestation. In this case, the water bowl was removed and water was misted only once in the morning (09:00). At the same time, 84 control females (more than 2-year-old adults, $n = 74$, yearlings, $n = 10$) were maintained with the ad libitum water conditions described above. These treatments mimic natural conditions with permanent (e.g., bog habitat) or periodic access to water (e.g., dry meadows where morning dew is the only available source of free water; Dupoué et al. 2017). Previous studies showed that water restriction induced significant changes in body mass, plasma osmolality (i.e., an index

of body hydration), and activity time of lizards (Lorenzon et al. 1999; Dupoué et al. 2017).

Experimental manipulation of the post-natal environment

Females gave birth from 23 June to 14 July 2015; juveniles were sexed counting their ventral scales (Lecomte et al. 1992). The day of parturition, two to four juveniles per litter (equal sex ratio whenever possible) were randomly selected from each litter (171 litters, 422 juveniles; 204 females and 218 males). Exploration behavior was measured the day following birth (i.e., juvenile stage) using neutral arena tests. The experiment was done in a temperature-controlled room (25 °C) during activity time of the day (09:00 to 17:00). Each behavioral test was performed during 30 min in a neutral arena (25 × 15 × 15 cm) heated from above with a lamp (40 W) and illuminated with white light. During the first 10 min, the individuals had time to recover from handling stress and to habituate to the arena. We used the last 20 min to record the immediate behavioral responses. The acclimation time allowed for lizards to initiate exploration and the recording time typically corresponds to the time period where individuals normally explore the space of the neutral arena (Le Galliard et al. 2015). We randomly assigned each arena either to a dry or a wet treatment (i.e., post-natal environment). The substratum (fine sand) was dried before each trial at 150 °C during 2 h in a stove. In the dry treatment, dry sand was used, and in the wet treatment, the sand was sprayed homogeneously with water (ca. 30 mL) immediately before the trial to saturate the sand with water. Sand was changed, and terraria were cleaned between each trial in order to avoid the presence of conspecifics' odor. Each lizard was tested four times (i.e., four trials) with two repeats per soil moisture treatment. Each lizard was tested with a pseudo-random sequence to ensure that treatment was not confounded with trial number. Each trial was recorded with a webcam at a high frequency (five images/second). Behavioral experiment lasted from 24 June to 15 July and included 1474 analyzable videos out of 1688 records. Non-usable records had corrupted files or a camera with an inappropriate angle of view.

After experiments, each litter was randomly released in 1 out of the 24 outdoor enclosures between early July and early August. In May 2016, we recaptured all individuals that survived over the year with a high success of capture (Le Galliard et al. 2005). The day of capture, individuals were identified with their toe clipping, measured, and weighed. We calculated annual growth rate ($\text{mm}\cdot\text{day}^{-1}$) by dividing the SVL increment from birth to recapture by the total number of days between birth and recapture. Due to a lower survival rate than the average, inter-annual portrait (survival rate of 14% similar to mean value reported in Dupoué et al. 2017 but lower than the ca. 30%

inter-annual mean), we recaptured only 26 males and 34 females from the sample of individuals tested at juvenile stage. We also recaptured individuals that had not been tested but that were from the same litters (37 males, 25 females). Yearlings were kept for 3 days in the laboratory without food to ensure that all individuals were in a similar post-absorptive state. We then recorded their behavior in neutral arenas (44.5 × 24 × 26 cm) larger than those used earlier in life to scale with the body size increase (ca. 100 mL). Setups also differed in the location of the heat source: at juvenile stage, heat lamps were above the corner of the box, while they were centered above the box at the yearling stage. Except for arena size and light placement, the exact same neutral arena protocol as the one used for juveniles was used for yearlings. Experiment lasted 8 days between 19 May and 30 May, and 479 usable video records were obtained.

Behavioral data

To minimize observer bias, blinded computer-based methods were used when all behavioral data were processed. We extracted the spatial coordinates of each lizard inside the neutral arena and the spatial location of edges of the neutral arena with a threshold detection procedure in ImageJ (version 1.49, <https://imagej.nih.gov>). We used the movement path records to calculate several relevant measures of the exploration and movement behavior. First, we calculated the distance between two locations from two consecutive images (movement step length). This variable followed a clear bimodal distribution with the lowest mode corresponding to motionless lizards. We thus extracted the second mode of the distribution from each record using the *Rmixmod* package in R (Lebreton et al. 2015) and calculated the value of the 99 percentile of the distribution with the lowest mean. When distance values were below this distribution, lizards were considered inactive; otherwise, a positive step length (i.e., distance between two locations of two consecutive images) was recorded. We calculated the relative time spent active (T), the total distance walked by the lizard (D), the number of activity bouts (i.e., number of sequences of consecutive images with positive step length, N_{bouts}), the average distance walked in a bout (D_{bouts}), the average distance walked between two images in a bout (M_{bouts}), and the mean standard deviation of distances walked between two images in a boot (homogeneity of displacements; SD_{bouts}). Second, we added a buffer zone along the walls of the neutral arena (corresponding approximately to a lizard length) in order to measure the behavior of the lizard when they moved along or close to the wall. Movements towards or away from the walls are called “thigmotaxis” behavior and have been used as an index of “anxiety” in

rodents (Treit and Fundytus 1988; Simon et al. 1994) and in lizards (Maximino et al. 2014). Thigmotaxis is not frequently measured in behavioral ecology studies, but Maximino et al. (2014) observed that this behavior is inhibited by anxiolytics in a reptile, when exploratory behaviors were enhanced, indicating that exploration and thigmotaxis are indeed distinct behavioral traits. We calculated the time spent by the lizard in the buffer zone along the walls (T_{walls}), the total distance walked out of the buffer zone ($D_{1\text{walls}}$), the mean distance to the walls ($D_{2\text{walls}}$), and the standard deviation of the distance to the walls (SD_{walls}). Third, we subdivided the neutral arena into 24 equal squares, to estimate the total area visited by the lizards including the proportion of squares visited at least once by the individual (τ_{explo}) and the standard deviation of the number of locations per square or heterogeneity of the exploration (SD_{explo}).

Statistical analyses

All statistical analyses were carried out in R version 3.3.0 (R Core Team 2016). Prior to analyses, the distribution of each behavioral trait was transformed using a Box-Cox power function with “*AID*” package to meet the requirements of the Gaussian distribution (Asar et al. 2017). The identification of suites of correlated behavioral traits (i.e., behavioral syndromes) was explored using principal component analyses (PCAs) on the centered and scaled individual values of each behavioral trait with the “*ade4*” package (Dray and Dufour 2007). The number of components in the analysis was chosen using the broken stick method (Legendre and Legendre 1998), and we identified the contribution of each variable to each dimension of the PCA by calculating the inertia. A contribution was significant when it was higher to the average contribution (Legendre and Legendre 1998). In the subsequent analyses, each PC axis was considered as a behavioral syndrome; individual PC scores were extracted, and individuals were ranked according to them. This analysis was conducted on both years separately. We also repeated this analysis with a data set of juveniles and yearling records in order to study repeatability of behavioral syndromes during early life (see below).

Possibly due to handling and novelty stress, some individuals were motionless during the whole duration of a test leading to a bimodal distribution of behavioral traits related to mobility and exploration (see below). We calculated the proportion of these records and excluded these immobile individuals from our analyses of mobility and exploration behavior. To do so, we fitted the best bimodal distribution to the data based on loglikelihood maximization and deleted observations that had more than 50% chance of being part of the motionless mode of the distribution.

Question 1: are behavioral syndromes repeatable within and between life stages?

We calculated a repeatability index of the PC scores using a linear mixed model (LMM, Verbeke and Molenberghs 2009; package *nlme*) including the soil moisture treatment (i.e., dry or wet) as fixed effect and individual identity as a random effect. Repeatability R was calculated from the variance components following model results (see Eq. 1). The model was run with separate data from each year with a random individual variability around the intercept. Significance of the intra-individual variance was tested with a loglikelihood ratio test (LRT). We further tested the correlations of behaviors between the 2 years. Since PC axes were similarly structured across years (see below), we merged data from the 2 years from recaptured individuals and calculated a mean PC score for each year for each individual. We then tested the correlation between the individual scores of the 2 years.

$$R = \frac{Var^{Interindividual}}{Var^{Interindividual} + Var^{Residual}} \quad (1)$$

Question 2: are behavioral syndromes a result from pre-natal and post-natal interactions?

We tested the effects of the maternal treatment (i.e., water restriction or control), soil moisture treatment (i.e., dry or wet), trial number (i.e., trials 1, 2, 3 to 4), and their interactions on behaviors. We built LMMs with each PC score as a response variable, and lizard identity, mother identity, and the enclosure of origin of the mother as random factors to account for repeated measures on the same individual, non-independence among siblings, and differences among enclosures, respectively. The full model included a three-way interaction between trial, maternal treatment, and the soil moisture treatment. When testing behaviors at birth, we also included the standardized time since first laying, a measure of the developmental stage of offspring in utero during the maternal treatment, in two-way interactions with both treatments. We first checked for the Gaussian distribution and homoscedasticity of the residuals of the full model. We then selected a minimum adequate model using backward elimination of the non-significant terms based on LRT. We first tested the significance of random effects and then removed non-significant fixed effects.

Question 3: do juvenile exploration behaviors influence their fitness?

For each individual record at birth, we calculated the mean individual PC score from the four measurements, and the

plasticity of each PC score (difference between mean score in the wet and the dry conditions). We tested the effects of mean and plasticity in PC scores on annual survival using generalized linear mixed models (GLMM, package lme4) with a binomial error. We also tested the effects of mean and plasticity in PC scores in interaction with maternal treatment on survival. We tested the effects on annual growth rate using LMMs. Mother and enclosure of release identity were treated as additive random effects.

Results

Repeatability of behavioral syndromes

In both years, the broken stick method selected only two significant PC axes (Table 1). Variables associated with locomotor activity (distance walked by the lizard, number of movement bouts, distance per activity bout, average distance between each images of bouts, standard deviation of the distance, distance walked along the walls) and exploration

Table 1 Eigenvalues and relative contributions of each measured behavioral variables (in percentage) to the variance of each PCA axes. A contribution is considered significant when it is higher than the mean (i.e., 8.33%). The sign of the contribution indicates if it positively (no sign) or negatively (–) correlates with the PC axis. Behavioral traits are total distance walked by the lizard (D), relative time spent active (T), number of activity bouts (N_{bouts}), average distance walked in a bout (D_{bouts}), average distance walked between two images (M_{bouts}), mean standard deviation of distances walked between two images in a bout (SD_{bouts}), time spent by the lizard in the buffer zone along the wall (T_{walls}), total distance walked in the buffer zone ($D_{1\text{walls}}$), mean distance to the wall when the lizard is in movement ($D_{2\text{walls}}$), standard deviation of the distance to the walls or heterogeneity of the distance to the walls (SD_{walls}), proportion of squares visited at least once by the individual (τ_{explo}), and standard deviation of the number of locations in the square visited or heterogeneity of the exploration (SD_{explo})

	2015		2016		Both	
	PC1	PC2	PC1	PC2	PC1	PC2
Eigenvalues	52.5	19.4	49.8	26.1	57.7	19.7
D	13.46	4.58	16.10	-0.12	11.82	6.10
T	9.69	3.70	13.29	0.12	10.20	2.52
N_{bouts}	1.63	3.23	3.27	0.04	5.70	0.001
M_{bouts}	11.84	3.92	14.10	-0.66	10.88	4.32
SD_{bouts}	12.34	3.59	13.55	-0.15	10.27	6.35
D_{bouts}	11.91	2.88	11.67	-0.33	7.95	8.47
T_{walls}	3.50	-21.56	-1.11	-25.35	3.84	-23.25
$D_{1\text{walls}}$	10.77	-7.72	14.94	1.52	10.93	-0.58
$D_{2\text{walls}}$	0.20	-31.15	-0.86	-28.07	1.23	-29.04
SD_{walls}	6.79	-14.98	-0.29	-28.10	7.58	-15.81
τ_{explo}	9.25	-2.69	4.35	-12.90	9.05	2.61
SD_{explo}	-8.62	0.001	-6.50	2.65	-10.55	0.95

(proportion of time spent walking, proportion of the space visited) were positively correlated with the first axis (PC1). Lizards with positive values of the PC1 score were also characterized by a lower heterogeneity of exploration suggesting that all the space was visited equally. Thus, PC1 provided a score of activity and exploration in the neutral arena, which we subsequently describe as the exploration score. On the other hand, three behavioral variables related to movement relative to the walls of the neutral arena were correlated with the second axis (PC2, Table 1) with negative correlations with mean distance to the walls and time spent out the buffer zone and negative correlation with standard deviation of the distance to the walls. Thus, PC2 provided a score of thigmotaxis.

Short-term repeatability was higher in 2016 in yearlings (PC1: $R = 64.9\%$ and PC2: 39.8%) than in 2015 (PC1: 27.4, PC2: 17.9), but was significant in each life stage (juveniles, PC1: LRT = 104.33, $p < 0.001$; PC2: LRT = 56.6, $p < 0.001$; yearlings, PC1: LRT = 228.34, $p < 0.001$; PC2: LRT = 86.4, $p < 0.001$). In addition, PC scores at the yearling stage were not significantly correlated with PC scores at the juvenile stage (PC1: Pearson's correlation coefficient $R^2 = 0.08$, $t = 0.6$, $df = 58$, $p = 0.53$; PC2: $R^2 = -0.08$, $t = -0.6$, $df = 58$, $p = 0.55$).

Maternal effects on behavioral syndromes

Exploration score was best fitted with a bimodal distribution in 2015 and 2016 (Supplementary Fig. 1): 147 observations in 2015 and 17 in 2016 were considered as immobility records and were removed from the dataset. The probability of being motionless was significantly higher during the first trial and the lowest during the third trial (LRT = 98.74, $p < 0.001$) and in wet environments (LRT = 26.59, $p < 0.001$) at the juvenile stage. In yearlings, this probability was also greater explained by the trial number (LRT = 27.15, $p < 0.001$), but was not related to neutral arena wetness (LRT = 1.95, $p = 0.16$). In yearlings, the maternal treatment did not affect the probability of being motionless (juveniles: LRT = 26.59, $p < 0.001$; yearlings: LRT = 0.10, $p = 0.75$).

The best models for each PC score had no significant effects of the mother enclosure identity (PC1 in 2015: LRT = 1.09, $p = 0.30$; PC2 in 2015: LRT = 0.06, $p = 0.81$; PC1 in 2016: LRT = 1.60, $p = 0.21$; PC2 in 2016: LRT = 1.46, $p = 0.23$; see details on the best models in Tables 2 and 3). Exploration score was not influenced by an interaction between soil moisture treatment and maternal treatment (juveniles: LRT = 0.96, $p = 0.37$; yearlings: LRT = 0.69, $p = 0.41$; Fig. 1). In juveniles, exploration was higher for individuals from water-restricted mothers than for controls when mothers laid early; on the contrary, individuals from latest clutches from water-restricted mother had a lower exploration rate than controls (Table 2). Maternal treatment significantly enhanced thigmotaxis score at the juvenile stage (Table 3, Fig. 1c), but

Table 2 Best statistical models describing significant effects of maternal water restriction treatment, soil moisture treatment, and trial number on exploration behaviors. Minimum adequate models were selected by backward elimination of non-significant terms (see main text). Description of the effect of each numeric variable and of each level of the factors in the best models selected for exploration rate in

juveniles and yearlings. These effects are presented as the difference to the reference value called intercept (trial 1; wet soil moisture conditions; control mother). In italics are effects that are significantly different from 0. The standard deviation explained by the random effects in each model are also displayed

	<i>ndf</i>	<i>ddf</i>	<i>F</i> statistics	<i>p</i> value		Estimate	SE	DF	<i>t</i> value	<i>p</i> value	
Exploration score at the juvenile stage (<i>N</i> = 1327)											
Trial number	3	900	33.00	< 0.0001	Intercept	-0.93	0.18	900	-5.15	< 0.0001	
					Trial 2	0.98	0.21	900	4.67	< 0.0001	
					Trial 3	1.72	0.17	900	9.86	< 0.0001	
					Trial 4	1.17	0.21	900	5.66	< 0.0001	
Soil moisture treatment	1	900	30.87	< 0.0001	Dry	1.16	0.21	900	5.56	< 0.0001	
Trial number × soil moisture treatment	3	900	4.74	0.0028	Trial 2: dry	-0.32	0.34	900	-0.96	0.3374	
					Trial 3: dry	-0.82	0.23	900	-3.55	0.0004	
					Trial 4: dry	-0.12	0.34	900	-0.37	0.7127	
Scaled time since first laying	1	246	0.24	0.62		0.06	0.12	246	0.49	0.6219	
Scaled time since first laying × soil moisture treatment	1	900	7.98	0.0048	Dry	0.22	0.08	900	2.83	0.0048	
Maternal water restriction treatment	1	169	0.76	0.39	Stress	0.13	0.15	169	0.87	0.3856	
Scaled time since first laying × mat. water restric. treat.	1	246	7.04	0.0085	Stress	-0.41	0.15	246	-2.65	0.0085	
Random effects						Intercept		Residual			
						Mother	0.7274				
						Juvenile in mother	0.6293	1.3829			
Exploration score at the yearling stage (<i>N</i> = 463)											
Soil moisture treatment	1	340	21.29	< 0.0001	Intercept	0.10	0.19	340	0.54	0.5855	
						Dry	-0.60	0.12	340	-5.03	< 0.0001
Random effects						Intercept		Residual			
						Mother	0.7594				
						Juvenile in mother	0.6247	1.3888			

had no effect at the yearling stage (LRT = 1.12, $p = 0.29$) and did not interact with soil moisture treatment (juveniles: LRT = 0.51, $p = 0.47$; yearlings: LRT = 1.29, $p = 0.26$; Fig. 1).

Exploration score was higher in dry than in wet soil moisture treatment in both life stages (Fig. 1a, b). In addition, in juveniles, this effect was stronger in individuals from latest clutches (Table 2). Thigmotaxis score was higher in dry than in wet soil moisture conditions at the juvenile stage (Fig. 1c), but this difference was reversed at the yearling stage (Fig. 1d). Exploration score of juveniles increased on average with trial number until the last trial, where scores were slightly lower than in trial 3, and the difference between wet and dry soil moisture conditions was maximum in the first and last trial (Fig. 2). Similar effects of trial number were found for mean exploration score of yearlings and mean thigmotaxis score of juveniles (Fig. 2c). On the contrary, thigmotaxis score of yearlings decreased with trial number (Fig. 2d).

Relationship between behavioral traits and fitness components

Annual survival was not influenced by the mean exploration score at birth (LRT = 0.59, $p = 0.44$), plasticity in exploration score (LRT = 0.72, $p = 0.40$), mean thigmotaxis score (LRT = 1.01, $p = 0.32$), nor by plasticity of thigmotaxis score (LRT = 0.84, $p = 0.36$). Survival was not influenced by the interaction of the maternal treatment with the mean exploration score at birth (LRT = 0.47, $p = 0.49$), plasticity in exploration score (LRT = 0.41, $p = 0.52$), mean thigmotaxis score (LRT = 0.55, $p = 0.46$), nor by plasticity of thigmotaxis score (LRT = 1.00, $p = 0.32$). Similarly, annual growth rate was not impacted by the mean exploration score at birth ($F_{1,7} = 0.38$, $p = 0.56$), plasticity of exploration score ($F_{1,7} = 0.14$, $p = 0.72$), mean thigmotaxis score ($F_{1,7} = 0.04$, $p = 0.84$), nor by plasticity of thigmotaxis score ($F_{1,7} = 2.66$, $p = 0.15$).

Table 3 Best statistical models describing significant effects of maternal water restriction treatment, soil moisture treatment, and trial number on thigmotaxis behaviors. Minimum adequate models were selected by backward elimination of non-significant terms (see main text). Description of the effect of each numeric variable and of each level of the factors in the best models selected for thigmotaxis rate in

juveniles and yearlings. These effects are presented as the difference to the reference value called Intercept (trial 1; wet soil moisture conditions; control mother). In italics are effects that are significantly different from 0. The standard deviation explained by the random effects in each model are also displayed

	ndf	ddf	<i>F</i> statistics	<i>p</i> value		Estimate	SE	DF	<i>t</i> value	<i>p</i> value
Thigmotaxis score at the juvenile stage (<i>N</i> = 1474)										
Trial number	3	1048	5.89	<i>0.0006</i>	Intercept	-0.89	0.17	901	-5.38	< <i>0.0001</i>
					Trial 2	0.98	0.21	901	4.62	< <i>0.0001</i>
					Trial 3	1.75	0.18	901	10.00	< <i>0.0001</i>
					Trial 4	1.16	0.21	901	5.58	< <i>0.0001</i>
Maternal water restriction treatment	1	169	4.99	<i>0.0267</i>	Stressed mother	0.23	0.10	169	2.23	<i>0.0267</i>
Soil moisture treatment	1	1048	54.64	< <i>0.0001</i>	Dry conditions	0.53	0.07	1048	7.39	< <i>0.0001</i>
					Intercept			Residual		
					Mother	0.3334		Juvenile in mother	0.5355	1.3483
Thigmotaxis score at the yearling stage (<i>N</i> = 480)										
Trial number	3	354	4.33	<i>0.0052</i>	Intercept	0.56	0.18	354	3.16	<i>0.0017</i>
					Trial 2	-0.26	0.17	354	-1.50	0.1351
					Trial 3	-0.36	0.17	354	-2.06	<i>0.0398</i>
					Trial 4	-0.63	0.18	354	-3.58	<i>0.0004</i>
Soil moisture treatment	1	354	16.02	<i>0.0001</i>	Dry conditions	-0.49	0.12	354	-4.00	<i>0.0001</i>
					Intercept			Residual		
					Mother	0.5484		Yearling in mother	0.9678	1.3427

Discussion

We investigated the age-dependent effects of pre-natal and post-natal hydric conditions on space use behavior of offspring. We used the neutral arena test, which provides a simple and standard procedure to score a variety of exploration, locomotor, and space use behaviors in ground-dwelling vertebrates such as rodents or lizards (Réale et al. 2007; Gould et al. 2009; Le Galliard et al. 2013). In addition, by using the neutral arena test under two conditions representing extremes from a substratum wetness gradient, we were able to score not only the mean lizard behavior but also the behavioral flexibility of individuals. We acknowledge that this simple test protocol did not allow to quantify the boldness of individuals and their habitat choice behaviors that could be tested in further studies with more complex arenas including shelters and micro-habitats. Our results show that two behavioral scores related to exploration and thigmotaxis (a proxy of anxiety) could be extracted from movement paths of lizards at both life stages.

Exploration behavior relates to the ability to gather spatial information in a novel or changing environment and has been measured by metrics of locomotor activity, spatial sampling, and information gathering similar to

ours in recent studies with lizards (e.g., Rodríguez-Prieto et al. 2011). As expected, exploration behavior was enhanced in the dry soil moisture treatment at the juvenile and yearling life stages in line with previous studies of natal dispersal behavior in the same species (Massot et al. 2002). Individuals did not differ consistently in the behavioral sensitivity of exploration to soil moisture treatment. We also found that individuals from latest clutches increased their exploration behavior in response to the dry soil treatment with more amplitude than individuals from early clutches. This indicates differences in the behavioral flexibility of offspring associated with differences in laying dates of females, most probably because of some unknown maternal effect. In general, dry environments may be challenging for lizards on the very short term given the physiological constraints on water balance (e.g., higher rate of water losses; Summers and Norman 1988; Dupoué et al. 2015a). A more pronounced locomotor activity and spatial sampling may therefore indicate more active exploration to evade such conditions and search for water. Such enhanced behavioral exploration could be crucial for survival, especially in juvenile lizards that disperse quickly in the month following birth. Individuals

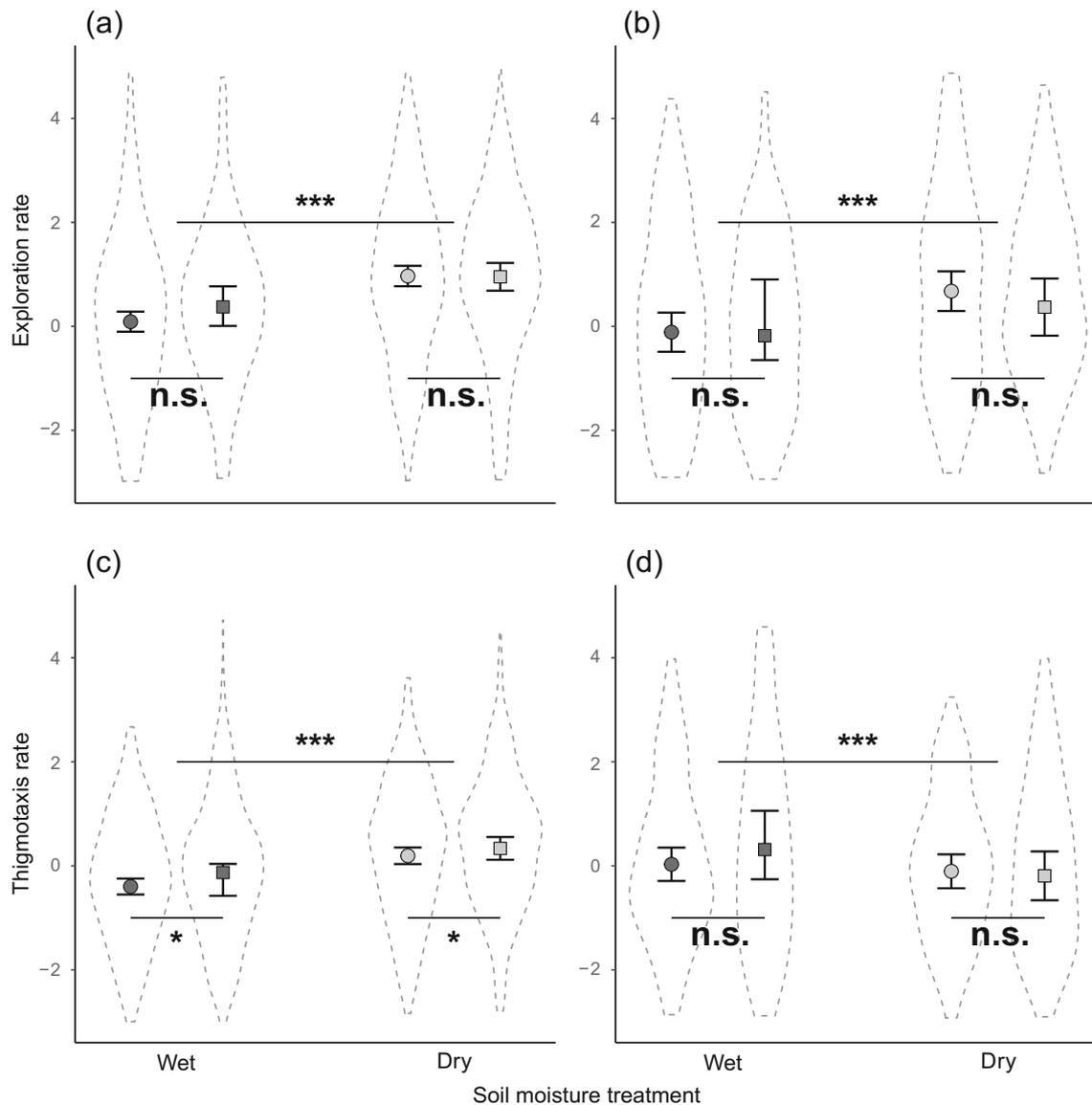


Fig. 1 Behavioral syndrome estimated for **a** PC1 in 2015 (juveniles), **b** PC1 in 2016 (yearlings), **c** PC2 in 2015 (juveniles), and **d** PC2 in 2016 (yearlings) for each treatments. Soil moisture treatments are differentiated with colors: dark gray symbols are for wet soil moisture conditions, and light gray symbols are for dry soil moisture conditions. Maternal treatments are differentiated with the shape of the symbols: circles are for control mothers, and squares are for water restricted mothers. Light

gray dashed violin plots represent raw data distributions. Error bars are for 95% confidence intervals. Stars represent p values. n.s. non-significant; $0.05 < * < 0.01$; $0.01 < ** < 0.001$; $*** < 0.001$. Upper p values are comparing soil moisture treatments; lower p values are comparing maternal treatments. Significance of the effects and their estimates are presented in Tables 2 and 3. R library “ggplot2” and Inkscape 0.91 were used to create the artwork

showing more exploration behavior have indeed a higher probability to disperse in this species (Massot et al. 2002; Cote and Clobert 2007). Yet, we did not observe any influence of neither behavioral traits nor behavioral plasticity of juveniles on their annual survival. As all enclosures were similar in density and predation was prevented, food availability, parasitism, meteorological conditions, and social interactions were the main selection pressures in this study (Le Galliard et al. 2015). The absence of natural selection on exploration behavior could therefore

be the consequence of a low predation, although it was also reported in previous studies including some allowing for predation mortality (Le Galliard et al. 2013, 2015).

In a previous study, Lorenzon et al. (1999) demonstrated that a chronic water restriction decreased locomotor activity in yearling common lizards in contrary to what we found in this study simulating an acute change in hydric conditions. This highlights that chronic exposure to water stress might trigger specific behavioral adjustments. Individuals may initiate a flight response by increasing exploration behavior on the short

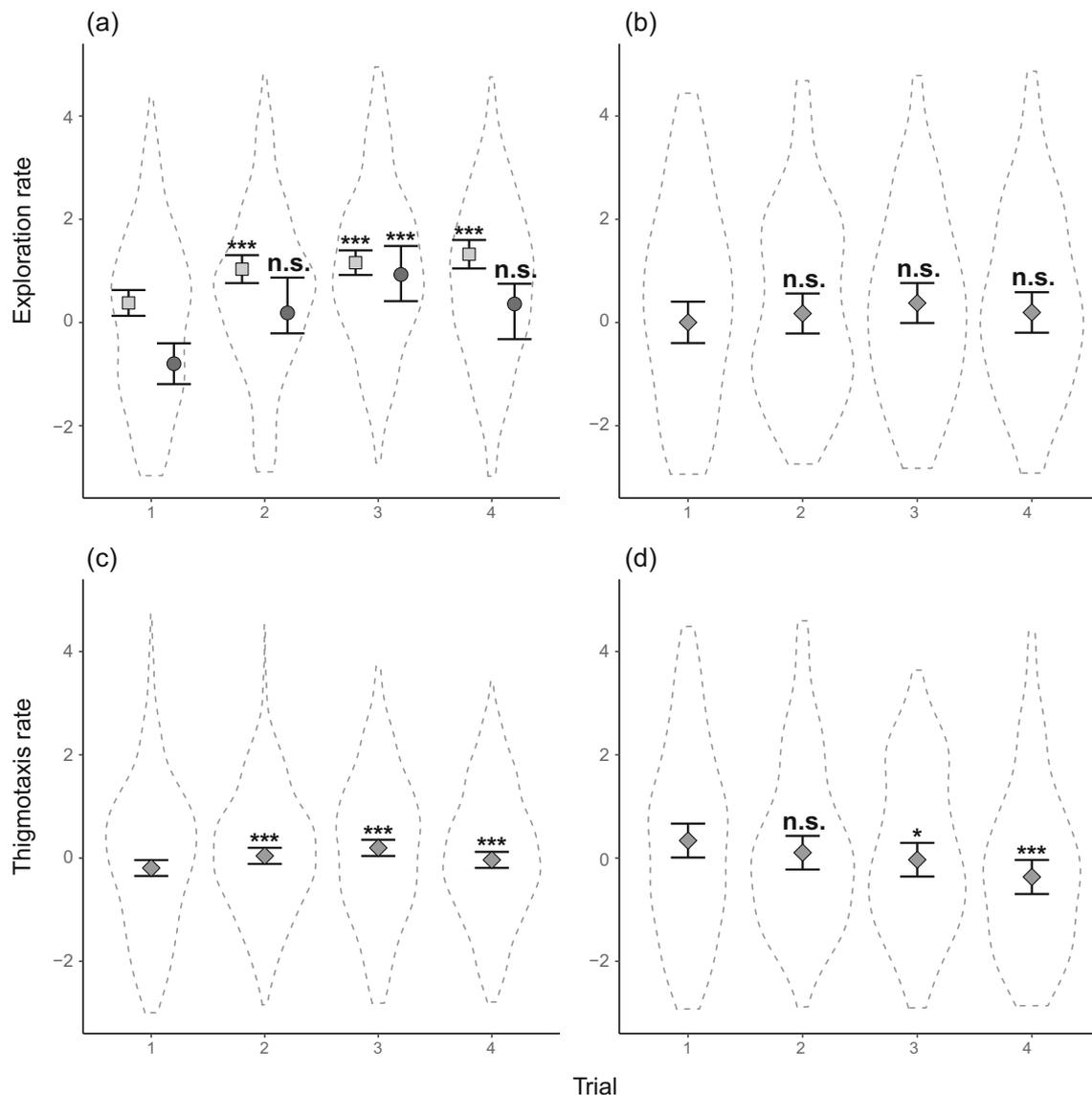


Fig. 2 Behavioral syndrome estimated for **a** PC1 in 2015 (juveniles), **b** PC1 in 2016 (yearlings), **c** PC2 in 2015 (juveniles), and **d** PC2 in 2016 (yearlings) for each trials. In **a**, soil moisture treatments are differentiated by the color of the symbols: light gray squares for dry soil moisture conditions, and dark gray circles for wet soil moisture conditions. In **b**, **c**, and **d**, as soil moisture treatments had no effect, gray diamonds are for trials whatever the treatment. Light gray dashed violin plots represent raw

Trial

data distributions. Error bars are for 95% confidence intervals. Stars represent *p* values comparing each estimate to the estimate in trial 1. n.s. non-significant; $0.05 < * < 0.01$; $0.01 < ** < 0.001$; $*** < 0.001$. Significance of the effects and their estimates are presented in Tables 2 and 3. R library “ggplot2” and Inkscape 0.91 were used to create the artwork

term (Greenberg 2002). Whenever the exposure to dry conditions becomes more chronic, individuals might then decrease exploration and switch to energy-saving mechanisms that would reduce the rate of water loss and limit the risks of dehydration. Future studies would benefit from examining the behavioral responses to short- or long-term exposure to changes in hydric conditions.

Thigmotaxis relates to anxiety in neutral arena tests with laboratory rodents (Simon et al. 1994). Therefore, the proportion of time spent near the walls relative to the time spent elsewhere can be a good proxy of this behavior (Maximino

et al. 2014) and was best summarized by PC2 score in this study. We observed a higher thigmotaxis score in dry soil moisture conditions in juveniles, consistently with the hypothesis that dry conditions are stressful and initiate a flight response. For example, lizards exposed to an acute physiological stress display more scratching behaviors (de Fraipont et al. 2000). However in yearlings, the thigmotaxis score was lower in dry soil moisture conditions despite the fact that lizards were more active and exploratory on average at this life stage. We expected that behaviors would be less sensitive to habitat humidity in yearlings because older animals should be more

resistant to desiccation (due to their bigger size) and yearling common lizards disperse much less than juveniles (Newman and Dunham 1994; Massot et al. 2002; Meylan et al. 2002), but we did not predict an opposite response. In addition, we do not know how stressful are dry soil moisture conditions since we did not measure any indicator of physiological stress (hormones or body mass change for example). It is however unlikely that our short-term behavioral test treatment caused a significant water imbalance and subsequent stress responses because average water fluxes imply significant physiological responses within hours not minutes. Instead, we suggest that the immediate behavioral responses of lizards allow them to anticipate the future physiological costs of dehydration in the dry soil treatment.

Pre-natal exposure to water restriction increased the thigmotaxis behavior of juveniles independently from soil moisture treatment, but environmental conditions during gestation did not influence the behavior of yearlings. These results highlight that a stress-related behavior (thigmotaxis) scored at birth was positively influenced by the level of hydric stress experienced by females during pregnancy. Water restriction can result in higher physiological stress levels as shown by higher plasma corticosterone levels (e.g., Dauphin-Villemant and Xavier 1987; Dupoué et al. 2016), and this was especially true for mothers during gestation in this study (Dupoué et al. 2017). In turn, increased maternal physiological stress could explain the higher thigmotaxis of their offspring (de Fraipont et al. 2000). For example, prenatal stress can potentially reduce glucocorticoid receptors in offspring with subsequent rise in the levels of anxiety (Maccari et al. 1995, 2003). These results thus indicate that water restriction during gestation enhanced maternal physiological stress, which led to a higher behavioral anxiety in their offspring. This change in thigmotaxis in response to pre-natal water stress suggests that stress-induced natal dispersal phenotypes might be mediated by thigmotaxis behavior in this species. We know very little about the role of anxiety in natal dispersal in animals (Cote et al. 2010), including in the common lizard, and the numerous studies using neutral arena tests have rarely quantified thigmotaxis in the same way than we did. Some earlier studies suggested that physiological and behavioral stress can influence natal dispersal and juvenile fitness (Belthoff and Dufty 1998; Meylan et al. 2002), but we did not measure natal dispersal in this study, and thigmotaxis was unrelated to annual survival. Annual survival was on average lower in juveniles from water-restricted females (Dupoué et al. 2017), but this was not explained by the higher behavioral anxiety of these juveniles at birth. Further studies should test if individuals showing more thigmotaxis at birth disperse more or further distances.

On average, pre-natal exposure to water restriction did not influence exploration behavior at birth, but contrasted effects were found depending on the laying date and therefore developmental stage of juveniles. In early clutches, i.e., in juveniles that experienced water restriction late in their development (i.e., 3 weeks to 10 days before birth), water restriction enhanced exploration. In late clutches, i.e., from juveniles that experienced water restriction during the middle of their development (i.e., 4–6 weeks before birth), water restriction decreased exploration. These stage-dependent effects of water restriction on offspring exploration are difficult to explain a posteriori. Water demands for embryos increase late in gestation in viviparous reptiles (Dupoué et al. 2015b; Lourdaïs et al. 2015). Water restriction at that stage may induce stronger physiological stress responses in gravid females and signals deteriorating environmental conditions that promote natal dispersal and associated increase in exploration behaviors. The relationship between exploration behavior and natal dispersal has indeed been well documented in numerous animal taxa (Dingemanse et al. 2003; Clobert et al. 2009; Debeffe et al. 2013). Instead, water restriction in the middle of development may impair juvenile quality and thus reduce their ability to explore. Previous studies argue that negative maternal effects on juvenile survival and morphology are stronger when they occur earlier in development (Heath et al. 1999; Lindström 1999). Future studies should test the links between water restriction, exploration behaviors, and life history traits with a protocol imposing the treatment explicitly at the beginning or at the end of gestation.

The inter- and intra-individual variability of behavioral traits we observed in this study also gave us further insights. First of all, correlation structure between all behavioral variables, allowing us to calculate exploration and thigmotaxis scores, remained qualitatively the same between the 2 years of study. Yet, no correlation was found between the juvenile and yearling behavioral scores, which is consistent with some other studies that observed strong intra-individual changes in personality across development (e.g., Bell and Stamps 2004). In addition, behaviors were less repeatable at birth than at the yearling stage: exploration rate and thigmotaxis rate showed a repeatability score high enough to be subjectively considered as personalities only at the yearling stage (Réale et al. 2007). A higher repeatability of exploration early in life was expected because natal dispersal mostly occurs few months after birth in this species and natal dispersal has been correlated to consistent behavioral traits such as exploration rate in several other species (Dingemanse et al. 2003). On the other hand, Hoset et al. (2011) observed a positive correlation between exploration behavior and dispersal status in a small rodent; still, there was a low repeatability of this behavioral trait like in our study. One possibility is that the exploration personality type was not well developed in the first days of life when individuals were more sensitive to environmental changes,

including handling and procedural stress. It is now accepted that personalities are not always stable in time during ontogeny or when the environment changes importantly (Stamps and Groodhuis 2010) and that exposure to environmental conditions early in life can drive the emergence of alternative personality types (e.g., Bell and Sih 2007).

Our results indicate that the behavioral responses of organisms to water availability involved independent pre-natal and post-natal effects of hydric conditions on behavioral traits associated with exploration and anxiety. In general, dry conditions and water restriction elicited flight responses (i.e., higher exploration and anxiety), especially in juveniles and late in development, but pre-natal and post-natal environmental conditions influenced differently behavioral traits related to exploration and anxiety. Exploration and anxiety were sensitive to acute changes in hydric conditions in both life stages. Maternal effects influenced average anxiety of juveniles but were not significant at the yearling stage suggesting vanishing long-term effects of the maternal environment on offspring behavior. These results indicate that different behavioral items are involved in plastic responses to water restriction during embryogenesis and fetal development than in behavioral flexibility. The behavioral response of an organism to a changing environment is thus likely to be a combination of independent behavioral items shaped differently by stage-specific environmental cues. We suggest that the life history strategy linking together these behavioral changes in the European common lizard is natal dispersal. In order to elucidate better this complexity, additional behavioral traits and the natal dispersal phenotype should be tested, in particular the link between natal dispersal, anxiety syndromes, and environmental stress.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. Animal care and behavioral protocols were performed in accordance with laws on animal experimentation in France and Europe, especially EU Directive 2010/63/EU, and were approved by national ethics committee for animal experimentation under file number APAFIS#5108-2016040811272391. Animal care and breeding was performed by authorized personnel under

permit DTTP-2008-449 issued to J-FLG. Experiments were conducted under agreement A77-341-1 delivered by the Préfecture de Seine-et-Marne. Animals were captured and manipulated under authorization 2007-198-005 delivered by the Préfecture de Seine-et-Marne.

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