Behavioral Ecology and Sociobiology (2023) 77:90
https://doi.org/10.1007/s00265-023-03362-2

ORIGINAL ARTICLE

Behavioural response to predation risks depends on experimental change in dehydration state in a lizard

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Received: 25 February 2023 / Revised: 26 June 2023 / Accepted: 29 June 2023 / Published online: 15 July 2023

Abstract

Optimal regulation of body temperature and water balance is essential for the survival of terrestrial ectotherms in a changing world. A behavioural trade-off exists between these two constraints because maintaining a high body temperature usually increases evaporative water losses. In addition, the evaluation of predation risk is a key factor in behavioural decision for prey species, and predation threat can cause shift in individual behaviours due to the modification of the cost-benefit balance of thermo-hydroregulation. However, little is known on how prey integrate these different biotic and abiotic stressors when combined. Here, we performed an experimental study on the common lizard, a terrestrial ectotherm prey species, sensitive to water restriction and able to detect specialised predator scents in its environment. We analysed changes in thermo-hydroregulation behaviours, activity patterns and body temperature in response to a chronic water stress coupled with simulated punctual occurrences of predator scents. Water restriction and predator threat had mostly additive effects on lizard thermoregulation behaviour. They both reduced the time spent basking and thermoregulation precision. They also had opposite effects on the time spent active, water restriction reducing activity whereas the presence of predator scents increased it. Yet, we also found an interactive effect on hydroregulation behaviour, as water-restricted lizards showed a wet-shelter preference only in absence of predator odours. This study demonstrates the existence of some hydration state dependent behavioural responses to predator threat and suggests that fear of predators may compromise thermo-hydroregulation and thus prey performances.

Significance statement

In this paper, we show that the fear of predators induces significant changes in the thermo-hydroregulation behaviours of a widespread terrestrial lizard species, some of which are influenced by a physiological increase in dehydration induced by an experimental restriction of water availability. There is a general lack of understanding about how prey respond to simultaneous changes in biotic and abiotic stressors; in particular, our comprehension of the non-energetic costs of thermoregulation caused by the presence of predators and the absence of water in the environment is extremely limited. Our findings indicate that predators have state-dependent effects on the behaviour of their prey and that joint changes in water availability and predation risks can compromise the thermo-hydroregulation strategies of their prey, potentially affecting their physiological performances.

Keywords Thermoregulation · Lizards · Dehydration · Predation risk · Reptiles · Activity pattern

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Communicated by S. Joy Downes

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Introduction

Water is one of the most essential resources for the survival and reproduction of organisms, and natural selection has led to several behavioural adaptations and acclimation strategies enabling terrestrial organisms to cope with predictable and unpredictable reductions of water availability (Davies 1982; Chown et al. 2011; Pirtle et al. 2019; Fuller et al. 2021). In ectotherms, thermoregulation is primarily behavioural (Angilletta 2009) and there is a potential conflict between water balance and body temperature regulation because thermoregulation effort and high body temperatures generally increase evaporative water loss through the skin and during respiration (e.g., Lourdais et al. 2017). Thus, water constraints influence thermoregulation accuracy and dehydration should lead to "sub-optimal" body temperature in terrestrial ectotherms (Huey and Slatkin 1976; Anderson and Andrade 2017; Rozen-Rechels et al. 2019). Indeed, there is now accumulating evidence that dehydration is associated with lower field body temperatures during activity (Ladyman and Bradshaw 2003), reduction in preferred body temperatures in the laboratory (Sannolo and Carretero 2019), decrease of behavioural activity or shifts in the daily and seasonal activity patterns (Rozen-Rechels et al. 2020). This surge of interest for the understanding of the joint mechanisms involved in the regulation of body temperature and water balance led to the development of the thermo-hydroregulation concept (Rozen-Rechels et al. 2019), defined as the integrated suite of behavioural and physiological processes enabling homeostatic regulation of both body temperature and hydration state.

Biotic interactions such as predation are also a major selective force shaping behavioural strategies. The detection of specialised predators in the habitat can induce significant behavioural changes in their prey (Clinchy et al. 2013). Anti-predator behavioural responses include temporal and spatial shifts in activity, changes in dispersal behaviour or differential investment in vigilance effort of the prey (Brown et al. 1999; Martin 2011). However, to date, little is known about the combined influences of dehydration and predation risks on thermo-hydroregulation behaviours and whether these two stressors have additive or interactive effects on thermoregulation. Yet, this is highly relevant to patterns and processes of thermo-hydroregulation because these two constraints should influence jointly the non-energetic costs of thermo-hydroregulation behaviours and these effects should be driven by their spatiotemporal variations in natural populations. For example, simultaneously avoiding predation and fulfilling thermo-hydroregulation needs may be in conflict, as shown in recent studies of ecological interactions between ungulates and their predators in semi-arid areas, such as African savannahs (Veldhuis et al. 2019). In these habitats, large predators are attracted by waterholes such that water dependent ungulate species also experience a higher exposure to predation risks, leading to temporal or spatial shifts in their thermo-hydroregulation strategies (Valeix et al. 2009a). Another possibility includes shifts in social behaviour in response to water deprivation that increase the risks of predation, such as huddling behaviours in amphibians (Rohr and Madison 2003). In such situations, the benefits of thermo-hydroregulation responses to water deprivation may be cancelled by a simultaneous increase in predation risks (Rohr and Madison 2003).

In addition to interactions between predation risks and water availability caused by their level of complementation in the landscape, prey may react to predation risks differently depending on their hydration state. This is especially likely in organisms that can tolerate a wide range of osmotic states and display large variations in their hydration status, such as many terrestrial ectotherms (Lillywhite 2016). According to classical behavioural models (Lima 1998), if a trade-off exists between avoiding predators and getting necessary water resources, dehydrated individuals should be more prone to take risks in the presence of predators than well-hydrated individuals. Alternatively, since the dehydration state of the individual also influences the potential costs and benefits of thermoregulation in a risky environment (Rozen-Rechels et al. 2019), anti-predator responses may involve changes in thermoregulation, such as reduction in behavioural activity or changes in micro-habitat selection. Changes in body condition induced by chronic dehydration could also influence an individual's response to the fear of a predator, which is generally condition-dependent (e.g. in lizards, Martín and López 1999; Martín et al. 2003).

In many terrestrial ectotherms, thermoregulation plays an important role in predator avoidance because high locomotor performances allowing prey to escape from their predators are closely related to an optimal regulation of body temperature (Landry Yuan et al. 2021). However, behavioural thermoregulation often involves increased activity (i.e. shuttling behaviours) and preferential use of open habitats (i.e. basking behaviours), which can draw the attention of predators and increase predation risks. Therefore, there is a proximate trade-off between active thermoregulation strategies and the exposure to predation (Angilletta 2009). For example, terrestrial reptiles can adjust their escape tactics and flight initiation distances in relation to their body temperature and opportunities for optimal basking in their environment (Cooper 2009). Furthermore, reptiles often use burrows or crevices as shelters to protect themselves from predators and they will use differentially these shelters depending on their thermal quality and their perception of predation risks (Amo et al. 2004; Lorioux et al. 2013). Generally, the perception of predators triggers a decrease in behavioural activity and may reduce the accuracy of thermoregulation (Downes 2001; Herczeg et al. 2008; Angilletta 2009; Lorioux et al. 2013). These organisms thus provide relevant models to address interaction between predation risks, thermoregulation and water constraints, even though this facet has been poorly studied.

Here, we set up a laboratory experiment with a ground-dwelling lizard (the common lizard, *Zootoca vivipara*) to quantify changes in thermo-hydroregulation behaviours when animals are exposed to simultaneous changes in dehydration risks and the threat of predation. Common lizards are widespread lizards from cold and wet habitats across Eurasia and they are preyed upon by a diversity of generalist and specialist predators, including snakes such as the adder (Prestt 1971) and the smooth snake (Drobenkov 2014). Previous studies have demonstrated that there is an overall reduction in thermoregulation effort for animals under water stress (Rozen-Rechels et al. 2020). Common lizards and their snake predators rely on chemical cues in their environment to detect each other, and previous studies have shown that common lizards can recognise scent from a specialised snake predator and differentiate it from the scent of food or of conspecifics (Thoen et al. 1986; Van Damme et al. 1990). Here, we examined the following hypotheses. First, we expect a reduction in the proportion of time spent basking (and thus being more vulnerable to predators) and a delay in emergence time for individuals confronted to scents of their predators. Lizards could also lower their body temperature (Martin and Huey 2008; Anderson and Andrade 2017) and/or shift towards more thermo-conformity under stressful conditions as predicted by Huey and Slatkin (1976). We also expect adult males to be more prone to take risks than females, as it has been suggested in this species by Antczak et al. (2019). Second, we posit that lizards confronted to predator scents in addition to water stress will respond differently than well-hydrated lizards, as antipredator behaviours are often condition dependent. Dehydrated lizards would take greater risks, searching for water despite the presence of predators, and thus being more active than expected. Additionally, they may reduce body temperature to limit water loss, even though it impacts their sprint performance when encountering predators.

To test these hypotheses, we submitted lizards to two different conditions including a control with access to ad libitum drinking water and a treatment group with restricted access to drinking water, hereafter referred to as the water treatment. Before and after this manipulation, we recorded lizards' behaviours and activity, as well as their body temperature, under two conditions of predator threat (absence or presence of predator scents in the environment). This experimental design allows us to detect a potential interactive effect between the two stressors.

Material and methods

Studied species and acclimation conditions

The common lizard *Zootoca vivipara* is a small lacertid lizard (Reptilia: Lacertidae; adult snout-vent length 50–70mm) with a wide Euro Siberian distribution (Surget-Groba et al. 2006). It inhabits mesic environments such as humid grasslands and peat bogs and is highly sensitive to water deprivation due to its high standard water loss rates (Lorenzon et al. 1999; Massot et al. 2002; Dupoué et al. 2017). The species is mainly predated by birds and snakes including the adder (Viperidae, *Vipera berus*) and several species of Colubridae (Prestt 1971; Steen et al. 2011; Drobenkov 2014). Common lizards used in this study were captured after the reproduction period (in early July 2019) in semi-natural populations maintained in 10 fenced, outdoor enclosures in CEREEP-Ecotron IleDeFrance in Saint Pierre lès Nemours, France (48°17′N, 2°41′E), without natural predators. We captured 72 adults (≥ 2 years old) with a 1:1 sex ratio, measured their snout-vent length with a plastic ruler (± 0.5mm) and weighed them for body mass (± 1mg). Lizards were then placed in individual terraria (18 × 11 × 12cm) for acclimation in a temperature-controlled room (23°C from 8:00 to 19:00, 15°C otherwise) and fed with living crickets (*Acheta domestica*) ad libitum. During acclimation, drinking water was available ad libitum in a water cup and terraria were sprayed 3 times a day with water to maintain a wet environment

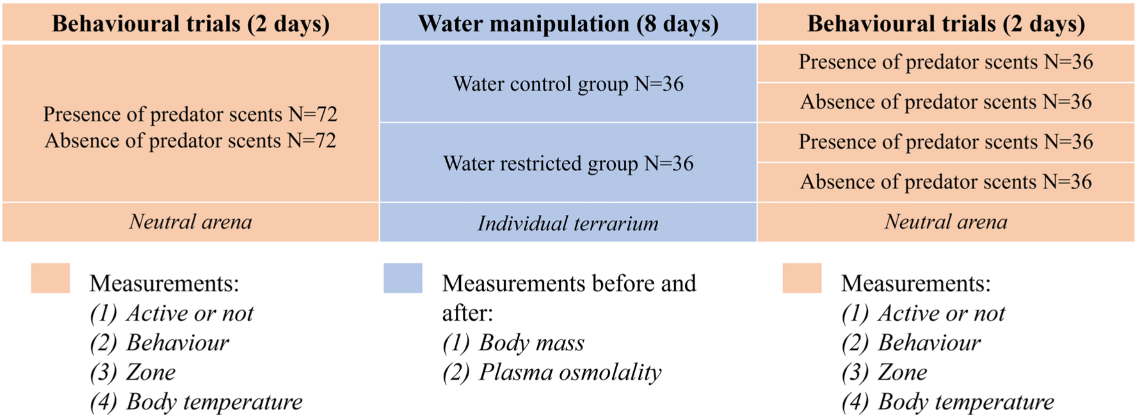
Experimental design

After a 1-week acclimation period, lizards were divided into 3 trial groups (24 individuals per group, 12 females and 12 males) tested successively. Inside each group, individuals were paired in couple (one male and one female of similar body size) and behavioural observations were recorded on pairs of individuals. The day before the first behavioural observations, each pair was transferred to a neutral arena (79 × 57 × 42cm) in a temperature-controlled room maintained at 25°C between 8:00 am and 5:30 pm. Arenas were equipped with a substratum of sterilised peat soil, a water cup and, on one side, two 40-W light bulbs placed above two artificial shelters in order to provide them with basking spots and refuges in the so-called hot zone of the arena and a retreat site without refuge in the "cold part" of the arena. One shelter was maintained humid at ground level with a wet sponge, whereas the other one was maintained dry with a dry sponge. In addition, a UV neon tube (Reptisun 10.0, white light) provided UV-enhanced light above each arena during daytime. Mean temperature in wet shelter was slightly lower than in dry shelter (wet: 27.1°C ± 3.4 SD; dry: 27.9°C ± 4.2 SD), and mean relative humidity was much higher in the wet one (wet: 54.4% ± 10.4 SD; dry: 35.4% ± 9.4 SD). On the cold side of the arena (without the heating lamps above), ground temperatures stayed below *Zootoca vivipara* preferred temperature all day long whereas the hot part offered optimal temperatures for thermoregulation (temperature during behavioural trial: cold mean = 26.5°C, maximum = 28.5°C ; hot mean = 35.4°C, maximum = 39.8°C, Gvoždík and Castilla 2001).

The experimental design consisted in 2 days of behavioural observations prior to manipulation, 8 days of manipulation of water availability, and 2 days of observations after this manipulation period (see Fig. 1). First, behavioural observations (see below) were performed with lizards maintained in standard conditions (including ad libitum water) for each pair with a random succession of each of the two predator trial groups ("control" trial group with no scent or "odour" trial group with predator scents added in the arena) during one day each. We referred to this sequential test as the "test day sequence" variable and our sequential test was motivated by the need to avoid habituation of lizards to scents since they were tested against predator scents only during one day (Parsons et al. 2018). The odour trial group was obtained by combining scents of two natural predators of the common lizards. We used a standardised quantity of shed skins of the adder (*Vipera berus*) that we cut into pieces and combined with the substrate layer before spreading it out in the arena. In addition, we used shelters installed in a live smooth snake's (*Coronella austriaca*) terrarium for at least 24h, in order to imitate a realist situation as these two predators can be sympatric. Shed skins were obtained from adders ($N = 40$) captured in Western France and temporarily maintained in capacity at Centre for Biological Studies of Chizé, France (Dezetter et al. 2021). The smooth snakes ($N = 2$) were captured in natural habitats at CEREEP-Ecotron in late June 2019. Next, after these 2 days, lizards were put back in their individual terrarium for 8 days without odours of predators. Water treatment (control *ad libitum* or restricted water) was randomly attributed to each pair following standard protocols: in control conditions, each terrarium had a water cup filled with drinking water in the morning whereas we removed the water in restricted conditions (Dupoué et al. 2018). In addition, we reduced water spray to once every day in restricted conditions instead of 3 times a day in control conditions. Lizards were fed with living cricket *Acheta domestica* throughout the experiment. Finally, after these 8-day manipulation period, pairs of lizards were placed back in the neutral arena (with an empty water cup for the water-restricted lizards) for 2 additional days of behavioural observations involving a new random sequence of each of the two predator trial groups (see Fig. 1).

Behavioural observations

During each observation trial (see Fig. 1), we quantified the behaviours of lizards with a focal sampling survey every 30 min from 08:30 to 17:00. At each focal sampling, we observed if the individual was "active" (i.e. visible to the observer) or "inactive" (i.e. hidden in a shelter or buried in the soil). When the individual was not visible, we searched gently under the shelters and noted if it was found under the wet or dry one. When the lizard was still not found, we assumed that it was buried into the soil and did not disturb it. In this case, the individual was reported as "hidden". When it was "active", we further recorded whether the individual was basking (immobile position, flatten body oriented towards light bulb under the hot spot), moving (active movement of any kind) or drinking. We reported in which part of the arena the individual was located (either on the hot part or the cold part away from the hot spots and shelters). We also measured from the same distance the surface body temperature on



Behavioural trials (2 days)	Water manipulation (8 days)	Behavioural trials (2 days)
Presence of predator scents N=72 Absence of predator scents N=72	Water control group N=36	Presence of predator scents N=36
		Absence of predator scents N=36
	Water restricted group N=36	Presence of predator scents N=36
		Absence of predator scents N=36
Neutral arena	*Individual terrarium*	*Neutral arena*

🟧 Measurements:
(1) Active or not
(2) Behaviour
(3) Zone
(4) Body temperature

🟦 Measurements before and after:
(1) Body mass
(2) Plasma osmolality

🟧 Measurements:
(1) Active or not
(2) Behaviour
(3) Zone
(4) Body temperature

Fig. 1 Timeline of the experimental design including behavioural trials with and without predator odours (2 days), then a chronic water treatment during 8 days (water restriction or water control) followed by a repetition of behavioural trials with and without predator odours (2 days). Lizards were transferred to the arena on the day before the observations began the back of each active lizard using an infrared thermometer (Raynger MX2, Raytek) following standard protocols and previous work showing a strong correlation between surface and core body temperature (Chabaud et al. 2022).

Plasma osmolality assays

We measured body mass and collected blood samples from the post-orbital sinus using 1–2 micro-capillary tubes (ca. 20–40 µl whole blood) before and after the 8 days of manipulation to measure plasma osmolality, which provides a standardised assay of physiological dehydration. Samples were centrifuged at 11,000 rpm for 5 min to separate plasma from red blood cells. Plasma samples (approx. 10–15 µl) were immediately frozen at −28°C until further analyses in the lab. Then, plasma osmolality was determined using a vapour pressure osmometer (model Vapro 5600, ELITechGroup) with the protocol described in Wright et al. (2013) and adjusted to small plasma volumes (Dupoué et al. 2017). Before analyses, plasma was diluted (1:3) in standard saline solution (Osmolarity = 280 mOsm l^{-1}) to obtain 2 duplicates per sample (CV = 1.5%). Mean value from the 2 duplicates was used in subsequent analyses. Due to their manipulation, a few samples could not be analysed so we only got 55 out of 72 values for osmolality change, randomly distributed among the sex and water treatment.

Statistical analyses

Statistical analyses were performed using R statistical software (version 3.6.3). First, intra-individual changes in osmolality and body mass during the manipulation were compared with ANCOVA on linear models including effects of treatment, sex and their interaction and the additive effects of initial value (of osmolality or body mass) and of trial group. Second, inter- and intra-individual variations in different behavioural items and in body temperature were analysed with different statistical methods depending on the behavioural item. We first summed the number of times the behaviour was recorded each day relative to the total number of focal sampling in the day, and calculated relative frequency for 5 behavioural items: (1) the proportion of surveys spent active, (2) the proportion of active surveys spent basking, (3) the choice of a wet shelter (proportion of surveys seen in the wet shelter among surveys in a shelter), (4) the proportion of surveys spent hidden and (5) the proportion of surveys spent in hot zone. These behavioural items were analysed with generalised linear mixed models using the *glmer* function from the ‘lme4’ package (Bates et al. 2015) with a binomial family and a logit link. We added the experimental arena and the individual as random factors to account for the inter-individual variability and for potential differences among arenas. Next, body temperatures were analysed with linear mixed models using the *lme* function from the ‘nlme’ package (Pinheiro et al. 2006). In all cases, we tested the three-way interaction between predator scent trial (absence or presence), water treatment (water restricted or water control) and time period (before or after the manipulation), in addition to additive effects of sex, trial group and test day sequence (day 1 or day 2). Finally, we analysed emergence hour (first time of the day the individual was observed “active”) with a mixed effect Cox model using the *coxme* function of package ‘coxme’ (Therneau 2012). This model assumes that the emergence time of the lizard can be best described by a proportional hazards model with a single random intercept per group. We fitted the model with additive fixed effects of the predator scent trial, water treatment and time period and their three-way interactions and additive fixed effects of sex, test day sequence and trial group. Random intercept effects were included for arena and individual groups, respectively.

For each analysis, we built a full model and checked its assumptions with graphical analyses of residuals and predictions, for example to test the Gaussian and homoscedastic distribution of residuals. For *glmer* models, we also performed goodness-of-fit tests to confirm the absence of overdispersion. For Cox models, we used a graphical test of proportional hazards provided with the package ‘survminer’ (Kassambara et al. 2017). Data were slightly over-dispersed only for one behavioural item (proportion of surveys spend hidden, $\chi^2 = 407$, $p<0.0001$), so we used an observation-level random effect to correct it as recommended in this situation (Harrison 2014). Then, starting with the full model, the best model was selected using stepwise removal of non-significant effects based on standard *F* statistics computed with the *Anova* function from package ‘car’ (Fox and Weisberg 2011). Results are shown as means ±SE unless otherwise stated. If the odour trials have an effect on behavioural items, it should appear in the models as a mean effect independently of time period, as it is designed as a one-time effect. On the other hand, the water treatment is designed as a chronic manipulation, and its potential effect should therefore appear as an interactive effect of water treatment and the time period. In particular, we expect no difference between water treatment groups before the manipulation and potential contrasts after the manipulation (see Fig. 1). Finally, interactive effects of water restriction and predator scents presence should appear as a three-way interaction between water treatment, time period and predator scent trial.

Results

Effect of water deprivation on plasma osmolality and body mass

Water restriction influenced significantly body mass change, with a negative effect on females (water treatment × sex: $F_{1,64} = 9.65$, p=0.0028), water-restricted females losing on average 0.12 ± 0.03 g (3% of their initial body mass) whereas control females gained 0.04 ± 0.02 g (1% of their initial body mass; estimate= -0.16 ± 0.04, p=0.0009). However, water treatment did not impact males (estimate=0.05 ± 0.05, p=0.32), male body masses remained constant. We also found an effect of trial group, animals from trial 2 losing more body mass than the two other trials ($F_{2,64} = 6.73$, p=0.002). In addition, water restriction increased osmolality by an average of 17 mOsm kg^{-1} in male and female lizards, whereas non-restricted ones decreased their osmolality by an average of 2 mOsm kg^{-1} (water treatment: $F_{1,55} = 14.63$, p=0.0003; initial value: $F_{1,55} = 65.03$, $p < 0.001$).

Changes in thermo-hydroregulation behaviours

A lizard was reported active on average 8.4 ± 0.2 times a day out of 18 observations. Activity probability increased significantly in the presence of predator scents prior to the water manipulation ($\chi^2 = 13.23$, df = 1, $p = 0.006$, Fig. 2) but this difference was smaller after the water manipulation since lizards were slightly less active in presence of odours after the 8-day manipulation period than before (time period × predator scent trial: $\chi^2 = 3.96$, df = 1, p=0.05). Activity also decreased through time with water restriction compared to the control treatment (time period × water treatment: $\chi^2 = 22.96$, df = 1, $p < 0.0001$, Fig. 2) independently from predator scent treatment. Other factors influencing the proportion of time spent active include test day sequence as lizards were less active on the second day of observation trials ($\chi^2 = 20.95$, df = 1, $p < 0.0001$).

When lizards were active, the time they spent basking under the hot spot, immobile and exposed was influenced additively by our two experimental constraints as the time spent basking decreased in presence of predator scents (predator scent trial: χ^2 =5.34, df = 1, p=0.02, estimate = -0.37 ± 0.16, p=0.02) and in the water-restricted group (time period × water treatment: $\chi^2 = 3.97$, df = 1, p=0.05, estimate = -0.46 ± 0.23, p=0.046). We also found an effect of time period alone ($\chi^2 = 10.63$, df = 1, p=0.001) since lizards spent more time basking after than before the manipulation and an overall effect of trial group ($\chi^2 = 7.96$, df = 2, p=0.019). In addition, when lizards were active, they were situated in the hot part of the arena on average 11.4 ± 0.2 times a day. The predator odour trials influenced the time spent in the hot zone ($\chi^2 = 15.99$, df = 1, $p<0.0001$) but not the water treatment. Test day sequence also impacted the time spent in hot zone ($\chi^2 = 6.87$, df = 1, p=0.009) as well as the trial group ($\chi^2 = 7.35$, df = 2, p=0.025). Lizards were less often seen on the hot part of the arena in presence of predator odours and during the second day of the observation sequences.

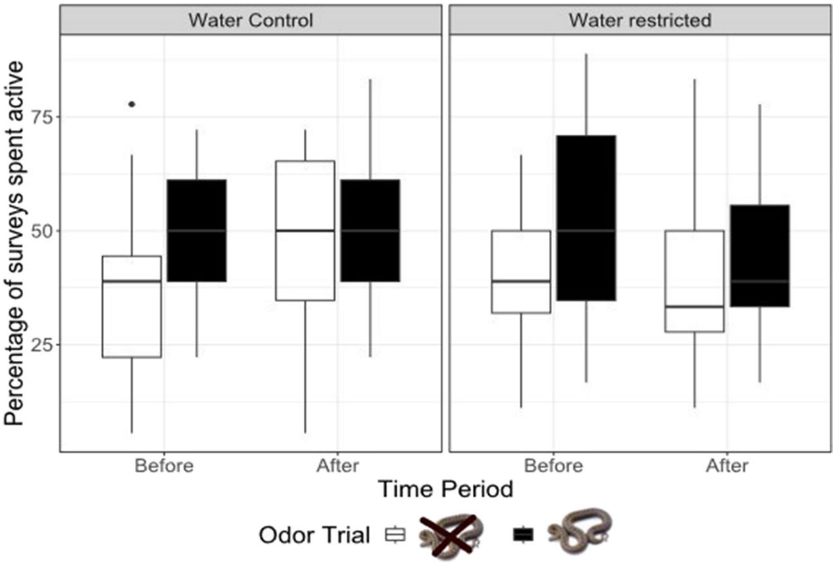


Fig. 2 Proportion of time spent active between 8:30am and 5:00pm in water treatment groups: water control lizards on the left panel and water-restricted lizards on the right panel. Behavioural trials are separated according to the presence (black) or absence (white) of predator scents in the environment. Data are reported for measurements "before" the start of the water restriction manipulation, and "after" the end of the water restriction manipulation. The thick black lines represent the medians, the boxes encompass the interquartile ranges, the whiskers extend to the most extreme data points within 1.5 × the interquartile range outside the box, and the circle show data point beyond the whiskers

Lizards were found on average 3.8 ± 0.2 times a day under a shelter and only slightly more than half of the time under the wet shelter (2.18 ± 0.15 times a day). The water treatment influenced the proportion of time lizards spent under the wet shelter differently between the predator scent trials (time period × water treatment: $\chi^2 = 22.92$, df = 2, $p<0.0001$; time period × water treatment × predator scent trial: $\chi^2 = 14.11$, df = 2, $p=0.0009$, Fig. 3). In the water-restricted group, lizards were seen more often under the wet shelter than in control group when no predator odour was present (estimate = 1.04±0.51, $p=0.044$). Wet shelter preference was not found when shelters and the substrate had predator odours ($p=0.25$).

Lizards were hidden in the soil on average 5.8 ± 0.2 times a day. Water treatment did not explain the variation in the number of times they were buried (time period × water treatment: $\chi^2 = 2.12$, df = 2, $p=0.34$) but the interaction between the predator scent and time period did (predator scent trial: $\chi^2 = 0.42$, df = 1, $p=0.52$; time period × predator scent trial: $\chi^2 = 5.38$, df = 1, $p=0.02$), lizards being more often buried in presence of predator odours after the manipulation. The other factor influencing burrowing included test day sequence ($\chi^2 = 26.70$, df = 1, $p<0.0001$), lizards being more often buried on day 2 than on day 1 of behavioural trials. We found no effect of sex on either of the thermo-hydroregulation behaviours (all $p>0.05$).

Change in emergence time

On average, most lizards emerged between the 2nd and the 3rd observation of the day (9:00 to 9:30 am) with 50% of individuals being active by 9:30 am (Fig. 4). Emergence time was influenced significantly by the predator scent presence and its interaction with time period (predator scent trial: $\chi^2 = 8.79$, df = 1, $p=0.003$; time period × predator scent trial: $\chi^2 = 9.29$, df = 1, $p=0.0023$). Lizards emerged slightly later in the presence than in the absence of predator scents (Log-rank test, $p=0.0039$, Fig. 4), but this was less the case after the manipulation irrespective of the water treatment group. We also found an effect of the test day sequence ($\chi^2 = 6.29$, df = 1, $p=0.01$), with lizards emerging slightly earlier on the second consecutive day of observation than on the first. The water treatment had no detectable effect on the emergence time (time period × water treatment: $\chi^2 = 0.77$, df = 1, $p=0.38$). We found no effect of sex on emergence time ($\chi^2 = 2.06$, df = 1, $p=0.15$).

Change in body temperature

Mean surface body temperature during activity was 34.3±0.1 °C. The mean body temperature during the day was slightly reduced by the presence of predator odours ($\chi^2 = 4.2$, df = 1, $p=0.04$, Fig. 5) but only marginally by the

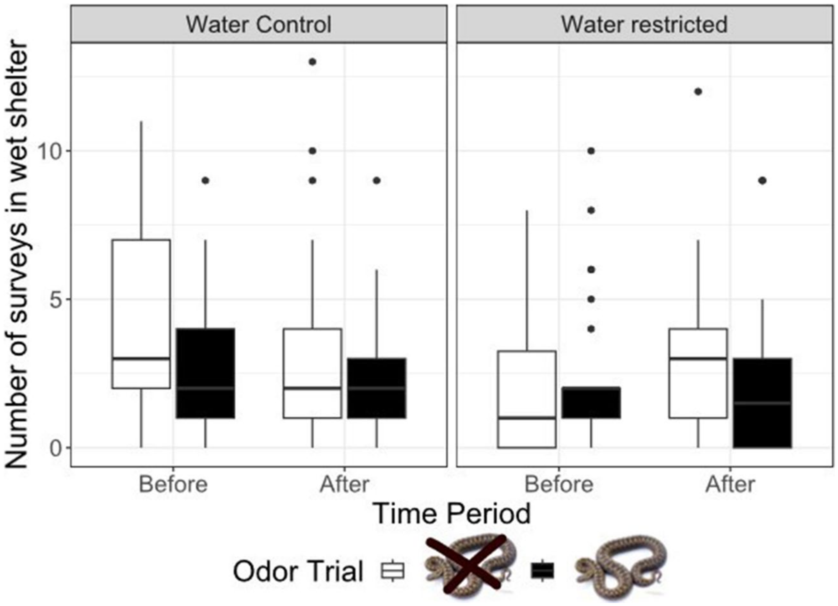


Fig. 3 Number of observations in wet shelter between 8:30am and 5:00pm depending of water treatment groups: water control lizards on the left panel and water-restricted lizards on the right panel. Behavioural trials are separated according to the presence (black) or absence (white) of predator scents in the environment. Data are reported for measurements "before" the start of the water restriction manipulation, and "after" the end of the water restriction manipulation. The thick black lines represent the medians, the boxes encompass the interquartile ranges, the whiskers extend to the most extreme data points within 1.5 × the interquartile range outside the box, and the circles show data points beyond the whiskers

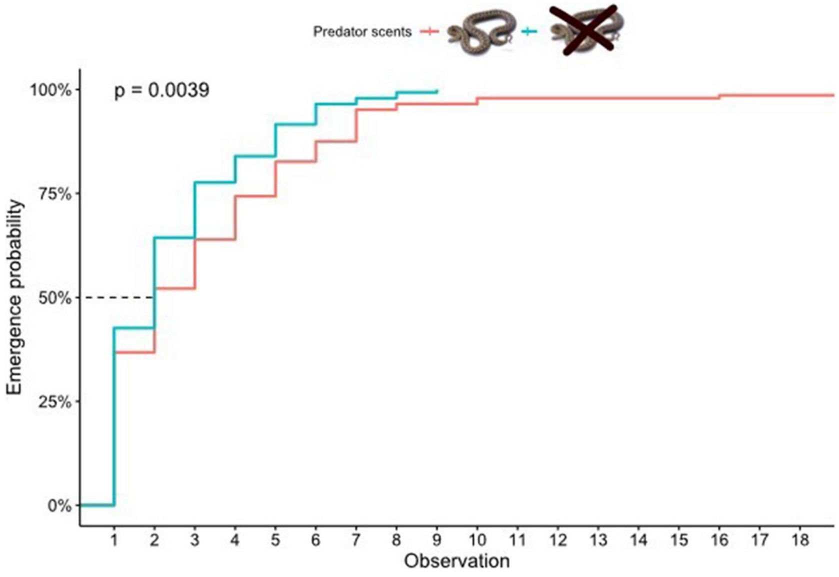


Fig. 4 Emergence time depending on the presence (red line) or absence (blue line) of predator scents from observation 1 starting at 8:30am to observation 18 ending at 5:00pm. Emergence was scored every 30 mins. Representation are Kaplan-Meier survival curves, produced with *survfit* function

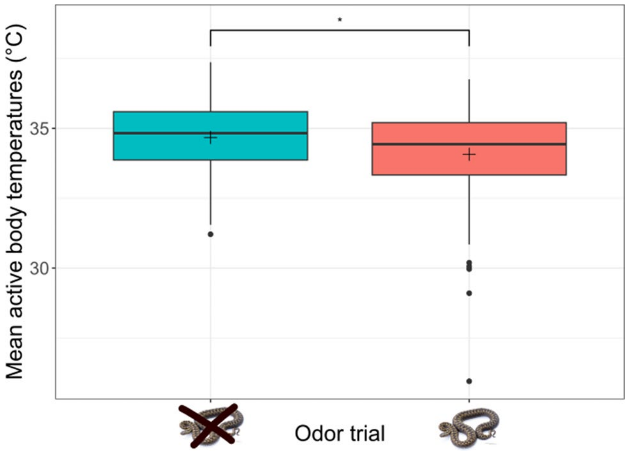


Fig. 5 Boxplot of body temperature during the reported active observations depending on the absence (blue) or presence (pink) of predator scents in the arena. The plus sign represents mean value, N=72 individuals observed two times each in both odour trials. The thick black lines represent the medians, the boxes encompass the interquartile ranges, the whiskers extend to the most extreme data points within 1.5 × the interquartile range outside the box, and the circles show data points beyond the whiskers. The asterisk indicates a significant difference between the two mean values of body temperature (p<0.05)

water restriction (water treatment × time period: $\chi^2 = 2.8$, df = 1, p=0.09). Time period alone ($\chi^2 = 7.2$, df = 1, p=0.007) and test day sequence ($\chi^2 = 9.49$, df = 1, p=0.002) also influenced the body temperature, lizards having a higher mean body temperature after the manipulation, but a lower one on the second consecutive day of observation than on the first. We found no effect of sex on the mean body temperature (χ^2 = 0.04, df = 1, p=0.84).

Discussion

Our experiment was designed to study the simultaneous effects of water availability and predator threat on thermo-hydroregulation behaviours and activity patterns. We used male and female adult lizards but found no effect of sex on any of the behavioural variables, maybe because the manipulation period was outside reproduction season for this species and different trade-offs between water needs and fear of predation between sexes occur only when reproduction is at stake (Dupoué et al. 2018; Rozen-Rechels et al. 2020). We simulated a mild water deprivation using a chronic stress experiment over several days, whereas predation threat was simulated as a one-time effect using behavioural trials in both presence and absence of predator scents during one day. Thus, our design contrasted the short-term responses of well-hydrated and dehydrated animals to a punctual occurrence of predator scents, as might occur in natural populations when predators traverse the home range of several prey and patrol more distances than their prey. Thanks to this experimental design, the behaviours of animals were tested before and after water manipulation, and we could control for inter-individual variation in mean behaviour, including thermo-hydroregulation temperaments (Cote and Clobert 2006), to strengthen the statistical power. In addition, a chronic exposure to predator scents without direct physical encounters would have been less relevant as animals can learn that the risk is not associated with danger and behavioural responses will thus fade with time (Parsons et al. 2018). We indeed found that some behavioural traits were influenced by a slight effect of time period, possibly explained by habituation to odours of predators; for example, predator scent effects on wet shelter use and emergence time were weaker after the 8-day water manipulation. Lizards also exhibited decreased activity and were less frequently found in the hot zone on the second day of trials, with increased burying behaviour and lower body temperatures. This pattern suggests that lizards became accustomed to the arena environment and their paired partner, resulting in reduced exploration and overall activity, which subsequently impacted the other observed effects.

Our study reveals interesting results on how predator threat affects activity and emergence time in this terrestrial ectotherm. The presence of predator scents increased activity rate but in the meantime it decreased basking rate during activity. Increased activity can be associated with a higher level of vigilance and also more frequent escape attempts (via scratching behaviours, see Kawamoto et al. 2021), but this was not correlated with a better thermoregulation. On the contrary, lizards spent less time basking, which is consistent with the observed reduction of mean active body temperature in presence of predation threat. Overall, this suggests that the presence of predator scents led to less optimal thermoregulation. Previous works on other lizard species also demonstrated a reduction of basking behaviours when a predation risk was perceived, both in laboratory experiments (Downes 2001; Robert and Thompson 2007) and in the field (Lister and Aguayo 1992). The lower basking effort and less accurate thermoregulation in the presence of predators scents also conform with predictions of the cost-benefit model of thermoregulation (Huey and Slatkin 1976) and other similar studies on ectotherms (Herczeg et al. 2008; Gvoždík et al. 2013). These behavioural responses may represent a significant fitness cost over the long term if maintenance of an optimal body temperature is important for the detection of future threat or foraging efficiency (Amo et al. 2004). For example, a reduction of basking effort had consequences on juvenile growth rates in one study due to the reduced time spent in temperature-dependent activities such as foraging and digestion (Downes 2001).

We also found that lizards emerged later in presence of predators' scents, which might be a strategy to shift their activity towards periods of the day with a more limited predator activity or to reduce overall daytime activity period. This shift of the daily activity pattern is interesting given that smooth snakes emerge earlier in the morning during the hottest months of the year (de Bont et al. 1986), so emerging later could be a strategy for common lizards to limit encounters with this specialised predator. Prey often need to adjust their behavioural decisions and activity patterns according to geographic or temporal variation in predation risks (reviewed in Lima and Dill 1990). This shift is particularly important to study for lizards in natural conditions as during the summertime, when drought is combined with high temperatures, activity in the morning is favoured to avoid heat stress and dehydration (Rozen-Rechels et al. 2020).

In addition, our investigation of behavioural changes in water-restricted animals mostly confirmed our predictions and previous works on this species (Rozen-Rechels et al. 2020). Dehydration was on average mild in manipulated lizards, with small relative decrease in body mass and small relative increase in plasma osmolality compared to maximum sustainable values that common lizards can tolerate under laboratory conditions (up to 25–30% body mass decline and up to 50–70 mOsm kg^{-1} increase, see Dupoué et al. 2020). Despite this, dehydrated lizards were significantly less active and had lower basking rates than water control ones, which led to a less accurate thermoregulation given the trend, albeit not significant, for lower body temperatures in the treatment group. Dehydrated lizards also increased their use of the wet shelter, probably as a hydroregulation strategy to reduce evaporative water loss rates and conserve more water (Dezetter et al. 2022). Thus, our data confirmed the existence of a behavioural trade-off between thermoregulation and hydroregulation, as predicted for terrestrial ectotherms in Rozen-Rechels et al. (2019) and observed in several recent studies (e.g. Greenberg and Palen 2021; Nervo et al. 2021). However, these behavioural adjustments did not allow the water-restricted lizards to totally compensate for the lack of water, as their plasma osmolality slightly increased compared to non-restricted ones.

From our independent analysis of six behavioural traits and body temperature, we found interactive effects of these two constraints on only one behaviour, which suggests that the two stressors had primarily additive effects on thermoregulation and activity patterns. These conclusions run against our hypotheses that anti-predator responses could depend on hydration state or that thermo-hydroregulation responses are dependent on the fear of predation, as might be the case for example when one environmental constraint has dominant effects on behavioural plasticity and is given priority over the other (Rozen-Rechels et al. 2019). Water stress and the fear of predators additively impacted activity and thermoregulation behaviours, but sometimes in an opposite way. Indeed, as the presence of predator scents in the environment increased activity rate, chronic water stress decreased it; yet, we found no interactive effect. However, water stress and the fear of predators interactively impacted the use of wet shelter, as dehydrated animals used it more often only in the absence of predator scents. In our experimental design, resting under the wet shelter represents a good strategy to optimise both temperature, since the shelter is located in the hot zone closed to the basking area, as well as water balance, since a wet shelter allows lizards to reduce evaporative water losses thanks to the high ambient relative humidity (Pintor et al. 2016). However, we used shelters with or without fresh scents of a specialised predator (the smooth snake) implying that shelters were potentially perceived as a danger for dehydrated lizards and priority was given to other, safer behavioural responses to dehydration than shelter use. Thus, these results suggest that a behavioural response to limit dehydration while maintaining a high body temperature (hot shelter use) was modified by the risk of predation (Angilletta et al. 2002). Similar results on habitat selection were found in geckos, with the avoidance of retreat site with predator scents at the expense of thermoregulation (Downes and Shine 1998). These results highlight that anti-predator behaviours can have consequences on the regulation of crucial parameters such as body temperature and water balance. If the starvation-predation risk trade-off has been studied in other ectotherm species (e.g. Bennett et al. 2013), few studies have considered how predation risk can influence the non-energetic costs to the maintenance of water balance (Valeix et al. 2008, 2009a, b). We need a deeper understanding of the interactive effects of these two constraints in more ectothermic species.

In conclusion, we found mostly additive effects of water and predator threat on thermoregulation behaviours, but an interactive effect was observed for the use of shelter that shift from optimal to sub-optimal in the presence of predators' odours. This change in shelter use driven by both water restriction and perception of predation risk could have consequences for thermo-hydroregulation in natural conditions including shelter use during daytime in response to hot temperatures but also shelter use during night time when lizards need to rest at lower body temperatures (Rutschmann et al. 2021). In turn, ecological effects of water restriction should be enhanced in prey species and their predators when they use the same habitat (Valeix et al. 2009a, b) as it is the case here for common lizards and *Vipera berus*, which live both in the same wet microhabitats (Guillon et al. 2014). Our results suggest that hydroregulation may be critical in lizard populations with a lot of adders as the fear of predation can affect optimal hydroregulation strategies, and "the ecology of fear" (Clinchy et al. 2013) should be taken into account when making predictions about the life history strategies of lizards facing changes in climate conditions.

Acknowledgments The authors want to thank Théo Bodineau and Jérémy Lefèvre who helped with the experiment and animal care, and Elsa Martin for help with the data cleaning and preliminary analyses, as well as the CEREEP Ecotron IleDeFrance staff. We would also like to thank the reviewers for their constructive and helpful comments on our manuscript.

Funding This study received the financial and technical support from the Centre National de la Recherche Scientifique (CNRS), and was funded by the Agence Nationale de la Recherche under the 'Aquatherm' project (ANR-17-CE02-0013 to JFLG).

Data availability Data generated during the current study is available in a Zenodo repository at 10.5281/zenodo.8084341.

Declarations

Ethical approval The experimental procedures involving vertebrate animals were carried out in accordance with institutional guidelines and ethical standards, under licence from the French Ministry of the Environment (permits APAFIS#25252-2020042722118884). Research protocol was approved by the Darwin ethics committee on animal experimentation, regarding animal welfare.

Informed consent Informed consent was obtained from all individual participants included in the study.

Conflict of interest The authors declare no competing interests.

References

Amo L, López P, Martín J (2004) Thermal dependence of chemical assessment of predation risk affects the ability of wall lizards, *Podarcis muralis*, to avoid unsafe refuges. Physiol Behav 82:913–918. https://doi.org/10.1016/j.physbeh.2004.07.013

Anderson RCO, Andrade DV (2017) Trading heat and hops for water: dehydration effects on locomotor performance, thermal limits, and thermoregulatory behavior of a terrestrial toad. Ecol Evol 7:9066–9075. https://doi.org/10.1002/ece3.3219

Angilletta MJ (2009) Thermal adaptation: a theoretical and empirical synthesis. Oxford University Press, Oxford, UK

Angilletta MJ, Niewiarowski PH, Navas CA (2002) The evolution of thermal physiology in ectotherms. J Therm Biol 27:249–268. https://doi.org/10.1016/S0306-4565(01)00094-8

Antczak M, Ekner-Grzyb A, Majláth I, Majláthová V, Bona M, Hromada M, Tryjanowski P (2019) Do males pay more? A male-biased predation of common lizard (*Zootoca vivipara*) by great grey shrike (*Lanius excubitor*). Acta Ethol 22:155–162. https://doi.org/10.1007/s10211-019-00318-6

Bates D, Mächler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. J Stat Softw 67:1–48. https://doi.org/10.18637/jss.v067.i01

Bennett AM, Pereira D, Murray DL (2013) Investment into defensive traits by anuran prey (*Lithobates pipiens*) is mediated by the starvation-predation risk trade-off. PLoS One 8:e82344. https://doi.org/10.1371/journal.pone.0082344

Brown JS, Laundre JW, Gurung M (1999) The ecology of fear: optimal foraging, game theory, and trophic interactions. J Mammal 80:385–399

Chabaud C, Berroneau M, Berroneau M, Dupoué A, Guillon M, Viton R, Gavira RSB, Clobert J, Lourdais O, Le Galliard J-F (2022) Climate aridity and habitat drive geographical variation in morphology and thermo-hydroregulation strategies of a widespread lizard species. Biol J Linn Soc 137:677–685. https://doi.org/10.1093/biolinnean/blac114

Chown SL, Sørensen JG, Terblanche JS (2011) Water loss in insects: an environmental change perspective. J Insect Physiol 57:1070–1084. https://doi.org/10.1016/j.jinsphys.2011.05.004

Clinchy M, Sheriff MJ, Zanette LY (2013) Predator-induced stress and the ecology of fear. Funct Ecol 27:56–65. https://doi.org/10.1111/1365-2435.12007

Cooper WE (2009) Flight initiation distance decreases during social activity in lizards (*Sceloporus virgatus*). Behav Ecol Sociobiol 63:1765–1771. https://doi.org/10.1007/s00265-009-0799-1

Cote J, Clobert J (2006) Social personalities influence natal dispersal in a lizard. Proc R Soc Lond B 274:383–390. https://doi.org/10.1098/rspb.2006.3734

Davies SJJF (1982) Behavioural adaptations of birds to environments where evaporation is high and water is in short supply. Comp Biochem Physiol A 71:557–566. https://doi.org/10.1016/0300-9629(82)90204-3

de Bont RG, van Gelder JJ, Olders JHJ (1986) Thermal ecology of the smooth snake, *Coronella austriaca Laurenti*, during spring. Oecologia 69:72–87. https://doi.org/10.1007/BF00399040

Dezetter M, Le Galliard JF, Guiller G, Guillon M, Leroux-Coyau M, Meylan S, Brischoux F, Angelier F, Lourdais O (2021) Water deprivation compromises maternal physiology and reproductive success in a cold and wet adapted snake *Vipera berus*. Conserv Physiol 9:coab071. https://doi.org/10.1093/conphys/coab071

Dezetter M, Le Galliard J-F, Lourdais O (2022) Behavioural hydroregulation protects against acute effects of drought in a dry-skinned ectotherm. Oecologia 201:355–367. https://doi.org/10.1007/s00442-022-05299-1

Downes S (2001) Trading heat and food for safety: costs of predator avoidance in a lizard. Ecology 82:2870–2881. https://doi.org/10.1890/0012-9658(2001)082[2870:THAFFS]2.0.CO;2

Drobenkov SM (2014) Distribution, ecological traits and conservation of the smooth snake (*Coronella austriaca*) in Belarus. Acta Biol Univ Daugavp 14:21–27

Downes S, Shine R (1998) Sedentary snakes and gullible geckos: predator–prey coevolution in nocturnal rock-dwelling reptiles. Animal Behav 55(5):1373–1385

Dupoué A, Blaimont P, Rozen-Rechels D et al (2020) Water availability and temperature induce changes in oxidative status during pregnancy in a viviparous lizard. Funct Ecol 34:475–485. https://doi.org/10.1111/1365-2435.13481

Dupoué A, Le Galliard J-F, Josserand R, DeNardo DF, Decencière B, Agostini S, Haussy C, Meylan S (2018) Water restriction causes an intergenerational trade-off and delayed mother–offspring conflict in a viviparous lizard. Funct Ecol 32:676–686. https://doi.org/10.1111/1365-2435.13009

Dupoué A, Rutschmann A, Le Galliard JF, Miles DB, Clobert J, DeNardo DF, Brusch GA, Meylan S (2017) Water availability and environmental temperature correlate with geographic variation in water balance in common lizards. Oecologia 185:561–571. https://doi.org/10.1007/s00442-017-3973-6

Fox J, Weisberg S (2011) Multivariate linear models in R. An R companion to applied regression, SAGE

Fuller A, Mitchell D, Maloney SK, Hetem RS, Fonsêca VFC, Meyer LCR, van de Ven TMFN, Snelling EP (2021) How dryland mammals will respond to climate change: the effects of body size, heat load and a lack of food and water. J Exp Biol 224:jeb238113. https://doi.org/10.1242/jeb.238113

Greenberg DA, Palen WJ (2021) Hydrothermal physiology and climate vulnerability in amphibians. Proc R Soc B 288:20202273. https://doi.org/10.1098/rspb.2020.2273

Guillon M, Guiller G, DeNardo DF, Lourdais O (2014) Microclimate preferences correlate with contrasted evaporative water loss in parapatric vipers at their contact zone. Can J Zool 92:81–86. https://doi.org/10.1139/cjz-2013-0189

Gvoždík L, Castilla AM (2001) A comparative study of preferred body temperatures and critical thermal tolerance limits among populations of *Zootoca vivipara* (Squamata: Lacertidae) along an altitudinal gradient. J Herpetol 35:486–492. https://doi.org/10.2307/1565967

Gvoždík L, Černická E, Van Damme R (2013) Predator-prey interactions shape thermal patch use in a newt larvae-dragonfly nymph model. PLoS One 8:e65079. https://doi.org/10.1371/journal.pone.0065079

Harrison X (2014) Using observation-level random effects to model overdispersion in count data in ecology and evolution. PeerJ 2:e616. https://doi.org/10.7717/peerj.616

Herczeg G, Herrero A, Saarikivi J, Gonda A, Jäntti M, Merilä J (2008) Experimental support for the cost–benefit model of lizard thermoregulation: the effects of predation risk and food supply. Oecologia 155:1–10. https://doi.org/10.1007/s00442-007-0886-9

Huey RB, Slatkin M (1976) Cost and benefits of lizard thermoregulation. Q Rev Biol 51:363–384. https://doi.org/10.1086/409470

Kassambara A, Kosinski M, Biecek P, Fabian S (2017) Package ‘survminer.’ Drawing Survival Curves using ‘ggplot2’ (R package version 0.3.1). https://rpkgs.datanovia.com/survminer/index.html

Kawamoto A, Le Galliard J-F, Badiane A (2021) The role of social costs as a mechanism enforcing the honesty of ultraviolet-reflecting signals in a lizard. Biol J Linn Soc 133:1126–1138. https://doi.org/10.1093/biolinnean/blab008

Ladyman M, Bradshaw D (2003) The influence of dehydration on the thermal preferences of the Western tiger snake, *Notechis scutatus*. J Comp Physiol B 173:239–246. https://doi.org/10.1007/s00360-003-0328-x

Landry Yuan F, Ito S, Tsang TPN, Kuriyama T, Yamasaki K, Bonebrake TC, Hasegawa M (2021) Predator presence and recent climatic warming raise body temperatures of island lizards. Ecol Lett 24:533–542. https://doi.org/10.1111/ele.13671

Lillywhite HB (2016) An ecological and evolutionary viewpoint on the energy and water relations of ectothermic amphibians and reptiles. In: de Andrade DV, Bevier CR, de Carvalho JE (eds) Amphibian and Reptile Adaptations to the Environment - Interplay Between Physiology and Behavior. CRC Press, Boca Raton, FL, pp 1–25

Lima SL (1998) Stress and decision making under the risk of predation: recent developments from behavioral, reproductive, and ecological perspectives. Adv Stud Behav 27:215–290. https://doi.org/10.1016/S0065-3454(08)60366-6

Lima SL, Dill LM (1990) Behavioral decisions made under the risk of predation: a review and prospectus. Can J Zool 68:619–640. https://doi.org/10.1139/z90-092

Lister BC, Aguayo AG (1992) Seasonality, predation, and the behaviour of a tropical mainland anole. J Anim Ecol 61:717–733. https://doi.org/10.2307/5626

Lorenzon P, Clobert J, Oppliger A, John-Alder H (1999) Effect of water constraint on growth rate, activity and body temperature of yearling common lizard (*Lacerta vivipara*). Oecologia 118:423–430. https://doi.org/10.1007/s004420050744

Lorioux S, Lisse H, Lourdais O (2013) Dedicated mothers: predation risk and physical burden do not alter thermoregulatory behaviour of pregnant vipers. Anim Behav 86:401–408. https://doi.org/10.1016/j.anbehav.2013.05.031

Lourdais O, Dupoué A, Guillon M, Guiller G, Michaud B, DeNardo DF (2017) Hydric “costs” of reproduction: pregnancy increases evaporative water loss in the snake *Vipera aspis*. Physiol Biochem Zool 90:663–672. https://doi.org/10.1086/694848

Martín J, López P (1999) When to come out from a refuge: risk-sensitive and state-dependent decisions in an alpine lizard. Behav Ecol 10:487–492. https://doi.org/10.1093/beheco/10.5.487

Martín J, López P, Cooper WE Jr (2003) When to come out from a refuge: balancing predation risk and foraging opportunities in an alpine lizard. Ethology 109:77–87. https://doi.org/10.1046/j.1439-0310.2003.00855.x

Martin TE (2011) The cost of fear. Science 334:1353–1354. https://doi.org/10.1126/science.1216109

Martin TL, Huey RB (2008) Why “suboptimal” is optimal: Jensen’s inequality and ectotherm thermal preferences. Am Nat 171:E102–E118. https://doi.org/10.1086/527502

Massot M, Clobert J, Lorenzon P, Rossi J-M (2002) Condition-dependent dispersal and ontogeny of the dispersal behaviour: an experimental approach. J Anim Ecol 71:253–261. https://doi.org/10.1046/j.1365-2656.2002.00592.x

Nervo B, Roggero A, Isaia M, Chamberlain D, Rolando A, Palestrini C (2021) Integrating thermal tolerance, water balance and morphology: an experimental study on dung beetles. J Therm Biol 101:103093. https://doi.org/10.1016/j.jtherbio.2021.103093

Parsons MH, Apfelbach R, Banks PB et al (2018) Biologically meaningful scents: a framework for understanding predator–prey research across disciplines. Biol Rev 93:98–114. https://doi.org/10.1111/brv.12334

Pinheiro J, Bates D, DebRoy S, Sarkar D (2006) nlme: an R package for fitting and comparing Gaussian linear and nonlinear mixed-effects models. (R package, version 3.1-157) https://svn.r-project.org/R-packages/trunk/nlme/

Pintor AFV, Schwarzkopf L, Krockenberger AK (2016) Hydroregulation in a tropical dry-skinned ectotherm. Oecologia 182:925–931. https://doi.org/10.1007/s00442-016-3687-1

Pirtle EI, Tracy CR, Kearney MR (2019) Hydroregulation. A neglected behavioral response of lizards to climate change? In: Bels V, Russell AP (eds) Lizard behavior: Evolutionary and mechanistic perspectives. CRC Press, Boca Raton, FL, pp 343–374

Prestt I (1971) An ecological study of the viper *Vipera berus* in southern Britain. J Zool 164:373–418. https://doi.org/10.1111/j.1469-7998.1971.tb01324.x

Robert KA, Thompson MB (2007) Is basking opportunity in the viviparous lizard, *Eulamprus Tympanum*, compromised by the presence of a predator scent? J Herpetol 41:287–293. https://doi.org/10.1670/0022-1511(2007)41[287:IBOITV]2.0.CO;2

Rohr JR, Madison DM (2003) Dryness increases predation risk in efts: support for an amphibian decline hypothesis. Oecologia 135:657–664. https://doi.org/10.1007/s00442-003-1206-7

Rozen-Rechels D, Badiane A, Agostini S, Meylan S, Le Galliard J-F (2020) Water restriction induces behavioral fight but impairs thermoregulation in a dry-skinned ectotherm. Oikos 129:572–584. https://doi.org/10.1111/oik.06910

Rozen-Rechels D, Dupoué A, Lourdais O, Chamaillé-Jammes S, Meylan S, Clobert J, Le Galliard J-F (2019) When water interacts with temperature: ecological and evolutionary implications of thermo-hydroregulation in terrestrial ectotherms. Ecol Evol 9:10029–10043. https://doi.org/10.1002/ece3.5440

Rutschmann A, Dupoué A, Miles DB et al (2021) Intense nocturnal warming alters growth strategies, colouration and parasite load in a diurnal lizard. J Anim Ecol 90:1864–1877. https://doi.org/10.1111/1365-2656.13502

Sannolo M, Carretero MA (2019) Dehydration constrains thermoregulation and space use in lizards. PLoS One 14:e0220384. https://doi.org/10.1371/journal.pone.0220384

Steen R, Løw LM, Sonerud GA (2011) Delivery of Common Lizards (*Zootoca (Lacerta) vivipara*) to nests of Eurasian Kestrels (*Falco tinnunculus*) determined by solar height and ambient temperature. Can J Zool 89:199–205. https://doi.org/10.1139/Z10-109

Surget-Groba Y, Heulin B, Guillaume C-P, Puky M, Semenov D, Orlova V, Kupriyanova L, Ghira I, Smajda B (2006) Multiple origins of viviparity, or reversal from viviparity to oviparity? The European common lizard (*Zootoca vivipara*, Lacertidae) and the evolution of parity. Biol J Linn Soc 87:1–11. https://doi.org/10.1111/j.1095-8312.2006.00552.x

Therneau T (2012) coxme: mixed effects Cox models. R package version 2:2–3. http://CRAN.R-project.org/package=coxme

Thoen C, Bauwens D, Verheyen RF (1986) Chemoreceptive and behavioural responses of the common lizard *Lacerta rivipara* to snake chemical deposits. Anim Behav 34:1805–1813

Valeix M, Fritz H, Loveridge AJ, Davidson Z, Hunt JE, Murindagomo F, Macdonald DW (2009a) Does the risk of encountering lions influence African herbivore behaviour at waterholes? Behav Ecol Sociobiol 63:1483–1494. https://doi.org/10.1007/s00265-009-0760-3

Valeix M, Loveridge AJ, Chamaillé-Jammes S, Davidson Z, Murindagomo F, Fritz H, Macdonald DW (2009b) Behavioral adjustments of African herbivores to predation risk by lions: spatiotemporal variations influence habitat use. Ecology 90:23–30. https://doi.org/10.1890/08-0606.1

Valeix M, Fritz H, Matsika R, Matsvimbo F, Madzikanda H (2008) The role of water abundance, thermoregulation, perceived predation risk and interference competition in water access by African herbivores. Afr J Ecol 46:402–410. https://doi.org/10.1111/j.1365-2028.2007.00874.x

Van Damme R, Bauwens D, Vanderstighelen D, Verheyen RF (1990) Responses of the lizard *Lacerta vivipara* to predator chemical cues: the effects of temperature. Anim Behav 40:298–305. https://doi.org/10.1016/S0003-3472(05)80924-8

Veldhuis MP, Kihwele ES, Cromsigt JPGM, Ogutu JO, Hopcraft JGC, Owen-Smith N, Olff H (2019) Large herbivore assemblages in a changing climate: incorporating water dependence and thermoregulation. Ecol Lett 22:1536–1546. https://doi.org/10.1111/ele.13350

Wright CD, Jackson ML, DeNardo DF (2013) Meal consumption is ineffective at maintaining or correcting water balance in a desert lizard, *Heloderma suspectum*. J Exp Biol 216:1439–1447. https://doi.org/10.1242/jeb.080895