

Hydroregulation in a tropical dry-skinned ectotherm

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Abstract While temperature effects on species' vulnerability to climate change are well studied, desiccation effects receive comparatively little attention. In addition, we poorly understand the capacity of ectotherms, and especially reptiles, to control water loss rates behaviourally by selecting suitable microhabitats. This study examined water loss rates and behavioural hydroregulation in the tropical rainforest skink *Carlia rubrigularis* to assess whether this dry-skinned ectotherm actively avoids desiccation and whether trade-offs occur between desiccation avoidance and selection of optimal temperatures, as previously shown in amphibians. Higher temperatures elicited humid refuge choice despite placing individuals in suboptimal thermal conditions, as indicated by preferred substrate temperatures. This finding emphasizes the importance of water loss even for taxa traditionally assumed to be highly desiccation resistant, and highlights this factor's potential influence on vulnerability to climate change by limiting activity times or by restricting individuals to thermally suboptimal microhabitats.

Keywords Desiccation threshold · Climate change · Water loss · Skinks · Lizards

Introduction

Most ectotherms are highly susceptible to the climatic conditions to which they are exposed, because they have limited capacity to thermoregulate physiologically using metabolic heating or evaporative cooling, and thus use behavioural thermoregulation. Some recent studies predicting vulnerabilities of ectotherms to climate change suggest that tropical ectotherms are highly susceptible to environmental temperature increases, because they are currently experiencing temperatures that are already close to optimum temperatures for performance and to critical thermal maxima (Deutsch et al. 2008). Forest dwelling ectotherms might be particularly vulnerable in this respect because they are often thermoconformers (Huey et al. 2009).

Water loss rates (WLRs) are directly influenced by environmental temperatures (Warburg 1965; Dmi'el 2001) and are, consequently, likely to increase as temperatures rise with climate change (IPCC 2013), depending on species' capacity to mitigate environmental warming through behavioural thermoregulation (Sunday et al. 2014; Buckley et al. 2015). Changes in hydric conditions will likely contribute to such climatic effects on water balance but are less well understood than temperature changes: predictions include complex spatial and temporal variation globally (Suppiah et al. 2007), decreases in dry season precipitation and increases in moisture balance deficit across most of Australia (Hughes 2003; IPCC 2013). Even though environmental variables connected to water balance, such as humidity and precipitation, have long been known to affect the activity, abundance and distribution limits of some

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We show that behavioural desiccation avoidance can trade-off with thermoregulation in reptiles and contributes substantially to climate change vulnerability even in dry-skinned ectotherms.

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dry-skinned ectotherms (Bursell 1957; Messenger 1959; Andrewartha and Birch 1960), and even though WLRs vary among closely related species from habitats of different aridity even in comparatively desiccation resistant ectotherms such as reptiles (Hillman et al. 1979; Neilson 2002), measures of WLRs are not usually included in studies assessing the vulnerability of dry-skinned ectotherms to climate change with the exception of some recent work on insects (Chown et al. 2011). Especially in reptiles, interspecific differences in WLRs as well as the potential capacity to resist or avoid desiccation through behavioural mechanisms are greatly understudied, despite their potential to be of great importance to the vulnerability of ectotherms to changes in their environment (Chown et al. 2011; Kearney et al. 2013).

While behavioural thermoregulation has been studied extensively in ectotherms (see Angilletta 2009), active behavioural hydroregulation of individuals has received less attention (Davis and DeNardo 2010; Tracy et al. 2014) and has, so far, been studied largely in amphibians (Bundy and Tracy 1977; Tracy et al. 1993; Bartelt et al. 2010) and invertebrates (Tracy et al. 1979; Prange 1996). Whether reptiles employ behavioural hydroregulation to avoid desiccation, however, is less well known, despite some indications that increased desiccation levels modify temperature choice and other behaviours that influence water loss, such as gaping (Tattersall and Gerlach 2005; Scarpellini et al. 2015). Additionally, some reptiles select periods of high precipitation for activity (Davis and DeNardo 2010) or retreat to humid burrows during dry periods (Wilms et al. 2010), which further highlights the possible importance of hydroregulation in this taxon and warrants more detailed research.

If increasing temperatures pose a particular risk to tropical forest reptiles because they are thermoconformers (Huey et al. 2009), increased desiccation rates induced by higher body temperatures may exacerbate such vulnerability. It is, therefore, of great interest whether reptile species from tropical forest habitats, where water is currently not limiting but may become limiting in the future, are not only thermoconformers but also hydroconformers, or whether they can mitigate combined effects of high temperature and low humidity on desiccation through behavioural mechanisms.

The aim of this study was, therefore, to (1) quantify active behavioural thermoregulation as well as hydroregulation in a tropical rainforest lizard (*Carlia rubrigularis*), and to (2) estimate the species' desiccation resistance across temperatures. We predicted that *C. rubrigularis* would avoid desiccation at high temperatures by actively choosing humid refuge sites.

Materials and methods

Animal collection and husbandry

We collected 10 individuals of adult rainbow skinks (*C. rubrigularis*) by hand at different locations between Bramston Beach (−17.35S, 146.02E) and Mossman (−16.44S, 145.36E) and acclimated them to a 28–32 °C temperature regime under a 12 h:12 h light:dark cycle (representative of typical tropical conditions) at 60–90 % relative humidity for more than 17 weeks before experiments. Conditions were identical for all individuals but varied across days because cages were sprayed with water every 3 days to maintain high humidity levels. Acclimation temperatures were representative of the hot end of the scale of natural thermal conditions in Cairns (monthly mean maximum = 25.7–31.5 °C; monthly mean minimum temperature = 17.1–23.8 °C; www.bom.gov.au/climate/ Accessed 16 June 2016). Animals were “hot” acclimated to reflect the acclimation state they would naturally be in when facing increased water loss due to heat. The extensive acclimation time chosen for this study was necessary because previous work on rainbow skinks has shown that some physiological traits require 17 weeks to complete acclimation (Pintor et al. 2016). Animals were housed in 30 (D) × 20 (W) × 10 cm (H) plastic containers with mesh lids. Potting mix and leaf litter were dried at 65 °C and used as substrate and retreat sites. Lizards were fed crickets several times per week and provided with water ad libitum.

Trait measurements

Preferred substrate temperatures

Preferred substrate temperatures of 9 warm-acclimated individuals (mean body mass = 2.71 g; range 1.63–3.53 g) fasted for 2 days prior to experiments were measured within a 2-m thermal gradient with an aluminium base and opaque Perspex walls, heated at one end and cooled at the other by Peltier plates (temperature range from 5 to 65 °C). White sand paint was applied to the base to provide a more natural substrate, while optimizing contrast. Lizards were introduced into the hot end, to facilitate quick temperature selection away from unsuitable temperatures, and were left in the gradient for 1 h to adjust to experimental conditions. Subsequently, photographs were recorded every 60 s for 24 h from above, under a 12 h:12 h day:night regime. Dim red light was provided at night. Start times were chosen at haphazardly between 0700 and 2230 hours. For the analysis, only the first 2 h of recording was used, unless start time was after 1700 hours, in which case the first 2 h in

the morning (0700–0900 hours) was analysed instead. The measurements used for the final analysis were spread out across the whole day. Measurements from the dark photophase were not used. Using ImageJ (<http://imagej.nih.gov/ij/>) lizard positions (distance from cold end of gradient to the point between lizard front legs in pixels) were measured for each photo. The position of ten iButtons® (model 1922L), which measured the temperature at 20 cm intervals along the gradient every 60 s, was recorded in the same manner. Using a polynomial calibration curve on the temperatures recorded by the iButtons® in the gradient during the experiment, lizard positions were converted into selected substrate temperature at each 60-s interval. For each lizard, the median of the 120 measurements collected over 2 h was calculated and used for further analysis. Upper and lower limits of set point ranges of each individual were calculated as the 25–75 % quartile of the 120 temperatures. The median 50 % of selected body temperatures was chosen because these are often used as cutoff points for the set point range (Angilletta 2009). The median of all values of the median preferred substrate temperature, 25–75 % quartile across individuals, was recorded as the species' preferred substrate temperature, lower, and upper limits of set point range, respectively. Some animals became inactive during the recording and positioned themselves at very cold temperatures over extended time periods. If inactivity was suspected, the measurement was repeated several weeks later and the first measurement was discarded. Similarly, if shedding was noted within 7 days of the experiment, that instance was discarded and the measurement was repeated to standardize the experiments for non-shedding individuals because shedding appeared to greatly increase water loss (Pintor, personal observations) and may, consequently, also influence behaviour.

Behavioural hydroregulation

Behavioural hydroregulation was measured by testing lizards' choice of refuge in 30 (*D*) × 20 (*W*) × 10 cm (*H*) plastic containers with mesh lids and sand substrate. Each container had two refuges placed at opposite corners. Refuges consisted of microfiber cloths placed on sand-filled 9-cm diameter plastic dishes. One refuge had a wet cloth cover and moist sand, while the other was kept dry. Animals were introduced to containers near the dry refuge. Containers were then placed in a temperature- and humidity-controlled cabinet at ten different temperatures between 18 and 36 °C in randomized order. The position of the container in the cabinet (wet or dry hide towards the back) was also randomized. Humidity in the cabinet was set to 20 % (the lowest possible setting with a stable resulting cabinet humidity). The same 10 animals (mean body mass = 2.78 g, range 2.12–3.87 g) were tested at each

temperature. Experiments were started at 17:00 ± 1 h. The fraction of individuals that had chosen the wet refuge was recorded after 16 h. If animals were sitting on top of a refuge, they were assumed to have recently emerged from this refuge that morning and refuge choice was recorded accordingly. No food or water was offered during experiments but animals were well hydrated up to the start of experiments. Hygrobuttons® randomly placed in four of the wet and four of the dry refuges, respectively, in each experiment recorded differences in humidity and temperature between the two refuge options. Humidity in the open was recorded as well.

Refuge choice was analysed using logistic mixed effects generalized linear models in R (Bates et al. 2015; R Core Team 2014). The fixed effects component of the starting model included temperature and body mass as potential predictors of wet refuge selection, as well as a random term for individual ID, because the same 10 individuals were used at each of the ten temperatures. Backwards step-wise selection on fixed terms according to AIC and log-likelihood ratio tests was used to eliminate insignificant terms.

Water loss rates

WLR was measured in 9 warm-acclimated individuals (mean body mass = 2.83 g, range 2.12–3.64 g) at 20–30 °C in constant darkness in transparent plastic chambers for 16 h overnight. Atmospheric air was dried to under 5 % relative humidity (as measured by Hygrobuttons®) using a scrubber containing silica gel pearls and was pumped through each chamber to maintain a constant low relative humidity. These two experimental conditions (20–30 °C at 5 % relative humidity) were equivalent to 2.22–4.03 kPa vapour pressure deficit (VPD) of the air. After animals had adjusted to experimental conditions in the chamber for 1 h, each lizard was weighed with its chamber, and again the following morning. To avoid overestimation of WLRs, measurements were discarded if animals defecated during the experiment, shed within 7 days after the experiment, or were very active at the time of morning measurements. Such animals were re-tested after at least 2 days in case of defecation or activity and after at least 7 days post-shedding. The relationship of water loss in mg over 16 h with vapour pressure deficit was analysed using mixed linear models in R (package nlme; Pinheiro et al. 2013; R Core Team 2014) to allow for the inclusion of individual as a random effect. The model included a term for body mass to account for size differences in water loss. Log transformed values of water loss and body mass and untransformed values for temperature were used based on the well-known shape of the relationship between the variables (Withers et al. 2000).

Results

Thermoregulatory and hydroregulatory preferences

Median preferred substrate temperature of *C. rubrigularis* was 32.9 °C (range 29.7–37.3; Fig. 1) and did not vary with time of day (linear regression; $F_{(1,7)} = 0.04$, $p = 0.85$) even though it appears to increase linearly with time of day in some other *Carlia* species (Pintor, unpublished data). The set point range was between 31.1 (range 27.9–36.8) and 35.2 (range 29.9–38.6). There was no significant effect of body mass on preferred substrate temperature (linear regression; $F_{(1,7)} = 0.51$, $p = 0.50$), lower quartile of selected temperatures (linear regression; $F_{(1,7)} = 0.15$, $p = 0.71$) or upper quartiles of selected temperatures (linear regression; $F_{(1,7)} = 1.25$, $p = 0.30$).

Relative humidity in dry and wet refuges was 32.0 ± 3.4 and 95.7 ± 3.0 % ($M \pm SD$, $n = 4$ for both wet, and dry categories). Mean relative humidity decreased linearly with temperature in both refuge types (linear regression; wet refuge: $F_{(1,8)} = 11.58$, $p < 0.01$; dry refuge: $F_{(1,8)} = 285.7$, $p < 0.001$) but always remained above 90 % in wet and below 45 % in dry refuges, i.e. humidity in dry refuges was consistently and substantially lower than in wet refuges (Fig. 2). Temperatures were consistently lower in wet refuges.

Temperature was a significant predictor of the proportion of individuals in the wet refuge, whether temperatures

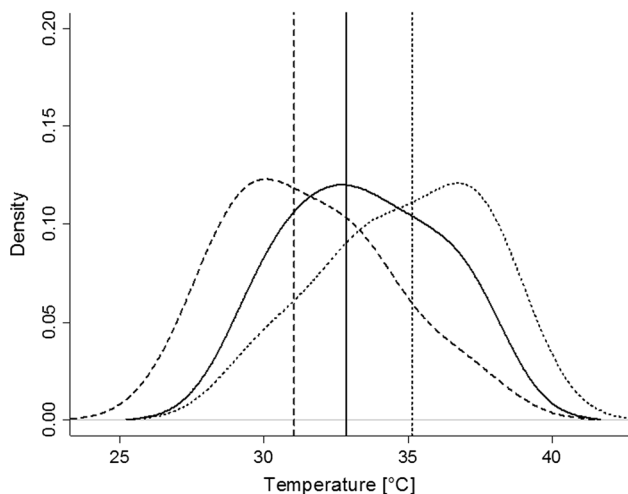


Fig. 1 Density plot of median preferred substrate temperatures (solid line, median indicated by solid vertical line) of *Carlia rubrigularis*, as well as lower (dashed line, median indicated by vertical dashed line), and upper (dotted line, median indicated by vertical dotted line) limits of set point range (median 50 % of selected substrate temperatures)

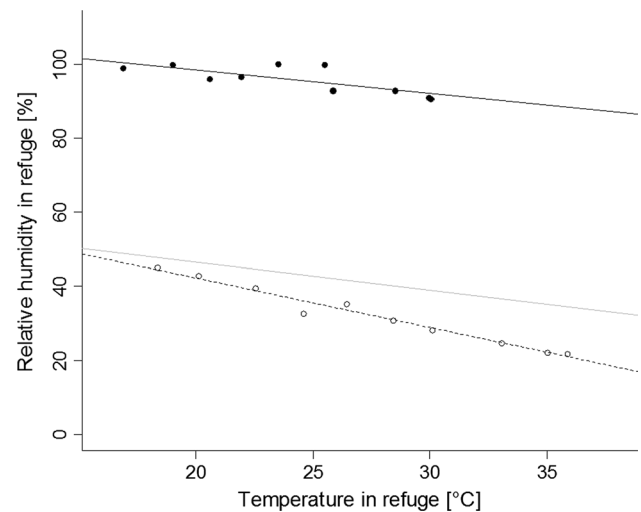


Fig. 2 Relative humidity in the wet (filled circles, solid black line) and dry (open circles, dashed black line) refuges across different temperatures in the same refuges, as well as humidity in the open at different controlled cabinet temperatures (solid grey line). Humidity increased with temperatures in both refuge categories but always remained high (>90 %) in the wet and substantially lower (<45 %) in the dry refuges

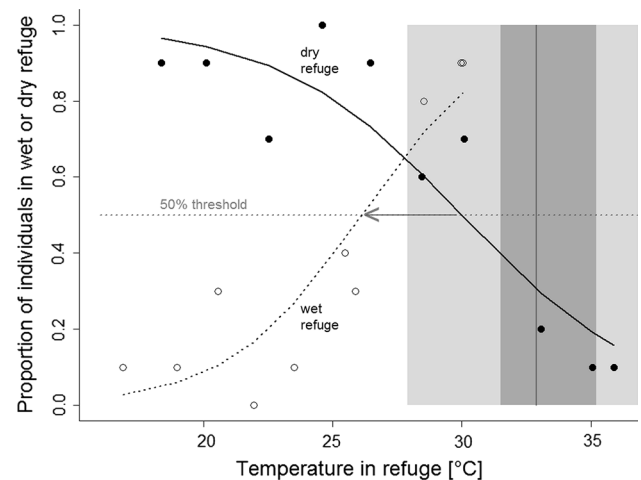


Fig. 3 Proportion of individuals selecting wet (open circles, dashed line) or dry refuges (filled circles, solid black line) at different temperatures, including fitted values of logistic regressions using temperature of the respective refuge as predictor of refuge choice. The median preferred substrate temperature (32.9 °C) dark grey vertical line), and median set point range of *C. rubrigularis* (31.5–35.2 °C, dark grey shaded area), as well as the temperature range delimited by the lowest and highest of the set point range boundaries recorded for any individuals (27.9–38.6, light grey shaded area) are shown for comparison with temperatures in chosen refuges. When the temperature in dry refuges reached 30 °C, the majority of individuals (>50 %, horizontal grey dotted line) began to select wet refuges instead, and thereby placed themselves in temperatures further below the range of preferred temperatures

in dry (logistic generalized linear mixed effects model, $Z = 5.06$, $p < 0.0001$) or wet refuges (logistic generalized linear mixed effects model, $Z = 5.08$, $p < 0.0001$) were used as predictor variables (Fig. 3). Including body mass as an additional predictor did not improve these models significantly ($\Delta AIC < 0.5$, $\chi^2 = 2.24$, $p = 0.13$). Above 30 °C in the dry refuge, equivalent to a VPD of 3.05 kPa, over 50 % of individuals selected the wet refuge, where the temperature was only 26 °C at this point (VPD = 0.24 kPa). This temperature (30 °C) at which dry refuge avoidance began was below the median preferred substrate temperature of the *C. rubrigularis* (32.9 °C) and below the lower limit of set point ranges of more than half of all examined individuals (see Fig. 1 for comparison). When temperatures in dry refuges were increased to within the set point range of *C. rubrigularis* (31.1–35.2 °C), an increasing majority of individuals selected the wet refuge, where temperatures (~26–30 °C) were well below the species' set point range.

Water loss budgets

There was a significant correlation of log transformed WLR over 16 h with vapour pressure deficit ($df = 6$, $t = 9.87$, $p < 0.001$) as well as with log transformed body mass ($df = 6$, $t = 3.70$, $p = 0.01$; mixed linear model with individual as random effect). The relationship was described by the following equation:

$$\ln[\text{WLR (mg)}] = 2.97 + 0.31 \times \text{VPD (kPa)} + \ln[\text{BM}^{0.62}(\text{g})], \quad (1)$$

where WLR is the water loss rate over 16 h, VPD is the vapour pressure deficit at the test temperatures at 5 % relative humidity, and BM is the body mass.

Body mass adjusted water loss rate (Fig. 4) is consequently described by the following rearranged equation:

$$\ln[\text{WLR (mg)}/\text{BM}^{0.62}(\text{g})] = 2.97 + 0.31 \times \text{VPD (kPa)}. \quad (2)$$

According to this equation, the WLRs of an average sized animal of 2.83 g at a VPD of 3.05 kPa (equivalent to 30 °C and 28 % relative humidity in the dry refuge; see Fig. 2), at which more than 50 % of animals preferred a wetter refuge, would be 95.63 mg. This equates to 3.4 % of body mass over 16 h, or 0.2 % per hour for an average sized individual (2.83 g). By choosing a wet refuge of ~26 °C and 93 % relative humidity instead (see Fig. 2), the resulting vapour pressure deficit would have been 0.24 kPa, resulting in an estimated water loss of 40.02 mg, or 1.4 % of body mass over 16 h (0.09 % per hour). While selection of a wet refuge under these conditions would have resulted in placement in a thermally suboptimal condition outside

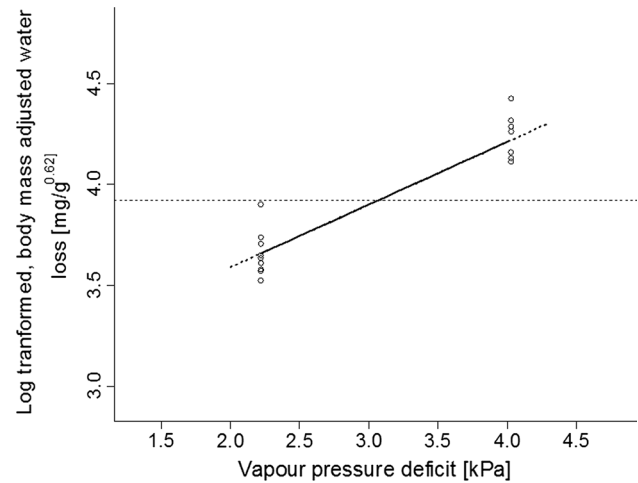


Fig. 4 Body mass adjusted WLR of *C. rubrigularis* over 16 h at different VPD (calculated from measurements at 20–30 °C with RH ~5 %), including predictor line of linear mixed effects model (solid), and extrapolation from the model (dotted). Predicted WLR at the voluntary threshold of 3.05 kPa would equate to 3.4 % of body mass over 16 h or 0.2 % per hour for an average sized animal (horizontal dashed line)

the set point range of the species (see Fig. 1), such a choice would have also more than halved the water loss rate.

Discussion

With increasing temperature, more rainbow skinks (*C. rubrigularis*) selected wet over dry refuges (Fig. 3). This could be interpreted as thermoregulatory behaviour, because temperatures were consistently lower in the wet refuge. However, the set point range of *C. rubrigularis* range lies between 31.1 and 35.2 °C (Fig. 1), whereas individuals began choosing a wet refuge around 30 °C. Therefore, the majority of individuals selected wet refuges with temperatures well below their preferred temperature, even though temperatures within their preferred temperature range were available in the dry refuges. Avoidance of high temperatures is, consequently, unlikely to be the cause of the observed preference. Thus, individuals in our experiment behaviourally thermoregulated when desiccation stress was low and selected dry (warmer) refuges at lower temperatures (Fig. 3). However, when the temperature in dry refuges approached their preferred temperature, they increasingly selected wet refuges at suboptimal temperatures and, thus, clearly avoided desiccation. This strongly suggests that these tropical rainforest skinks exhibit behavioural hydroregulation, either by selecting conditions that reduce desiccation in the first place, or by lowering their thermal preference when desiccated, similar to responses observed

in other reptiles (Ladyman and Bradshaw 2003). Both represent a form of active hydroregulation, either through preventative or through responsive behaviour. Contrary to previous suggestions (Huey et al. 2009), the tropical forest species in this study was, therefore, neither a thermoconformer, nor a hydroconformer, and the two behavioural mechanisms for optimization of thermal and hydric state clashed. Such behavioural trade-offs between optimization of hydration and thermal state are similar to those observed in amphibians (Bundy and Tracy 1977; Tracy et al. 1993; Köhler et al. 2011) and invertebrates (Tracy et al. 1979; Prange 1996) but have to date received much less attention in reptiles (Ladyman and Bradshaw 2003; Scarpellini et al. 2015).

At 30 °C and 28 % RH, when most individuals began to avoid the drier, thermally more suitable refuge, VPD reached 3.05 kPa. This suggests that there may be a voluntary desiccation threshold, either expressed as a water loss rate that is avoided (preventative) or as a maximum desiccation level that is tolerated before avoidance behaviours are initiated (responsive). If hydroregulation is preventative, our results suggest a voluntarily accepted hourly water loss rate of 0.2 % of body mass as the threshold for *C. rubrigularis*. However, there may, alternatively, be an absolute desiccation threshold, that when reached elicits avoidance behaviour. The desiccation level at which half of the individuals in our study selected a low VPD refuge was about 3.4 % of body mass over the experimental period. However, in the absence of definite observations of the time point at which individuals changed their refuge preference and corresponding measurements of desiccation state at that point, a reliable desiccation threshold cannot be determined. Comparison of our results with data from other species would be of great interest to establish whether closely related species with different water loss rates have similar desiccation avoidance behaviours, whether trade-offs between hydroregulation and thermoregulation influence species' distributions and activity times and what the exact decision mechanisms used by reptiles for hydroregulation (e.g. preventative vs. responsive) are.

Desiccation is likely to exacerbate the risks associated with high temperatures (Vickers et al. 2011) and may increase the vulnerability of species to climate change. Climate change will lead to increases in temperature as well as changes in precipitation, cloud cover, and relative humidity (IPCC 2013). High temperatures are strongly relevant to species' vulnerability, due to abrupt decreases in fitness to the right of the thermal optimum in most ectotherm species (Deutsch et al. 2008; Angilletta 2009). However, increased temperatures may also be detrimental because of associated increases in water loss, especially if humidity or water availability decreases as temperatures rise (Bartelt et al. 2010). Synergies between temperature and desiccation could directly expose reptiles to lethal conditions but

will also have indirect impacts if individuals are forced to seek hydric refuges (Kearney et al. 2013), thus potentially decreasing activity time (Bartelt et al. 2010; Kearney et al. 2013) and suitable habitats. Additionally, and perhaps more importantly, optimal temperatures may be avoided if conditions are too dry, necessarily leading to activity in sub-optimal thermal conditions. As opposed to the direct lethal effect of high temperatures or low humidity, these more subtle effects may severely reduce fitness, and could represent a substantial threat to species from habitats where aridity or seasonality increases with climate change. This is in accordance with recent predictions suggesting that environmental conditions are likely to change along several axes, leading to novel combinations of conditions and making environmental risks hard to predict (Williams and Jackson 2007; Williams et al. 2007).

In conclusion, we found strong behavioural hydroregulation in a reptile, trading off with thermoregulation. Comparative studies on reptiles from different habitats in combination with models predicting activity times and potential distributions based on these two interacting behavioural mechanisms are needed, to further clarify the likely impact such behaviours may have on different species' responses to climate change. Voluntary desiccation thresholds of species are of particular interest in this context. Especially in reptiles, the relevance of water loss is often underestimated (Kearney et al. 2013). The effects of changing temperature, however, should not be assessed in isolation from other climate variables.

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Author contribution statement AFVP, LS, AKK conceived and designed the experiment, AFVP performed the experiments, AFVP and AKK performed the statistical analysis, AFVP wrote the manuscript, LS and AKK provided editorial advice.

Compliance with ethical standards

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

Animal ethics All applicable institutional and national guidelines for the care and use of animals were followed. The research was conducted under animal ethics permit A2076 and animal collection for scientific purposes permit WISP10730612.

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