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Lizards in the wind: The impact of wind on the thermoregulation of the common wall lizard

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1. Introduction

The effects of climate change are increasing in both intensity and scope, altering many important abiotic factors. Temperature is perhaps the most studied climatic factor, but there is also evidence of changing atmospheric wind patterns (Deng et al., 2022; Wu et al., 2018). These predicted fluctuations will undoubtedly impact the thermal biology of organisms who rely on their environmental conditions to thermoregulate and conserve water. These changes will especially affect the thermal biology and accompanying energy budgets of ectotherms, especially actively thermoregulating heliotherms. This can be seen in lizards, who possess flexible thermal physiology and behaviors that can buffer them from environmental variation (Huey et al., 2018; Kearney et al., 2009; Leal and Gunderson, 2012; Muñoz and Bodensteiner, 2019; Nowakowski et al., 2018). However, their capacity to respond has limitations (Bodensteiner et al., 2021a; Huey et al., 2012; Kearney et al., 2009; Sunday et al., 2014). Species that are successful in novel environments display flexibility in their thermoregulatory behavior, and can shift it according to the unique challenges of their thermal environment (Gunderson and Leal, 2012; Logan et al., 2014; Nowakowski et al., 2018; Refsnider et al., 2018). Thermoregulatory behavior, however, is subject to trade-offs and constraints. For example, additional time thermoregulating can lead to decreased time for mating, foraging, and defending territory (Black et al., 2019; Brewster et al., 2013; Gvoždík, 2002). As climate change worsens, it creates more of these novel thermal environments, driving lizards to adapt or perish. Even in the absence of environmental buffering via thermoregulatory behaviors, plasticity in physiological traits can alleviate issues caused by exposure to sub-optimal temperatures (Gunderson and Stillman, 2015; Neel et al., 2020). However, previous studies have shown that when body temperatures increase, the plastic physiology of lizards may be insufficient to mitigate a decrease in thermal safety margins (Gunderson and Stillman, 2015).

Studying the effect of wind on thermoregulation becomes important in the context of the seasonal shifts and alterations in wind regimes caused by climate change. These fluctuations are further exacerbated by the increased urbanization of natural environments: urbanization can alter wind patterns (Klink, 1999; Ongoma et al., 2013; Zhang and Wang, 2021), and the thermal habitats of urban centers show increased ambient temperature and warm microhabitat availability due to the urban heat island effect (Battles and Kolbe, 2019). Lizards responding to urbanization must endeavor to find cooler, shadier habitats (Ackley et al., 2015) or potentially use wind to offset heat stress (Gontijo et al., 2018). The potential outcomes of thermoregulation under wind can be complex, as wind can alter body temperature in multiple ways-through the direct convective warming or cooling of the lizard itself, by warming or cooling the substrate said lizard resides in or on, or via increased evaporative cooling (Almeida-Santos et al., 2015; Hare et al., 2009; Maia-Carneiro et al., 2017; Ortega et al., 2016). Lower body temperatures reduce metabolic and energetic capacity, which in turn can reduce the capacity to perform ecologically important tasks such as foraging, mating, and territorial displays (Angilletta et al., 2004; Huey, 1982; Huey and Berrigan, 2001). This lowered energetic capacity also reduces the lizard's rate of movement (Maia-Carneiro et al., 2012), forcing the animal to adjust the balance of their thermoregulatory behavior (shuttling vs basking) to maintain homeostasis. However, there is evidence that in some circumstances, lizards use wind as a cooling mechanism to mitigate overly high substrate temperatures (Gontijo et al., 2018). Wind can also have long-term impacts on energy budgets, as demonstrated in biophysical models (Kearney and Porter, 2009). Yet only one previous

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study in a controlled laboratory environment demonstrated the effect of wind on ectotherm thermoregulation (Virens and Cree, 2022). This study found that McCann's skinks (*Oligosoma maccanni*) select a cooler range of temperatures in response to wind, suggesting they can anticipate oncoming risk of dehydration and offset it accordingly. Whether other lizard species have a similar response is cause for further investigation.

The common wall lizard, *Podarcis muralis*, is an active thermoregulator inhabiting a broad (and expanding) geographic range across much of Europe (Speybroeck et al., 2016). This species has successfully established in new locations, including highly urbanized areas that present novel climates and habitat structure (Davis et al., 2021; Engelstoft et al., 2020; Oskyrko et al., 2020; While et al., 2015). Given its cosmopolitan habits and flexible thermal biology (Bodensteiner et al., 2021a; Litmer and Murray, 2019), this is an ideal species in which to examine the potentially interacting roles of behavior and physiology in responding to variation along environmental gradients, temperature, and wind. Previous research on lizards with a similar thermal ecology demonstrates that the presence of wind alters lizards' ability to effectively thermoregulate (Kearney et al., 2013; Kearney et al., 2018; Le Galliard et al., 2021; Logan et al., 2014; Maia-Carneiro et al., 2017; Ortega et al., 2017; Rozen-Rechels et al., 2019; Sannolo and Carretero, 2019). Within the rich history of studies on lizard thermoregulatory behavior, there is a comparative scarcity of studies quantifying the effects of wind (but see Virens and Cree, 2022). To address this knowledge gap, we analyzed factors influencing thermoregulation in free-range lizards and the thermoregulation of wild-caught lizards in a lab experiment. For our field observations, we hypothesized that lizards would exhibit lower body temperatures as average wind speed increased, as a result of the cooling effect of wind. In our laboratory experiment, we first hypothesized that under wind conditions, *Podarcis muralis* from an urban environment will adjust their thermoregulatory behavior to balance obtaining their preferred temperature and the potential risk of dehydration. Specifically, we predicted that lizards in a thermal gradient will select lower temperatures in wind conditions while maintaining hydration status (as measured by change in body mass and relative blood plasma volume; Logan et al., 2014; Virens and Cree, 2022). Our second hypothesis was that lizards in windy conditions will move less, as they can use wind to counterbalance the heat, and effectively maintain body temperatures within their selected thermal range. Understanding the physiological and behavioral trade-offs inherent in responding to multiple abiotic factors is essential to both characterizing and predicting the effects of ongoing environmental change (Cadena and Tattersall, 2009; Pirtle et al., 2019; Rozen-Rechels et al., 2019; Sannolo and Carretero, 2019; Telemeco et al., 2022).

2. Methods

2.1. Field data and lizard collection

The Common Wall Lizard (*Podarcis muralis* Laurenti 1768) is small (average snout-vent length: 60 mm), diurnal, and employs active thermoregulation. This lacertid lizard is endemic to southern and central Europe (Speybroeck et al., 2016), but was introduced to Cincinnati, Ohio, USA in the early 1950s, where they have since flourished to become common and widespread across much of the city (Davis et al., 2021). We collected field body temperatures of adult male and female *Podarcis muralis* (N = 57) at seven sites in Cincinnati during the peak activity season (June–August 2021; Table S1). We recorded air temperature and relative humidity (5 cm off the ground in the shade; PTH8708 Digital Temperature & Humidity Pen, General Tools, New York, USA) and wind speed (at chest level; Kestrel 3000 Weather Meter, Nielsen-Kellerman, Boothwyn, Pennsylvania, USA) at the beginning and end of each ~2 h survey. Once a subject was located, we captured thermal images (Model T540, FLIR Systems, Wilsonville, Oregon, USA). We took images repeatedly until the subject was captured using a lasso attached to a long fishing rod (range of distances from lizard: 1.57–5.71 m). Body temperature was measured by inserting a type K thermocouple approximately 0.5 cm into the animal's cloaca immediately after capture (<10 s), and the cloacal temperature was recorded (HH801, Omega Engineering, Norwalk, Connecticut, USA). We note that a subset of the field body temperatures measured with the thermocouple were used in Amer et al. (2023). We measured lizard snout-vent length (SVL) to the nearest 0.01 mm with digital calipers (range: 49.0–70.6 mm) and weighed lizards to the nearest 0.01 g using a digital scale (Weigh Gram Top-100, Pocket Scale, Tulelake, California, USA) range: 2.6–9.1 g).

2.2. Lab experiment: thermal preference trials

We tested the effect of wind on preferred body temperatures in a thermal gradient, which permits an animal to select a body temperature free of constraints (Fig. 1; Taylor et al., 2021). We employed a repeated-measures experimental design, utilizing adult male lizards (N = 12) that had been acclimated to captivity for approximately one year (all caught in 2020; See husbandry conditions described in Vaughn et al., 2021; Table S1). Food was withheld from animals for 48 h prior to

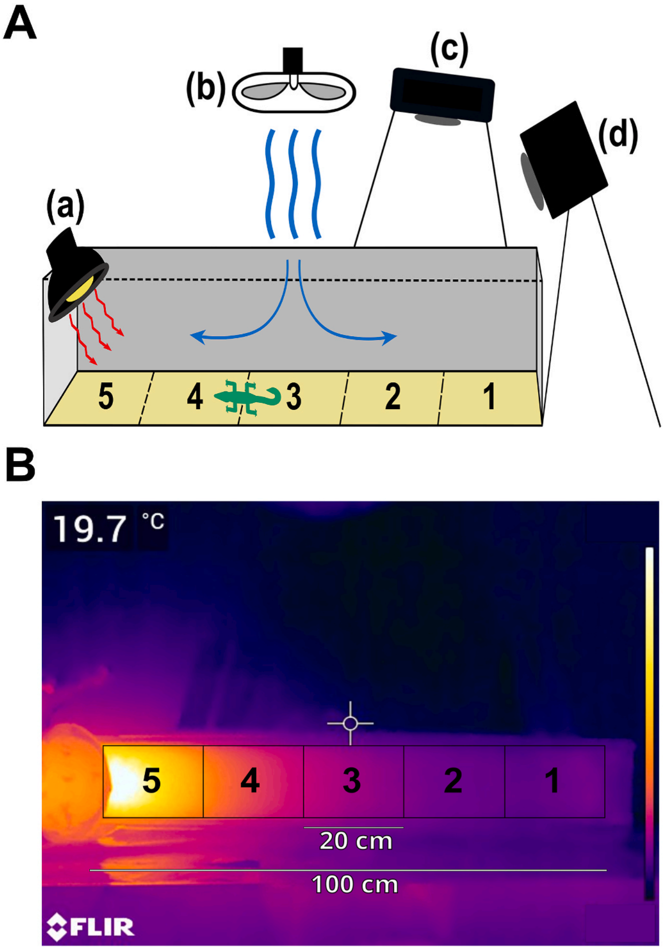

Fig. 1. **(A)** Schematic showing the thermal gradient, lateral view. Components include: (a) ceramic lamp; (b) fan placed 180 cm above the gradient (with corresponding blue arrows to show even air flow throughout the gradient); (c) digital video camera; and (d) thermal imaging camera. The numbers along the bottom of the arena denote the zones of the temperature gradient. **(B)** An aerial view of the thermal gradient, taken via thermal camera. The arena was divided into five zones, with Zone 1 being the coolest and Zone 5 being the hottest. Each zone was 20 cm long, and the overall gradient was 100 cm long. The heat lamp can be seen beside Zone 5. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

each trial to empty the digestive tract (Van Damme et al., 1991). Trials were conducted during the daytime activity period of lizards (09:00–18:00). Room conditions were controlled via thermostat (air temperature mean ± SD: 19.4 ± 0.57 °C, relative humidity mean ± SD: 50.4 ± 3.76%), and confirmed before and after each trial (PTH8708 Digital Temperature & Humidity Pen, General Tools, New York, USA). These conditions did not differ during trials with or without wind (air temperature: $t_{21.6} = -0.48$, $P = 0.64$, relative humidity: $t_{21.3} = -0.31$, $P = 0.76$). Second lizard trials occurred 11–12 days after the first trial (median: 12 days; range: 11–12 days). Each lizard underwent a trial under wind and non-wind conditions, the order of which was randomized such that six lizards began with wind treatment, and the other six began under the no-wind treatment. The arena measured 100 cm × 16 cm with plastic siding walls and lined with approximately 2 cm of white sand. We heated one end with a ceramic heat lamp (150 W) that was suspended 6–9 cm above the substrate and angled at one end of the arena, providing a gradient of ~50 °C (under the lamp) to 20 °C (room temperature). A fan was placed 180 cm above the gradient and pointed downward to the middle of the arena, providing an unimpeded and constant airflow of 0.4 ms^{-1} at the substrate level (Fig. 1A). This value is within the range of observed wind speed values from our field surveys (range: 0.2–0.9 ms^{-1}; median: 0.75 ms^{-1}). Lizards were given an acclimation period (30 min) in the arena before beginning data recording for each 2-h trial. We captured thermal images using the thermal imaging camera (FLIR T540) ~ 2 m (Playà-Montmany and Tattersall, 2021) from the center of the arena, programmed to take an image every 30 s for the duration of the trial. The preferred body temperature (T_{pref}) was calculated as the mean of the interquartile range (central 50%) of body temperatures (Hertz et al., 1993); the lower and upper limits of the interquartile range define the upper 50% and lower 50% limits of selected body temperatures (Upper and Lower Limits to T_{sel}, respectively). The absolute minimum and maximum body temperatures were recorded as the voluntary thermal minimum (VT_{min}) and voluntary thermal maximum (VT_{max}), respectively. Simultaneously, we recorded the arena from directly overhead with a digital camera (frame rate 29.97 fps, Sony DCR-SX40, Tokyo, Japan). Immediately preceding and following each trial, we weighed the lizard to the nearest 0.01 g, which serves as a measure of water loss during the trial (Le Galliard et al., 2021).

To properly calibrate the body temperature data, we conducted an additional experiment in October of 2023. In this, we placed adult male lizards (N = 6) that had been acclimated to captivity for approximately 2 years (all caught in 2021; See husbandry conditions described in Vaughn et al., 2021; Table S1) in the thermal gradient arena described above. Trials were conducted during the daytime activity period of lizards (09:00–18:00) in a thermostat-controlled room (air temperature mean ± SD: 18.9 ± 0.17 °C), and conditions were confirmed before and after each trial (PTH8708 Digital Temperature & Humidity Pen, General Tools, New York, USA). Lizards were given an acclimation period (30 min) in the arena before beginning data recording for each 2-h trial. During the trial, we captured thermal images using the thermal imaging camera (FLIR T540) ~ 2 m (Playà-Montmany and Tattersall, 2021) from the center of the arena, programmed to take an image every 5 min for the duration of the trial. We also collected body temperature via type T thermocouple adhered with tape approximately 0.5 cm into the animal's cloaca, recorded with an electric thermometer (HH801, Omega Engineering) every 10 s for the 2-h trial duration. From this data, we created a predictive equation and used it to calibrate the recorded body temperatures from the original thermal gradient experiment.

2.3. *Blood sampling and hematological measures*

Blood was sampled both from a subset of lizards in the field (N = 36) and after each gradient trial. The blood samples (5–50 μl) were collected with a heparinized glass capillary tube from the retro-orbital sinus (MacLean et al., 1973) within <5 min of capture for field samples, and immediately following the trial in the thermal gradient for lab measures. We stored samples on ice until spinning capillary tubes at 5000×*g* for 5 min on a centrifuge. We then measured relative volume of packed red blood cells and total blood volume with digital calipers (Model CD-6, Mitutoyo, Japan). Hematocrit (Hct) was calculated as the ratio of packed red blood cells to total blood volume.

2.4. *Data processing and analysis*

2.4.1. *Thermal image data extraction*

We extracted lizard body temperature from thermal images from both lab and field with FLIR Research Studio (v. 4.1.3). The measurement parameters were adjusted to reflect the average air temperature and relative humidity of the survey period or trial period and the emissivity set to 0.97 (Luna and Font, 2013). We measured distance from the camera to the lizard via the built-in laser distance meter and accounted for this in the data extraction. Body temperature was extracted using the ellipses ROI (region of interest) tool on the image that provided the sharpest focus of the lizard (median ROI ranges: field: 23 pixels; lab gradient: 32 pixels) An ellipsis was drawn over the body region of each lizard, and we recorded the average temperature and pixel number for each ellipsis.

2.4.2. *Digital video analysis & movement modeling*

We used ToxTrac software with the video file for each trial to extract location data for each video frame (Rodriguez et al., 2018). We then divided the test arena into five equal-sized zones across the thermal gradient (width: 20 cm) and determined which zone the lizard was in at each time step t, $\{Z_t\}_{t=1}^{T}$, with 27.9% missing frames, most commonly due to failure of software to identify the lizard. To match the temporal resolution of our thermal image data, we analyzed these data at 30 s time intervals (N = 240 observations per trial). Approximately 13% of temperature data (of 5760 total observations) were missing because lizard position precluded extraction of body temperature from thermal images; for these values we linearly interpolated body temperature based on the previous and subsequent value. We then implemented a Markov chain model to describe how lizards transition between zones at a given body temperature, while also accounting for missing data in the zones by treating these as if they were missing at random. The observation process, i.e. which zone the lizard is in, is taken to be a first order Markov chain whose evolution over time is governed by a transition probability matrix, $\boldsymbol{\Gamma}$, with entries, $\gamma_{ij} = \Pr(Z_t = j | Z_{t-1} = i)$ for $i, j \in \{1, \ldots, 5\}$ and $t \in \{2, \ldots, T\}$ where T denotes the last observation in the time series. The Markov chain initializes according to an initial state distribution, $\boldsymbol{\delta}$, with entries $\delta_n = \Pr(Z_1 = n)$, for $n \in \{1, \ldots, 5\}$. To assess how lizards may decide to switch between zones, we incorporated treatment and body temperature as covariates in the transition probability matrix using a multinomial logistic link for each row. We fit the model in a Bayesian framework using the software Stan in order to simulate from the joint posterior distribution using the dynamic Hamiltonian Monte Carlo algorithm (Carpenter et al., 2017; Leos-Barajas and Michelot, 2018).

2.4.3. *Statistical methods*

All analyses were conducted in the R Programming Language (v.4.1.3, R Core Team, 2023) and data figures were created via ggplot2 (Wickham et al., 2023). To describe the relationship between body temperatures measured via cloacal probe and those measured via thermal images in field-caught lizards, we used a linear regression model and paired *t*-test. We also tested the different influences of various factors on body temperature (body size, sex, hematocrit, wind speed) using linear models fitted with the lm function. We assessed model residuals by visually inspecting histograms and with a Shapiro-Wilks test. In the thermal gradient trials, we evaluated the effect of wind conditions on selected body temperatures (T_{pref}, Upper T_{sel}, Lower T_{sel}, VT_{min}, VT_{max})

and hydration status (hematocrit, change in body mass). To do so, we used paired t-tests. Further, we calculated constancy repeatability (Biro and Stamps, 2015), which here accounts for variation due to wind treatment, of physiological and behavior measures with the rptR package in R (Stoffel et al., 2017, 2019), using 1000 bootstraps to estimate 95% confidence intervals and likelihood ratio tests to estimate p-values.

3. Results

3.1. Field body temperature observations

Observed field body temperatures of active lizards measured using cloacal probes ranged from 29.2 to 38.2 °C (mean ± SD: 33.4 ± 2.5 °C) and using thermography from 28.7 to 44.7 °C (mean ± SD: 33.8 ± 3.1 °C). Using all measures of field body temperatures, the linear regression model demonstrates a clear correlation between the body temperatures recorded by the cloacal probe and the thermal camera in the field ($R^2 = 0.68$, $P < 0.0001$, slope estimate ± SE: 1.06 ± 0.10; Fig. 2A) and the measures did not differ (paired *t*-test: $t_{56} = -1.79$, $P = 0.079$). Model residuals indicate the deviation of observed data points from the line of best fit, indicating differences in body temperature measured via thermal imaging ranging from −2.7 °C to 6.3 °C. Field hematocrit values ranged from 0.20 to 0.65 (mean ± SD: 0.39 ± 0.09). In our linear model assessing factors influencing lizard body temperatures in the field, only hematocrit influenced body temperature, by which lizards with lower hematocrit selected lower body temperatures. These results were qualitatively the same when body temperature was measured with the cloacal probe (Table 1). Because hematocrit was measured on only a subset of animals ($N = 36$), we also constructed models without the fixed effect of hematocrit and found no factors influencing lizard body temperature (Table S2).

3.2. Calibrating thermal camera results

To address the differences in observed body temperature between the thermal camera and cloacal probe (Fig. 2A), a calibration experiment was conducted. The resulting linear regression model (Fig. 2B) showed a strong correlation between the body temperatures recorded by cloacal probe and thermal camera ($R^2 = 0.71$, $P = < 0.0001$, slope estimate ± SE: 0.88 ± 0.05; Fig. 2B) however, there was a significant difference between measurements taken from thermal camera and probe (paired *t*-test: $t_{124} = 12.27$, $P < 0.0001$). To rectify this discrepancy, we used these results (Fig. 2B) to calculate a correction equation for the experiment data recorded via thermal camera (**Eq. (1)**).

Table 1

Results of linear models testing the effect of intrinsic and extrinsic factors on field body temperatures of adult common wall lizards (*P. muralis*) measured with cloaca probe and thermography. See text for statistical details. Significant effects in bold and indicated by one asterisk ($P < 0.05$).

Source of Variation	T_b Probe	T_b Thermography
Sex		
Estimate (± SE)	−7.11 ± 10.32	−19.63 ± 13.83
F (df_n, df_d)	0.47 (5, 30)	2.02 (5, 30)
Pr > F	0.50	0.17
Snout Vent Length		
Estimate (± SE)	−0.14 ± 0.11	−0.12 ± 0.15
F (df_n, df_d)	1.46 (5, 30)	0.58 (5, 30)
Pr > F	0.24	0.45
Average Wind Speed		
Estimate (± SE)	−1.09 ± 0.58	0.014 ± 0.78
F (df_n, df_d)	3.53 (5, 30)	0.0003 (5, 30)
Pr > F	0.070	0.99
Hematocrit		
Estimate (± SE)	11.16 ± 4.96	14.90 ± 6.65
F (df_n, df_d)	**5.06 (5, 30)**	**5.02 (5, 30)**
Pr > F	**0.032***	**0.033***
Sex x SVL		
Estimate (± SE)	0.12 ± 0.17	0.33 ± 0.23
F (df_n, df_d)	0.50 (5, 30)	2.21 (5, 30)
Pr > F	0.48	0.15

$$T_{corr} = (T_{image} - 5.43442) / 0.87580 \quad (1)$$

Eq. (1): Where T_{image} is the temperature recorded with the thermal imaging camera, and the T_{corr} is the body temperature after correction.

3.3. Thermoregulation experiment

3.3.1. Thermoregulation and water loss

After accounting for wind treatment, the only repeatable trait was T_{pref} (Table 2). Lizards selected higher temperatures when exposed to wind, as demonstrated by higher values for T_{pref}, Upper T_{sel}, and VT_{max}, as well as a trend in Lower T_{sel}. (Fig. 3, Table 2). We did not observe differences in our measures of hydration status (hematocrit or mass change) between the treatments (Fig. 3, Table 2).

3.3.2. Thermoregulatory movement patterns

Our analysis of lizard movements demonstrated that temperature played a crucial role in determining what zones of the thermal gradient they selected, as well as differences in movement patterns between

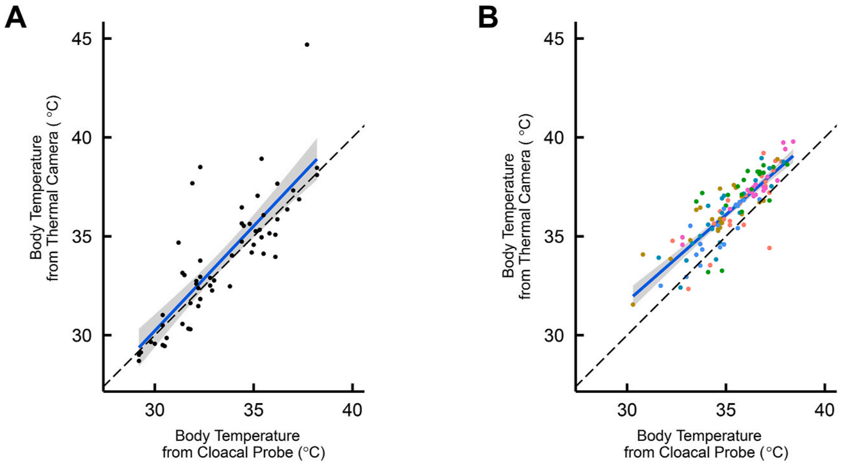

Fig. 2. Scatterplots and linear regressions of adult common wall lizard (*Podarcis muralis*) body temperatures measured via thermography and cloacal probe. Dashed black line indicates 1:1 correspondence. (A) Body temperatures collected from *P. muralis* in the field, (B) Body temperature collected from *P. muralis* during the calibration experiment.

Table 2

Results of paired *t*-test and constancy repeatability analyses of thermoregulatory behaviors and physiological measures in adult male common wall lizards (*Podarcis muralis*). Significant results in bold and indicated by one ($P < 0.05$) or two ($P < 0.001$) asterisks. See text for statistical details.

Variable	Repeatability results		Paired *t*-test results			
	R_c (95% CI)	*P* (LRT)	Mean ± SD (°C) Wind	Mean ± SD (°C) No wind	t-statistic$_{df}$	*P*
Upper T_{sel} Limit (°C)	0.430 0–0.804	0.0585	38.49 ± 0.49	37.62 ± 0.53	**−5.59$_{11}$**	**0.00016****
T_{pref} (°C)	**0.537** **0.019–0.857**	**0.022***	37.37 ± 0.60	36.61 ± 0.59	**−4.60$_{11}$**	**0.00077****
Lower T_{sel} Limit (°C)	0.353 0–0.792	0.103	36.12 ± 0.83	35.57 ± 0.74	−2.15$_{11}$	0.055
VT_{max} (°C)	0.353 0–0.772	0.103	41.30 ± 0.63	40.45 ± 1.38	**−2.42$_{11}$**	**0.034***
VT_{min} (°C)	0.209 0–0.707	0.232	29.54 ± 2.69	27.94 ± 4.54	−1.18$_{11}$	0.26
Hematocrit	0.00 0–0.563	0.50	0.40 ± 0.04	0.41 ± 0.05	0.31$_{11}$	0.76
Mass change (%)	0.00 0–0.532	>0.99	−1.50 ± 0.52	−1.29 ± 0.74	0.71$_{11}$	0.49

df = degrees of freedom; R_c = Constancy Repeatability; LRT = Likelihood ratio test.

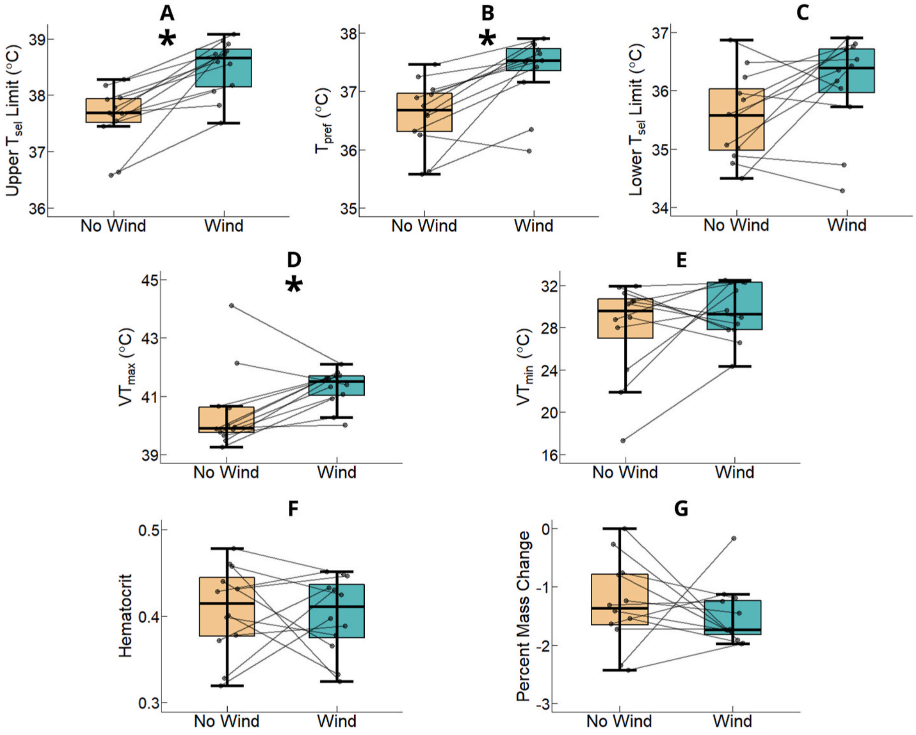

Fig. 3. Boxplots showing thermoregulatory behaviors and physiological measures in adult male common wall lizards (*Podarcis muralis*) under conditions of wind and no wind. (A) Upper limit of selected temperature (Upper T_{sel} Limit), (B) Preferred body temperature (T_{pref}), (C) Lower limit of selected temperature (Lower T_{sel} Limit), (D) Voluntary thermal maximum (VT_{max}), (E) Voluntary thermal minimum (VT_{min}), (F) Hematocrit, (G) Percent mass change. Lines connect values from same individuals. Significant difference between treatments is indicated by one asterisk ($P < 0.05$).

lizards in the wind and no wind treatments. Fig. 4 displays the marginal stationary distributions as a function of temperature and treatment to show the expected percentage of time the lizards spent in the five zones across different temperatures and treatment effects. Lizards in the wind treatment at body temperatures above approximately 36 °C would spend nearly all of their time in Zone 5, the warmest zone. Below this temperature, the lizards could be in any of the other four zones, while at temperatures below 30 °C the lizards were likely to be in Zones 3 or 4. Zones 1 and 2, the coolest areas of the arena, were inhabited most often when the lizard temperatures were between approximately 32-36 °C. For the no wind treatment, we see slight shifts in the curves in Fig. 4. For example, in Zone 5, lizards in the no wind treatment would spend nearly all of their time at temperatures >38 °C, showing an approximate one-degree difference in how they selected the zone. Similar rightward shifts for lizards not experiencing wind are displayed for the other four zones. We note that precision of estimates is much higher at warmer temperatures, due to the fact that lizards spent more time at these temperatures and our models are therefore informed with more observations.

4. Discussion

As climate change continues and wind patterns change, ectotherms face the daunting task of maintaining homeostasis while balancing their energetic budgets. Our thermal gradient experiment found that adult common wall lizards (*P. muralis*) select higher temperatures under mild

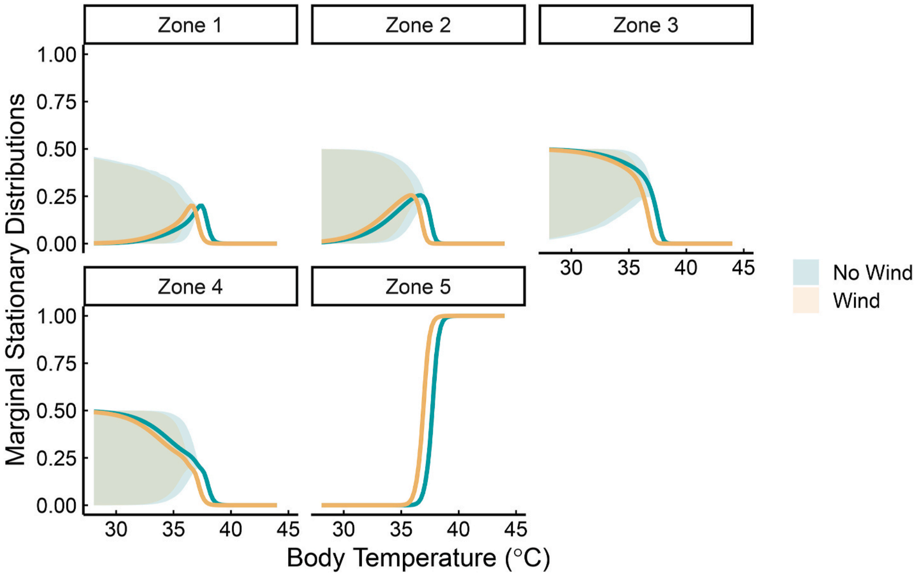

Fig. 4. Marginal stationary distributions from Markov chain models (see text for details) show the expected percentage of time the lizards remain in each zone when experiencing different body temperatures under different wind treatments. Lines correspond to the posterior mean for each treatment group. Pointwise 95% credible intervals are displayed for each group as shaded confidence bands; note that lizards spent less time at cooler temperatures so the models are informed with less data, resulting in wider confidence bands at cool temperatures.

wind conditions. This is opposite to our prediction that the lizards would select a lower body temperature in order to balance thermoregulatory behavior and hydration status (Rozen-Rechels et al., 2019; Virens and Cree, 2022). Despite selecting the higher temperatures (including higher preferred temperature, upper limit of selected temperatures, and voluntary thermal maximum), there was no difference in lizard hydration status between the treatments, as measured by change in body mass and hematocrit (Table 2 & Fig. 3). The observed changes in selected body temperatures were mirrored by changes in behavioral patterns. Between the wind treatments, both the distribution and body temperature of lizards shifted across zones (Fig. 4). Furthermore, our analysis of selected body temperatures in the field found no effect of wind speed on lizard body temperature. We did identify a significant positive relationship between hematocrit and field body temperature, suggesting that lizards at higher temperatures may be suffering from reduced hydration status. This result, combined with the results of our lab experiment, suggests that lizards selecting higher temperatures suffer from increased water loss. Nonetheless, it does not appear that hydration status (at least within the range we observed, likely well within the allostatic range), affects the selection of body temperatures in the lab or field.

The observed shifts in selected temperatures of lizards in a thermal gradient are counter to both our predictions and the only other study we know of that tested the effect of wind on lizard thermoregulation. McCann's skinks (*Oligosoma maccanni*) lowered body temperatures in wind, presumably in anticipation of potential water loss (Virens and Cree, 2022). Wall lizards might be exhibiting a sort of converse mechanism here, whereby they select higher body temperatures in anticipation of evaporative cooling via wind. This trend may become more apparent at higher wind speeds. For example, Logan et al. (2014) found that *Anolis* lizards reduce activity in wind speeds above 0.5 m s^{-1}. Angilletta et al. (2019) discussed a type of 'neural thermostat' whereby there is a coordination of movement between microclimates to remain within an individual's thermal preference. As wind gives sensory input to lizards, this could explain how they are able to 'anticipate' wind effects and adjust accordingly (Angilletta et al., 2019). In the context of our experiment, lizards experienced a mild wind treatment of 0.4 m s^{-1} (characterized as 'light air' on the Beaufort scale), which did not effect change in body mass or hematocrit values over the 2-h duration of the experiment (Table 2, Fig. 3). We speculate that this level of wind is high enough to be detectable by the lizard and induce behavioral shifts in thermoregulation, but not strong enough that it renders discernible effects on water loss over these time scales.

Because thermoregulation is an essential component of activity and energy budgets (Brewster et al., 2021; Huey and Slatkin, 1976), the fact that wind forces lizards to adjust said budgets can have long term consequences. However, this effect on energy and activity budgets could be beneficial if wind is used as a thermoregulatory tool. In our study, this is demonstrated by changes in thermoregulatory movement patterns between conditions of wind and no wind, whereby lizards exposed to wind were more likely to be found in the hottest zones with a lower body temperature. Lizards in the wind treatment were more likely to be in the outer zones (1, 2, and 5) at lower body temperatures. However, lizards in the no wind treatment were more likely to be in the intermediary zones (3 and 4) at lower body temperatures (Fig. 4). One possible explanation for this result was the position of the zones (Fig. 1)-wind-treated lizards were more willing to explore the slightly more extreme areas of the gradient at lower temperatures compared to their no-wind counterparts. Without this wind presence, lizards at lower body temperatures were more likely to be in the middle of the gradient (Figs. 1 and 4). Another behavioral pattern of note can be seen in zone 5 (Fig. 4), where lizards under non-windy conditions had higher body temperatures. This suggests that the presence of wind may offset thermoregulatory pressures to some degree, allowing lizards to explore the warmest zone without risk of overheating. It is also possible that lizards change other aspects of behavior that we did not measure, such as posture and limb position, to mitigate potential water loss in relation to radiation exposure (Bauwens et al., 1996; Brewster and Beaupre, 2019). While experimental tests of the use of wind to thermoregulate are rare, some field observations demonstrate that lizards may use wind to more effectively thermoregulate (Gontijo et al., 2018; Ortega et al., 2017). For example, a recent study using thermography found a positive trend between wind speed and field body temperatures of a frog and two lizard species (Blais et al., 2023). Further field observations and lab experiments are needed to test the hypothesis that lizards may be able to effectively use wind to their advantage in thermoregulating, anticipating that it will be easier to cool if needed. Future studies on this topic should seek to answer the paradoxical question: are lizards selecting hotter temperatures to balance hydration, or is the hydration status changing to account for high body temperature? Such work complements the broader program of understanding how abiotic factors other than temperature may affect thermoregulatory behaviors, as in recent work demonstrating the importance of UV exposure in basking behaviors (Conley and Lattanzio, 2022).

The results of our lab experiments and field study further validate the use of infrared thermography in studying the thermal biology of small diurnal lizard species. We found a strong correlation between body temperatures measured via thermography and the traditional method of inserting a thermocouple probe in the cloaca immediately after capture. However, despite the strong correlation between these methods, there is a significant difference in the measurements taken. The body temperature recorded by the thermal camera is slightly above that measured via cloacal probe (Fig. 2B), and 3 outliers were identified in our field body temperature data (Fig. 2A). With all three outliers, the body temperature estimated from thermal imaging was much higher than that measured by cloacal probe (up to 6.3 °C above the value predicted by the line of best fit, Fig. 2A). This is likely due to finding lizards at the onset of basking; as skin surface temperatures (measured by infrared thermography) will rise very quickly in the sun, while it will take a short amount of time for core body temperature (measured by cloacal probe) to equilibrate. But even when these outliers were included, the results of models testing factors that affect field body temperatures did not differ qualitatively between measurement methods. Furthermore, this difference can be resolved by conducting a preliminary study and calculating a correction factor (via the slope of a linear regression) to determine the correct body temperature measure (Fig. 2B; Eq. (1)).

Despite the preliminary work involved, the use of thermal cameras in biological research has created new methodological opportunities. In measuring body temperatures, infrared thermography offers several advantages over the traditional "grab-and-jab" methods, including the ability to characterize the thermal properties surrounding microhabitats (Goller et al., 2014), the ability to conduct surveys on animals without the need to catch or disturb them (Barroso et al., 2016), and the ability to measure temperatures on different parts of the body (Hodges, 2018; Luna and Font, 2013; Sannolo et al., 2014). These studies, along with our own, provide evidence of the benefits and limitations of infrared thermography as a data collection tool. Our study concludes that while there is an initial disconnect in the measurements reported by thermal cameras compared to cloacal probes, this disconnect can be resolved with preliminary work, and once corrected, can offer invaluable and innovative methodological opportunities in future thermal biological research.

Our results point to interesting shifts in thermal preferences within species, especially in the context of expanding geographical ranges and establishment in novel habitats. For example, previous work with *P. muralis* has identified variation in thermal preferences along an elevational gradient (Trochet et al., 2018) and variation in thermal tolerances among populations in the original species range (Bodensteiner et al., 2021b; Herrando-Pérez et al., 2020). We recorded substantially higher thermal preferences from lizards in their introduced range (mean of 36.6 °C without wind; Table 2) compared with those recorded from populations in Europe (34.2 °C from western and southwestern Europe, Bauwens et al., 1996; 32.6 °C from Greece, Sagonas et al., 2017; 32.9 °C from France, Trochet et al., 2018; and 32.8 °C from France, Bodensteiner et al., 2021b). This shift in preferred body temperature may be accompanied by other aspects of thermal biology, such as critical thermal limits, and could facilitate successful establishment (Litmer and Murray, 2019). These changes in important aspects of the organism's thermal biology can be attributed to evolutionary or plastic responses to urbanized habitat in the US (Campbell-Staton et al., 2020), or simply drift due to limited genetic variation of the small founding population (Davis et al., 2021; Homan, 2013; Lescano et al., 2021). Despite this change in thermal preferences under unconstrained laboratory conditions, our measures of field body temperature (mean of 33.8 °C by thermal camera; mean of 33.4 °C by probe) is only moderately higher than values from the native range (31.3 °C, Sagonas et al., 2017; 32.5 °C, Bodensteiner et al., 2021b). Consistently lower values for field body temperatures compared to thermal preferences measured in the laboratory across studies suggest that unmeasured constraints may be limiting thermoregulatory patterns in the field, for example wind or water availability. This can be especially useful to understand in the context of a recently-established urban population. Such a constraint is suggested by our result that selected body temperatures were positively correlated with hematocrit in the field. Future work can be directed toward uncovering the causality behind this relationship, especially given that hematocrit can vary with other aspects of physiology beyond hydration (Puerta et al., 1996). More direct methods of inferring hydration status, such as blood osmolality (Dupoué et al., 2018; Moeller et al., 2017; Weaver et al., 2023), may better indicate hydration status and may thus reveal more subtle shifts in thermoregulatory behaviors. For example, lower osmolality was associated with reduced activity in Gila monsters (*Heloderma suspectum*; Davis and DeNardo, 2009) and shifts in microhabitat preferences in common lizards (*Zootoca vivipara*; Rozen-Rechels et al., 2020). Additionally, future studies investigating wind effects on thermoregulation should consider testing the impacts across a wider range of wind speeds, including those present in both current and predicted future environments.

5. Conclusions

In conclusion, we first confirm that infrared thermography is an effective and accurate method to collect data on body temperatures without interrupting animal activity in the field. Our first hypothesis, that body temperatures of lizards in the field would decrease as average wind speed increased, was not supported by our data. The only factor impacting body temperature was hematocrit, a measure of hydration status, suggesting that lizards at higher temperatures may be suffering from reduced hydration status. Our second hypothesis, that lizards would select lower body temperatures in a thermal gradient, was also unsupported. Instead, we found the opposite: *P. muralis* selected higher body temperatures in the presence of wind, possibly due to anticipation of evaporative cooling. Lizards in the wind condition altered their movement patterns between temperature zones as well, potentially in a way to optimize thermoregulatory behaviors. The precise nature of potential fitness consequences and trade-offs with other physiological parameters will need to be explored in future studies. The lack of support for our predictions and surprising results provides fascinating new avenues for future research, ones that will hopefully aid in our ongoing fight to understand how organisms will adapt to the new world climate change creates.

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CRediT authorship contribution statement

Sierra Spears: Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Ciara Pettit:** Writing – review & editing, Methodology, Investigation, Funding acquisition, Conceptualization. **Sophie Berkowitz:** Writing – review & editing, Validation, Methodology, Formal analysis, Conceptualization. **Simone Collier:** Writing – review & editing, Validation, Methodology, Formal analysis, Conceptualization. **Cece Colwell:** Writing – review & editing, Investigation. **Ethan H. Livingston:** Writing – review & editing, Investigation. **Wyatt McQueen:** Writing – review & editing, Investigation. **Princeton L. Vaughn:** Writing – review & editing, Investigation. **Brooke L. Bodensteiner:** Writing – review & editing, Validation, Investigation. **Vianey Leos-Barajas:** Writing – review & editing, Visualization, Validation, Supervision, Project administration, Methodology, Investigation, Formal analysis, Conceptualization. **Eric J. Gangloff:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Project administration, Methodology, Investigation, Formal analysis, Conceptualization.

Declaration of competing interest

The authors declare no competing interests.

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Appendix A. Supplementary data

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