Thermal Ecology of Spiny-tailed Lizard and its Vulnerability to Climate Warming

Dissertation submitted to the
Saurashtra University Rajkot, Gujarat

In partial fulfillment of
Master's Degree in Wildlife Science

By
Avichal Tatu

Under the Supervison of

Dr. Sutirtha Dutta
Dr. Maria Thaker
Dr. Abhijit Das

भारतीय वन्यजीव संस्थान
Wildlife Institute of India

July, 2021

Acknowledgements

I have quite a few people to thank for supporting me throughout my dissertation journey. Firstly, I thank Dr. Sutirtha for giving me the freedom and support to explore my interests and ask challenging questions. Without his help, this study would not have been successful. Many thanks to Dr. Maria who gave me opportunities to expand my research in new directions and always gave her time when I needed it. Dr. Abhijit was present at all critical moments and offered timely help.

I am very thankful to the CAMPA-GIB project, LTEO Herpetofaunal Monitoring Project and UGC Indo-Israel Grant for funding this study.

Without Aradeen, this study would not have taken the shape it did. His help in the field was irreplaceable. I thank all CAMPA-GIB team members for making my field days a memorable experience. Stimulating discussions with Joshua and Varun brought a lot of clarity to my ideas.

Many thanks to Director, WII and Dean, WII for all the logistic support. Furthermore, I thank Dr. Samrat and Dr. Navendu for facilitating the course throughout. I am very thankful to the Rajasthan Forest Department for permissions and logistic support.

In the end, I would like to thank my friends and family, for supporting me from a distance, as this journey has taken me far from my home. To my parents, Ketan and Amita, I owe my love of science and my stubbornness to continue when I felt defeated.

Summary

Lizards and other ectotherms survive within their thermal limits and have a well-defined range of body temperatures within which their performance is optimal. Hence, as climate warming accelerates, ectotherms like lizards become increasingly constrained. *Saara hardwickii* survives in areas where environmental temperatures are already extreme. Therefore, they may be at the risk of extinction due to rising temperatures. In the field, we collected data on field body temperatures and opertative temperatures to evaluate and quantify the degree of thermoregulation observed in the lizard and to evaluate changes in activity pattern over months, In the laboratory, we quantified preferred temperature, thermal thresholds and locotmotor of the lizard. Using a combination of field and laboratory data, we described how *S. hardwickii* uses burrows to thermoregulate and evaluated how climate warming will impact locomotor performance and hours of activity in the future. We found that burrows provide an exceptional buffer to the lizards as the temperatures deep inside (~1 m) do not exceed the preferred temperature of the lizard, even in the worst-case climate change scenario (RCP 8.5). Currently, the lizards are restricted to their burrows for six hours during their active period. According to our model, by 2100, the lizards might get restricted to their burrows for 7 hours in the best-case scenario, and for 9 hours in worst-case scenario. Our model suggested decrease in locomotor performance by 2.1%, 9.5% and 28.3% in the best- (RCP 2.6), intermediate- (RCP 4.5), and worst- (RCP 8.5) case scenarios by 2100. Hence, the synergistic effect of loss of activity hours and decline in locomotor performance might result in decreased fitness of *S. hardwickii*, potentially leading to its extirpation.

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1. INTRODUCTION

Lizards and other ectotherms survive within their thermal thresholds and have a well-defined range of temperatures within which their performance is optimal (Bogert, 1949; R. Huey, 1988). Therefore, it is predicted that increasing environmental temperatures might have both direct (mortalities due to environmental temperatures exceeding thermal limits) and indirect impacts (increase in activity constriction (Deutsch et al., 2008; Huey et al., 2010; Sinervo et al., 2010). These effects will be more pronounced in lizards surviving in thermally extreme areas like deserts where thermal buffers like vegetation is scant and where lizards are already thermally constrained (Grant & Dunham, 1988). A common retreat site in deserts, where vegetation is limited, are burrows, which provide lizards thermal relief and aid them in predator evasion (Pianka, 1986). A lot of predictive models focus on broad-scale predictions that might lead to extinction (Huey et al., 2010; Sinervo et al., 2010) without taking into account intricacies like the use of refuge, thermal variability between different microhabitats, and the capacity to thermoregulate (Briscoe et al., 2016; Moore et al., 2018). Using activity restriction as a predictor, Sinervo et al., (2010) predicted that up to 20% of lizard species globally could go completely extinct and 39% of lizard species could go locally extinct by 2080. It is still unclear whether thermoconforming species or thermoregulating species will fare worse. This research created a new paradigm wherein restictions to lizard's activity period was considered when body temperatures are elevated above its thermal threshold, critical thermal maxima (CTmax).

In this study, we aim to understand how diurnal lizards existing in areas with extremely hot temperatures and low thermal heterogeneity thermoregulate and how rising temperatures might impact their activity patterns and fitness by investigating the thermal ecology of *Saara hardwickii*. *Saara hardwickii* is a diurnal and herbivorous lizard dwelling in arid and semi-arid areas of India, Pakistan, and Afghanistan. It is protected as a Schedule II species under the Indian Wildlife (Protection) Act, 1972. We chose this species because its density in one of the hottest parts of India is high (Ramesh & Ishwar, 2008). This species is adapted to extreme temperatures (Dutta & Jhala, 2007). Still, as ectotherms in deserts are already thermally constrained, we investigated the impact of global warming on the thermal ecology of this desert ectotherm. In addition to thermal constraints, this species faces severe poaching and habitat loss due to cropland expansion (Dutta & Jhala, 2014).

We focused on the thermal ecology of the species from the coolest (March) to the hottest month (May) within their active season with the goals of (1) evaluating and quantifying the degree of thermoregulation observed in the lizard (2) evaluating changes in activity pattern over months, (3) describing how *S. hardwickii* uses burrows to thermoregulate, (4) quantifying the locomotor performance curve of the lizard, (5) evaluating how climate warming will impact locomotor performance, (6) quantifying the number of hours for which the lizards are currently restricted to burrows due to extreme temperatures and (7) projecting how climate warming might impact these values.

2. GLOSSARY

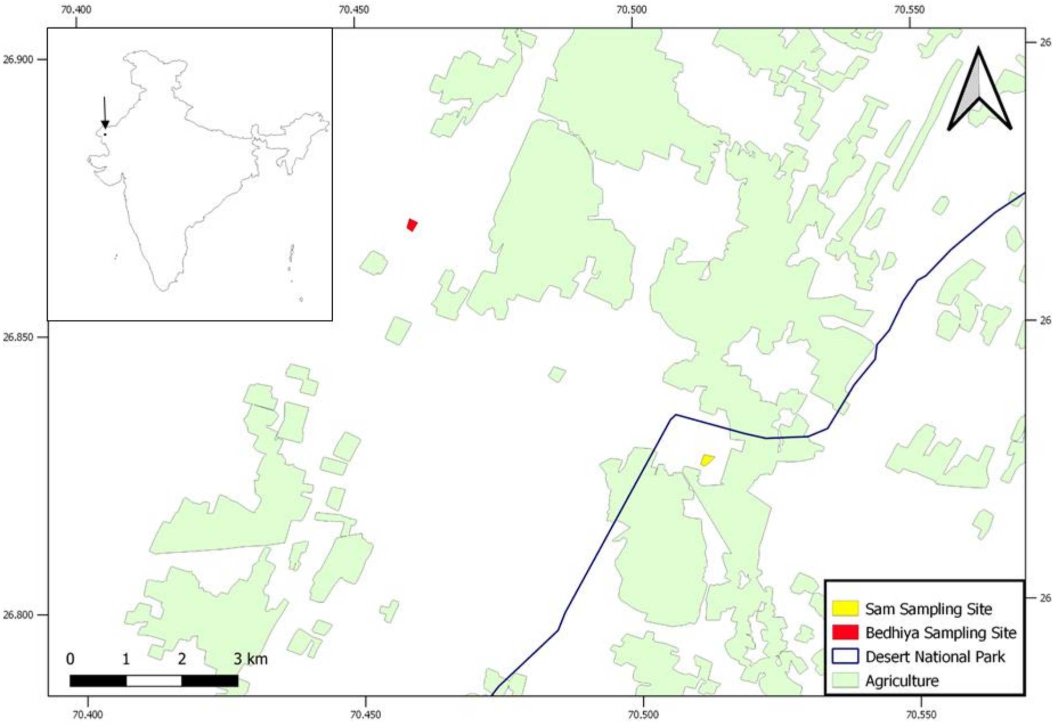
Abbreviation	Term	Explanation
T_b	Body temperature	The temperature of lizard's body
T_e	Operative temperature	Temperatures that a non-thermoregulating lizard attains based on conduction, radiation and convection often measured using copper models
T_{set}	Preferred temperature	Range of T_b selected/preferred by the lizard
VT_{max}	Voluntary maximum temperature	The upper T_b at which the lizard retreats to its refugia to prevent further heating
VT_{min}	Voluntary minimum temperature	The lower T_b at which the lizard retreats to its refugia to prevent further cooling
CT_{max}	Critical thermal maxima	The upper T_b at which onset of spasms is observed which indicates the loss of function in lizards
CT_{min}	Critical thermal minima	The lower T_b at which loss of righting response is observed which indicates the loss of function in lizards
B_{95}	95% Thermal performance breath	The range of T_b at which the performance is greater than or equal to 95% of V_{max}
B_{80}	80% Thermal performance breath	The range of T_b at which the performance is greater than or equal to 80% of V_{max}
T_{opt}	Optimum Temperature	The temperature at which maximum speed of the lizard is observed
TBAE	Temperature-Based Activity estimation	An IF-THEN-ELSE algorithm to predict the activity state of the lizard using absolute differences between T_e and T_b

3. STUDY AREA

The study was conducted in the Thar desert of Jaisalmer district in Rajasthan, India. We conducted all sampling at two sites (Map 1) in the Thar landscape for our study – Sam (26°49'32.5"N 70° 30' 42.3") and Bedhiya (26°52'07.3"N 70°27'36.6"E) near Desert National Park Wildlife Sanctuary. This area is characterized by extremely harsh, arid summers with air temperatures reaching up to 50˚C and cold winters with temperatures dropping as low as 0 ˚C. Rainfall in this area is erratic and usually ranges between 100 and 350 mm.

The ground vegetation in these sampling sites was characterized by *Dactyloctenium sp.* grasses interspersed with the invasive shrub *Dipterigyium glaucum* in Sam site, and *Dactyloctenium sp.* grasses under *Zizypus nummularia* trees in Bedhiya site. Common mammalian fauna seen in these sites include *Vulpes pusilla, Felis sylvestris ornata, Gazella bennettii* and *Sus scrofa.* Other than *S. hardwickii,* herpetofauna in these sites included *Varanus griesius, Echis carinatus sochureki, Acanthodactylus cantoris, Eryx johnii, Trapelus agilis,* and *Crossobamon orientalis*

Both Sam and Bedhiya were highly grazed by cattle and both had high burrow densities of *S. hardwickii* burrow densities, at 62 burrows/ha and 56 burrows/ha respectively, calculated using 20 100m * 5m belt transects in 100 ha plots. Bedhiya had higher thermal heterogeneity as it had shaded areas but during the reconnaissance observation of the lizards, it was established that the lizards avoid shade. Soil compaction was equally high in both areas (measured using a soil penetrometer), and the average grass height was less than 4 cm.



Map 1: Map of study area in Jaisalmer district of Rajasthan, India. The map depicts the unsuitable areas for S. hardwickii since it is not found in agricultural areas (Dutta and Jhala, 2007)

4. MATERIALS AND METHODS

This study was aimed at understanding the thermophysiology of the Spiny-tailed Lizard and its vulnerability to climate warming. To explore this, a combination of field data and mechanistic data was collected using both field and laboratory methods (Fig. 1). This data was analyzed to construct various climate models. The study was carried out between March and June 2021.

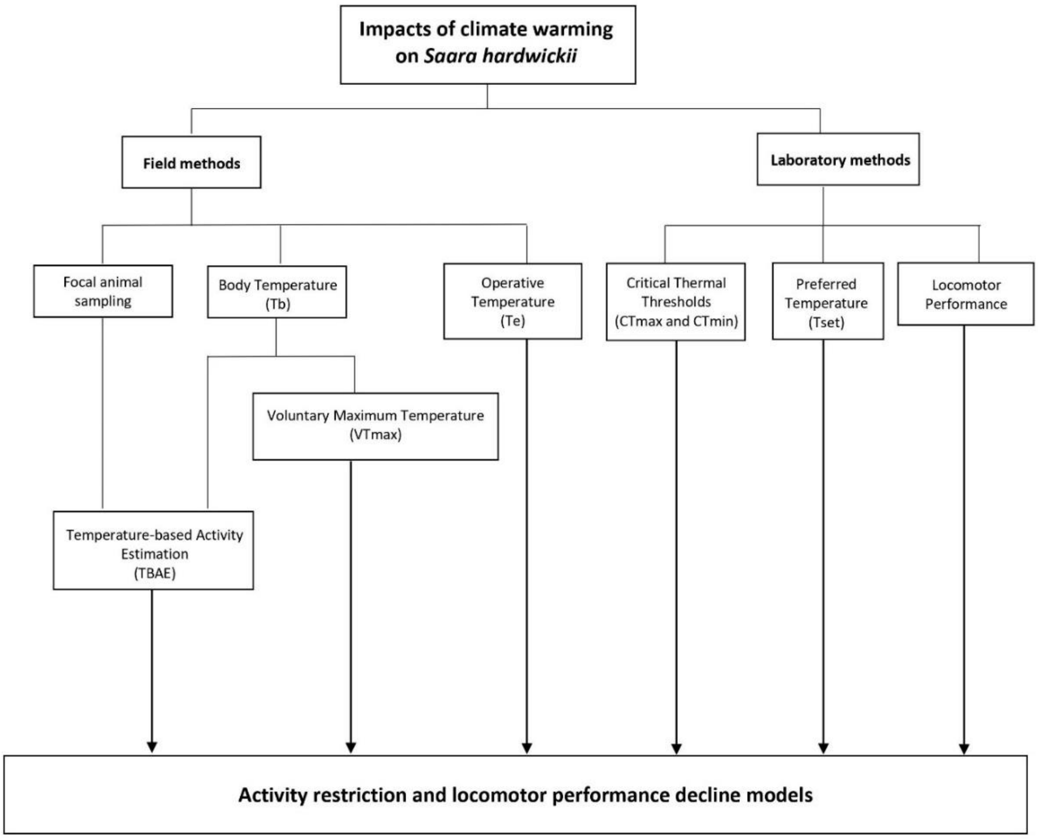


Figure 1: Flowchart depicting how both empirical and mechanistic data were used to construct activity restriction models.

4.1 Field Methods

4.1.1 Field Active Body Temperature (T_b)

Lizards (N = 25) were captured by noose near their burrows and marked using a nontoxic felt-tip permanent marker (Johnson, 2005). Their mass (Pesola® 500g precision scale, ± 0.5g), snout-vent length (SVL, ± 0.1 cm), sex, and gravidity (using abdominal palpations) were recorded. Lizard skin temperature was measured at 15-minute intervals using tiny temperature data-loggers (Maxim Thermochron iButton DS1921G; accuracy ±0.5°C) that were stitched into a breathable cotton harness such that only the sensing surface of the logger was exposed. These harnesses were attached to lizards such that the sensing surface of the logger touched the lizards' skin (Fig. 2). The combined weight of the logger and the harness was <6g (<5% of lizard body weight), and allowed free movements of lizards.

Lizard skin temperature (Tb) was used as a proxy for core temperature. Three lizards of different size classes were first used to validate this surrogacy approach. Their skin temperatures were measured using harnessed data-loggers as described above. Their cloacal temperatures (core temperatures) were measured using a k-type thermocouple, connected to a temperature logger (Amprobe model TMD-50). Data for both loggers was recorded at five-minute intervals. Skin temperature was always within ±1°C of the cloacal temperature and the relationship between the two was very strong ($R^2 = 0.985$, $F_{254} = 2381$, $P<0.001$).

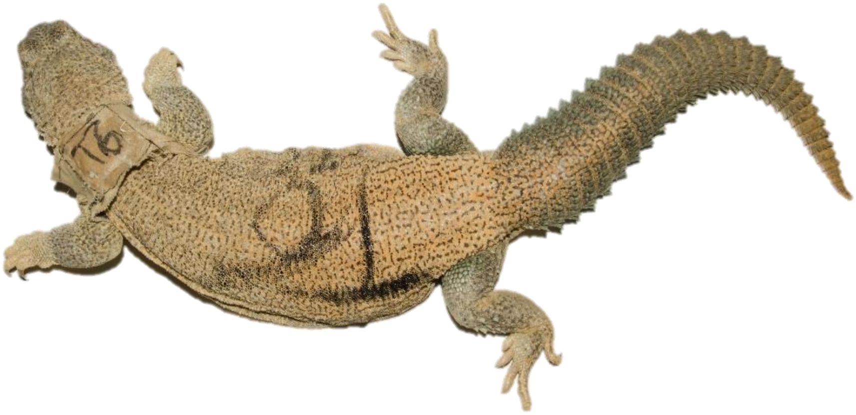


Figure 2: Photograph of a marked and tagged individual

4.1.2 Focal animal sampling

Marked/tagged lizards were observed from a hide using binoculars from 0700 to 1900 for 10 days spread over a month. Each day one tagged lizard was selected haphazardly. Activity and microhabitat of marked lizards were continuously recorded until it was out-of-sight following the focal animal sampling method (Altmann, 1974). The microhabitats recorded were: “burrow”, “burrow entrance” and “open”. If the lizard was in “open”, their activity states were recorded as: “basking”, “foraging” and “intraspecific interaction”. Duration of each activity state was recorded.

4.1.3 Operative temperatures (T_e)

Biophysical models made of copper were used to measure temperatures of microhabitats that the lizards would experience bereft of behavioural thermoregulation (Bakken, 1992; Bakken & Angilletta Jr, 2014). Copper models of two different sizes (400×35 mm and 250×25 mm) were used to represent adult and sub-adult lizards. Temperature loggers (Maxim Thermochron iButton DS1923; accuracy ±0.5°C) were positioned in the middle of the pipe using a plastic ring and recorded operative temperature (Te) every 15 minutes.

Three major microhabitats (open, burrow and burrow entrance) used by the lizards in the Thar landscape were sampled, and models were positioned in ways to imitate the posture of lizards in these microhabitats. Posture influences heating rates from radiation and conduction (Muth, 1977). In (1) Open habitats, full-body copper models (body + legs) were positioned in direct sunlight. For (2) burrow entrance, 3/4th of the copper model (body + legs) was positioned inside an inactive burrow and (3) within burrow, the copper model (body only) was placed ~1m inside an inactive burrow of *S. hardwickii*. Copper model temperatures were calibrated by comparing them with cloacal and skin temperatures of three size classes under different temperatures generated using a 150W infrared lamp.

4.2 Laboratory methods

Lizards (N = 20) with size range 14.5 to 24.2 cm SVL were captured and housed within individual terraria with a 150W heating lamp, artificially constructed refugia, and *ad libitum* access to food (*Dactyloctenium aegyptium*). Experiments were carried out in a cool room between 0800 to 1900 after acclimatization for 24 hours. On the first day, T_{set} experiment was performed with two running trials separated by a minimum of 4 hours of recovery (Angilletta et al., 2002). Next day, two running trials were conducted and CT_{min} was measured. On the last day, one running trial was performed, and CT_{max} was measured in the end. Thereafter, lizards were released near their respective burrows.

4.2.1 Preferred Body Temperature (T_{set})

Each lizard was introduced into a wooden frame (300×25×25 cm) with sand substrate, and a 150W infrared lamp at one end, creating a temperature gradient from 25°C to 52°C. Each lizard was allowed to acclimatize for two hours, after which, body (cloacal) temperatures were recorded every 5 minutes for an hour.

4.2.2 Critical thermal maxima (CT_{max}) and minima (CT_{min})

We used behavioural indicators of muscle performance limits, to measure CT_{max} and CT_{min} of the lizard. CT_{max} was the body temperature at which onset of muscle spasms (OS) was observed and CT_{min} was the body temperature at which loss of righting response (ability to turn over when placed on its back) was observed (Cowles & Bogert, 1944; Lutterschmidt & Hutchison, 1997a, 1997b).

For the experiment to measure CT_{max}, each lizard was placed in a metal container with a 150W infrared lamp 40 cm above it that ensured heating rate of 1°C/min. In each trial, cloacal temperatures, behaviour, and body temperature were constantly monitored. CT_{max} was recorded as the cloacal temperature at which OS was observed. Once lizards reached $CT_{max,}$ they were immediately removed from the container and transferred to a pre-cooled chamber to assist in lowering their body temperature.

For evaluating CT_{min}, each lizard was placed in a terrarium and its temperature was reduced until the lizard could right itself (Labra & Bozinovic, 2002; Laspiur et al., 2021). Then, the lizard was placed in room temperature and was flipped on its back every 15 seconds until it could right itself. The body temperature of the last flip when the lizard was unable to right itself was considered as the $CT_{min.}$ No lizard suffered mortality during these experiments, and all resumed normal activity (movement and feeding) within 2-5 hours after these experiments.

44.2.3 Locomotor performance

Locomotor performance for each lizard was measured at four body temperatures between 25-45°C with approximately 4°C intervals. A 150W infrared lamp at different heights over a metal container was used to increase the body of lizards above the room temperature, and a water bath with icepacks was used to reduce body temperature of lizards below room temperature. Each lizard was kept at the selected temperature for 1 hour before introducing them to a racetrack (250×25×25 cm). The racetrack was made of a wooden frame lined with 260-grit sandpaper to emulate the most common natural substrate - fine gravel plain (Ramesh & Ishwar, 2008). Each lizard was made to run two sprint trials per day separated by >4 hours. The trial consisted of five consecutive 0.5m runs, with a single initial stimulus (touching their rear thigh with a finger). This was repeated three times separated by five-minute rest. Nikon D7000 with Tokina 11-16mm was used to record all trials at 25 frames per second. The fastest run was used for the analysis.

4.3 Analytical methods

4.3.1 Body temperature

Field T_b data were checked manually for aberrant readings, which were removed. Linear Mixed Models (LMMs) and Linear models (LMs) were used to evaluate the degree of behavioural thermal regulation of the lizard. Field T_b (response variable) was modelled on open T_e, Body Condition Index (BCI), sex, SVL and site as fixed effects and individual identity as random intercept (Hertz et al., 1993). Variability in mass across lizards was incorporated into the BCI calculation:

$$\mathrm{BCI} = \mathrm{M_i} \times [(\mathrm{SVL_0})/(\mathrm{SVL_i})]^{\mathrm{b_{sma}}}$$

Where $\mathrm{M_i}$ and $\mathrm{SVL_i}$ are the mass and SVL of the individual respectively, $\mathrm{SVL_0}$ is the mean SVL of the population, and $\mathrm{b_{sma}}$ is the standardized major axis slope from the regression of natural log of mass on natural log of SVL for the population (Cecchetto et al., 2020; Peig & Green, 2009). Field Voluntary Maximum T_b (VT_{max}) was calculated as the average maximum daily T_b (Ivey et al., 2020).

4.3.2 Temperature-Based Activity Estimation (TBAE)

A dataset was compiled from dates, times, individual identification and activity state of tagged animals observed using focal animal sampling. We considered this as the test dataset. Plots with open T_e, burrow T_e and T_b were used to classify activity states of lizards using empirical rules: 1) steeper positive T_b slope compared to open T_e slope – “active”; 2) negative T_b slope when open T_e slope is positive – “inactive” and 3) all readings from 20:00 to 07:00 – “inactive”. These states were added to the test dataset. An IF-THEN-ELSE algorithm was created in R to assign activity states based on absolute differences between operative temperatures and T_b (Moore et al., 2018). Daily activity budgets were constructed for 20 lizards. The accuracy of the estimated activity budgets was assessed using Cohen’s Kappa test for agreement to assess the predictability of the relationship between estimated and observed activity (J. Davis et al., 2008). Mean hours of restriction (H_r) for current temperatures were quantified using this data.

4.3.3 Operative temperatures

GLMs were used to determine whether there were any differences between adult and juvenile models.

4.3.4 Preferred temperature (T_{set})

T_{set} was considered as the 25-75% interquartile range of the cloacal temperatures of the last hour of the 3-hour trial (Ivey et al., 2020). GLMs were used to examine the effects of BCI, sex and site on median T_{set}.

4.3.5 Critical thermal maxima (CT_{max}) and minima (CT_{min})

GLMs were used to examine the effects of BCI, sex and site on mean CT_{max} and mean CT_{min}.

4.3.5 Locomotor performance

All videos were analyzed in Avidemux 2.7.8. Optimum temperature (T_{opt}) was considered to be the T_b at which the lizard's speed was maximum (V_{max}). Performance breath (B_{80} and B_{95}) is the range of T_b at which the performance is greater than or equal to 80% and 95% of V_{max} respectively, was calculated (Hertz et al., 1993).

To calculate these variables, Generalized Additive Mixed Models (GAMMs) were fitted to the non-linear data using the package 'mgcv' in R 4.1.0 (R core team, 2020) where T_b, BCI, sex and site were considered as fixed effects and individuals were considered as a random effect.

4.3.6 Projecting the impact of climate warming

The projections were based on three scenarios: 1) RCP 2.6 where there would be an increase of 1.5°C by 2100 (+0.019°C /year); 2) RCP 4.5 where there would be an increase of 3°C by 2100 (+0.038°C /year) and 3) RCP 8.5 where there would be an increase of 5°C by 2100 (+0.063°C /year), which aligns with the projections for Jaisalmer based on CMIP6 (Almazroui et al., 2020). Impacts were projected vis-à-vis activity restriction and locomotor performance.

Activity restriction was projected using CT_{max}, VT_{max}, B_{95} and T_{set} as different thermal thresholds. H_r was projected for each threshold variable by adding projected increase in temperature to current biophysical model data unilaterally. It is likely that different microhabitats might have different rates of temperature increase but this model will provide a coarse estimate of how h_r might change with climate warming (Brusch et al., 2016). To project the locomotor performance, current performance set to 100% to evaluate the relative decrease in future (Neel et al., 2021).

5. Results

5.1 Study species

S. hardwickii is an obligate burrower that constructs and maintains a deep burrow. The average burrow length was 96 cm ± 7 cm. During our focal sampling from 0600 hrs to 2000 hrs, lizards never emerged before 0713 hrs and never emerged after 1943 hrs. Hence, we considered 0700 to 1900 the lizard's field active period. It was observed that the lizards used burrow entrances to defend territories and to passively forage. Morphological measurements were taken for 49 lizards (Table 1). There was a strong relationship between log-transformed SVL and log-transformed mass of *S. hardwickii* (β = 3.2, R^2 = 0.88, F_1 = 352.4, P<0.001; Fig. 3). There was no difference between sexes vis-à-vis log-transformed SVL (F_2 = 1.07, P = 0.35), log-transformed mass (F_2 =1.58, P = 0.21) and BCI (F_1 = 1.21, P = 0.3). Site had a significant but weak effect on log-transformed SVL (R^2 = 0.1, F_1 = 5.43 P = 0.02).

Table 1: **Morphological data of the 49 captured lizards.** Note that the lizard "ID" with E meant that the lizard was used for the experiments and others were used to measure field $T_{b.}$

ID	Mass	SVL	BCI	Sex	Site
TE1	360	24	170.48	Male	Sam
TE2	325	22.1	203.86	Male	Sam
TE3	215	19.6	203.04	Male	Sam
TE4	150	18	189.35	Male	Sam
TE5	125	16.9	195.62	Female	Sam
TE6	360	22	229.33	Female	Sam
TE7	90	16	169.72	Female	Sam
TE9	105	17	161.05	Male	Sam
TE11	140	19.2	141.83	Male	Sam

TE12	115	16	216.87	Female	Sam
TE13	175	19	183.73	Male	Sam
TE14	345	24.2	158.83	Male	Sam
TE15	105	16	198.01	Female	Sam
TE16	230	21.5	158.46	Female	Sam
TE17	300	21.5	206.69	Male	Sam
TE18	125	16.8	199.62	Male	Sam
TE19	325	23.2	172.76	Female	Sam
TE20	135	17.5	187.59	Male	Sam
TE21	105	17.2	154.76	Female	Sam
T1	370	22	235.70	Female	Sam
T2	390	23	213.52	NA	Sam
T3	280	20	246.83	Male	Sam
T4	285	20	251.23	Female	Sam
T5	125	16.5	212.26	Female	Sam
T6	390	23.5	198.43	Male	Sam
T7	190	19.5	182.58	Female	Sam
T8	405	22.5	238.98	Male	Sam
T9	180	17.4	255.05	Male	Sam
T10	310	23.5	157.73	Male	Sam
T11	225	21.8	147.87	Female	Sam
T12	165	16.5	280.18	Male	Sam
T13	320	24	151.54	Male	Sam
BE1	70	15.5	147.09	Male	Bedhiya
BE2	95	16.1	175.39	Female	Bedhiya
BE4	80	14.9	192.32	Male	Bedhiya
BE5	85	14.5	224.19	Female	Bedhiya
B1	125	15.5	262.67	Female	Bedhiya
B2	270	21	201.55	NA	Bedhiya
B3	335	22.2	206.93	Male	Bedhiya
B4	260	20	229.20	NA	Bedhiya

B5	265	22	168.82	Female	Bedhiya
B6	305	20.5	247.16	NA	Bedhiya
B7	300	19.5	288.29	Female	Bedhiya
B8	120	16	226.30	Female	Bedhiya
B9	135	16.9	211.27	Male	Bedhiya
B10	105	16	198.01	Male	Bedhiya
B11	165	18.9	176.38	Female	Bedhiya
B12	190	20	167.49	Female	Bedhiya
B13	145	17	222.40	NA	Bedhiya

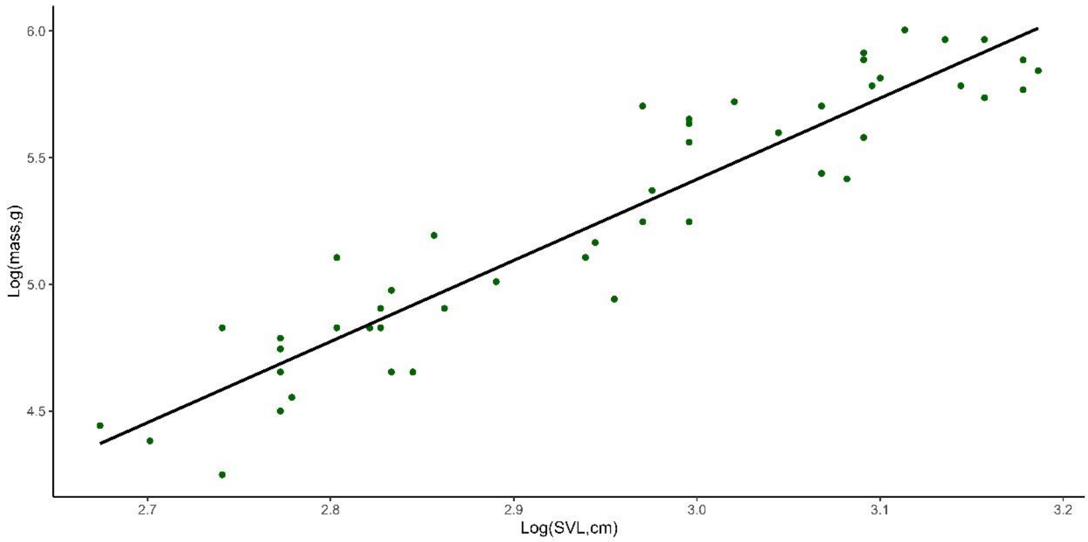


Figure 3: Relationship between log-transformed SVL and log-transformed mass of *S. hardwickii*

5.2 Biophysical Models

Above ground environmental temperatures in the open (T_e open) in the two sites did not show any significant difference (T_{6744} = 1.27, P = 0.13) Adult biophysical models and juvenile biophysical models did not show any significant differences in any microhabitat (open: T_{2861} = -0.189, P = 0.54; burrow: T_{2861} = 0.14, P = 0.37; burrow entrance: T_{2861} = -0.23, P = 0.6).

5.3 Field Body Temperature

Data were obtained for 19 *S. hardwickii* individuals between March to May. Each individual was monitored between 20 to 61 days resulting in 65950 field T_b data points. The effects of T_e open on field T_b was significant but weak ($\beta = 0.12$, $T_{65950} = 136.12$, $P<0.001$). A slope of 0.12 confirms that *S. hardwickii* shows a high degree of thermoregulation (Fig. 4). There might have been a slight effect of BCI ($\beta = -0.01$, $T_{16} = -0.01$, $P = 0.06$) but since the β slightly overlaps 0, we are skeptical. There was no effect of SVL ($\beta = -0.03$, $T_{16} = -0.04$, $P = 0.6$) on T_b. There was a significant random effect of 'individual' ($\chi^2 = 5866.5$, $P<0.001$) on T_b. The VT_{max} of *S. hardwickii* was 46.3°C ± 0.3°C and the VT_{min} of *S. hardwickii* was 27.5 ± 0.3°.

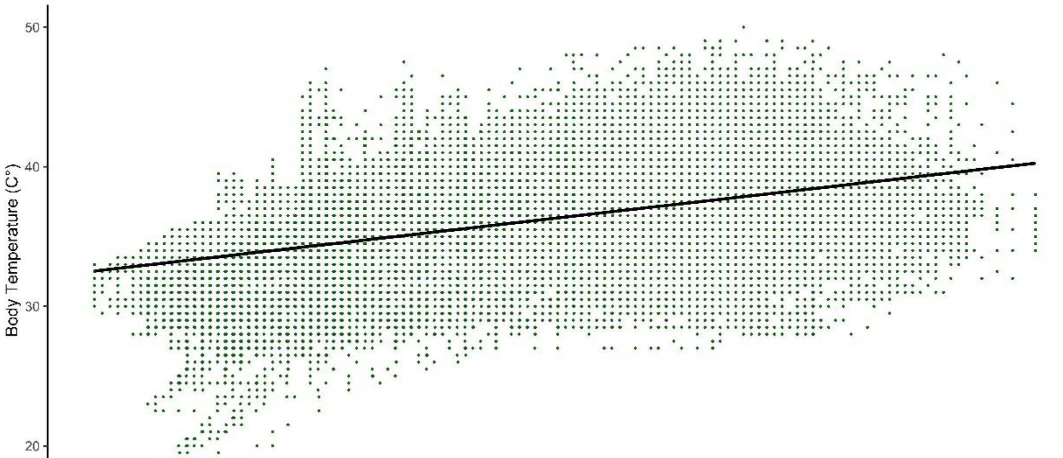
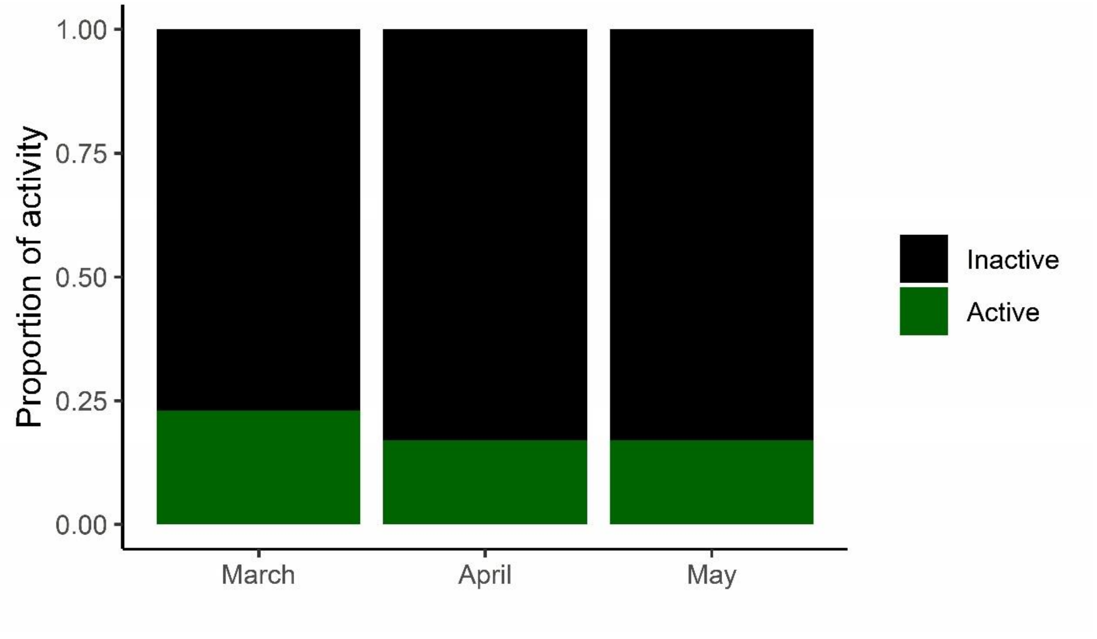


Figure 4: Body temperatures of S. hardwickii as a function of T_e in open.

5.4 Temperature-Based Activity Estimation (TBAE)

The results of TBAE had a substantial agreement with our test data (99.1%; K = 0.78). Using TBAE, we predicted that proportion of activity was 6% higher in March compared to April and May. April and May had the same proportion of activity but there was a slight shift in activity pattern (Fig. 5). In March the mean field T_b was 33.6°C ± 0.03°C compared to 35.2°C ± 0.01°C in April and 36.5°C ± 0.01 May. The mean environmental temperature (T_e open) in March was 33.3°C ± 0.2°C compared to 36.4°C ± 0.2°C in April and 38.9 °C ± 0.2°C in May. In May, the lizards showed a higher proportion of activity in the morning when the temperatures were comparatively lower and a lower proportion of activity in the afternoon when the temperatures were high.

a)



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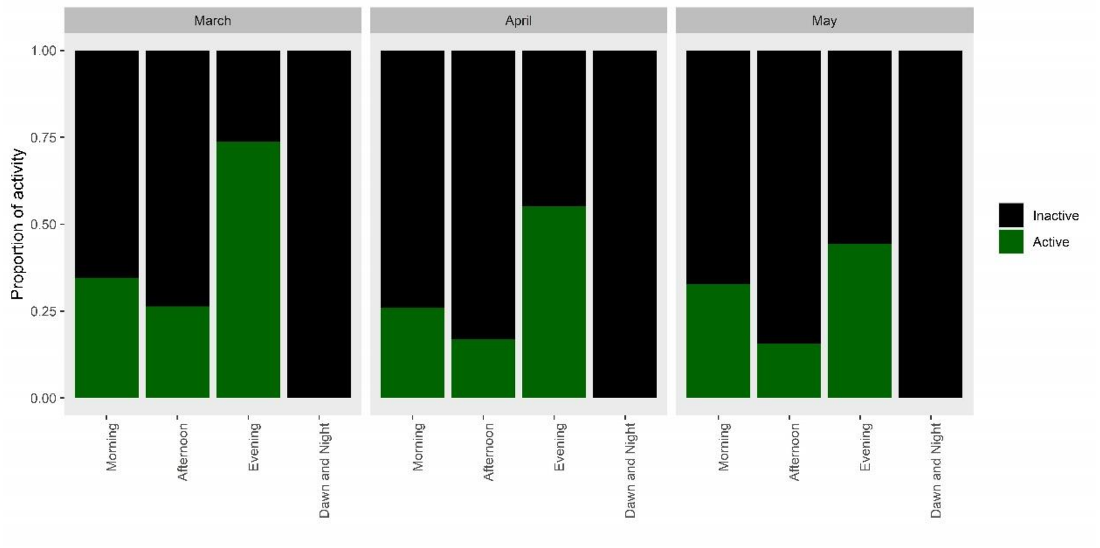

Figure 5: a) Total proportion of activity of the lizards over the course of their active season. b) Average daily activity pattern of the lizards over the course of their active season.

5.5 Preferred temperature (T_{set})

The median T_{set} of *S. hardwickii* was 39.2°C ± 0.3°C and the T_{set} range was 38.2°C ± 0.3 — 40°C ± 0.4°C. There was no effect of sex ($F_1 = 0.23$, $P = 0.64$), BCI ($F_1 = 1$, $P = 0.33$), and site ($F_1 = 0.07$, $P = 0.78$) on median T_{set}.

5.6 Critical thermal thresholds (CT_{max} and CT_{min})

The CT_{max} and CT_{min} of the species was 49°C ± 0.2°C and 12.7°C ± 0.27°C respectively. There was no effect of sex ($F_1 = 0.079$, $P = 0.78$), BCI ($F_1 = 0.001$, $P = 0.971$) and site ($F_1 = 2.03$, $P = 0.182$) on CT_{max}. There was a significant effect of site ($F_1 = 19.19$, $P = 0.001$) on CT_{min}. The mean CT_{min} for Sam was 13.06°C ± 0.26°C whereas the mean CT_{min} for Bedhiya was 11.3 ± 0.37°C. BCI ($F_1 = 2.2$, $P = 0.16$) and sex ($F_1 = 4.1$, $P = 0.07$) on CT_{min}. We only used CT_{max} for our predictions since the difference between VT_{min} and CT_{min} were large (14.8°C).

5.7 Locomotor performance

Thermal performance curves showed a significant effect of temperature on speed of *S. hardwickii* (GAMM: $F = 70.4$, $P<0.001$; Fig. 6). The GAMM with temperature as a fixed effect, 'individuals' as random effect, BCI, and site as covariates explained 80.5% of the deviance. The random effect of 'individuals' was significant (GAMM: $F = 7.5$, $P = 0.03$) Using the model, we found maximum speed (V_{max}) to be 2.55 (m/s) ± 0.09 (m/s) at 39.8 (T_{opt}). The T_{opt} fell in the T_{set} range 38.15°C ±0.3°C – 40°C ±0.4°C. Performance breath B_{80} ranged from 33°C to 43.5°C whereas B_{95} ranged from 36.5°C to 41.5°C.

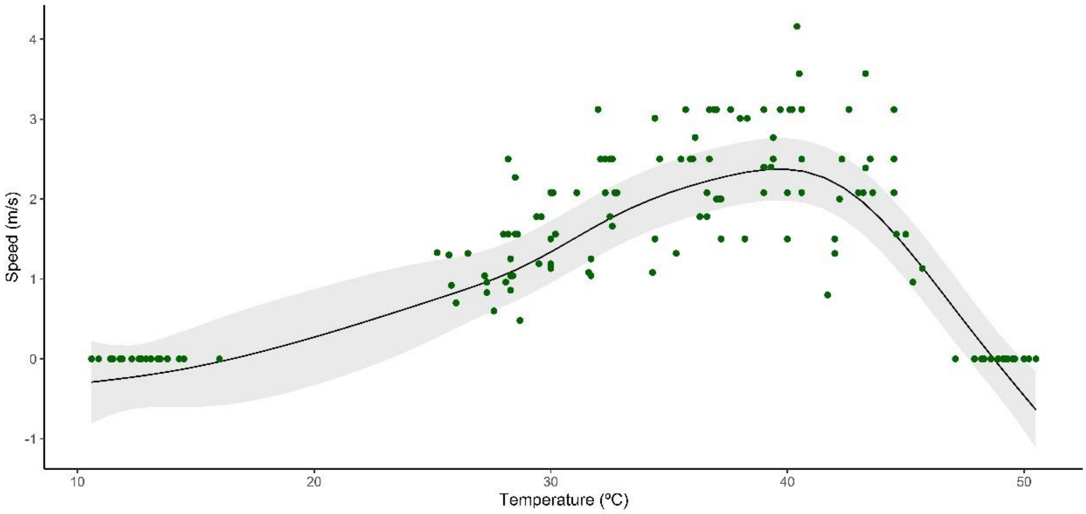

Figure 6: Locomotor performance curve of *S. hardwickii*

5.8 Microhabitat use

Burrows provided an exceptional buffer to the lizards from temperatures in the open. Burrow temperatures did not exceed 36.6°C which is considerably lower than VT_{max}, CT_{max}, B_{95} and T_{set}.

Temperatures in open regularly exceeded T_{set}, B_{95}, VT_{max} and CT_{max}. Temperatures at the burrow entrance exceeded T_{set} and B_{95} regularly, and were near to VT_{max} at mid-day but never exceeded CT_{max}. The lizards used all three microhabitats to thermoregulate (Fig. 7).

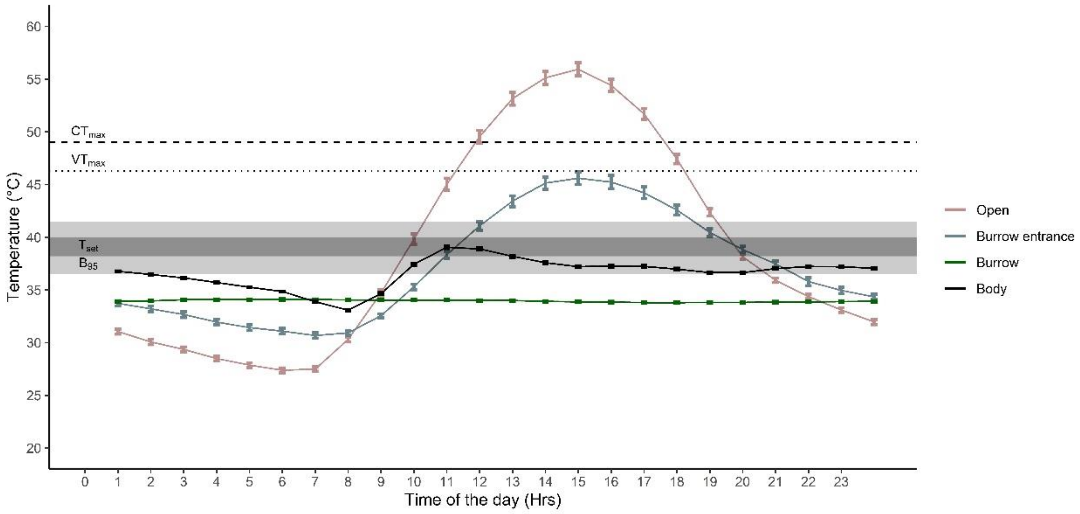

Figure 7: Average daily temperatures of field T_b of the lizards (N=19) and biophysical models in different microhabitats (N=6) during May (hottest month).

5.9 Activity restriction

During the hottest month of the year (May) the lizards were restricted to their burrows for six hours during their active period (07:00-20:00) as all microhabitat temperatures exceeded CT_{max}, VT_{max}, T_{set} and B_{95}

5.10 Projections

Our model suggested decrease in locomotor performance by 2.1%, 9.5% and 28.3% in the best- (RCP 2.6), intermediate- (RCP 4.5), and worst- (RCP 8.5) case scenarios by 2100 (Fig. 8). For hours of restriction, our model showed that there might be additional one-hour activity restriction in the best case scenario, and lizards might not be able to survive even at the burrow entrance for three hours and might have to seek refuge deeper inside their burrows (~1m), where temperatures, even in the worst-case scenario do not exceed T_{set} (Fig. 9).

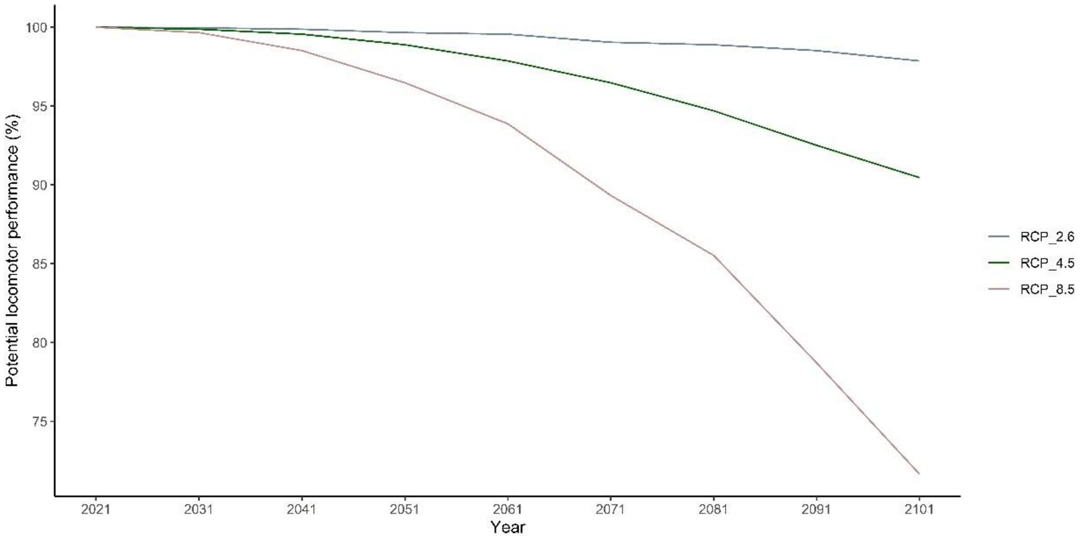

Figure 8: Potential loss of locomotor performance in *S. hardwickii.*

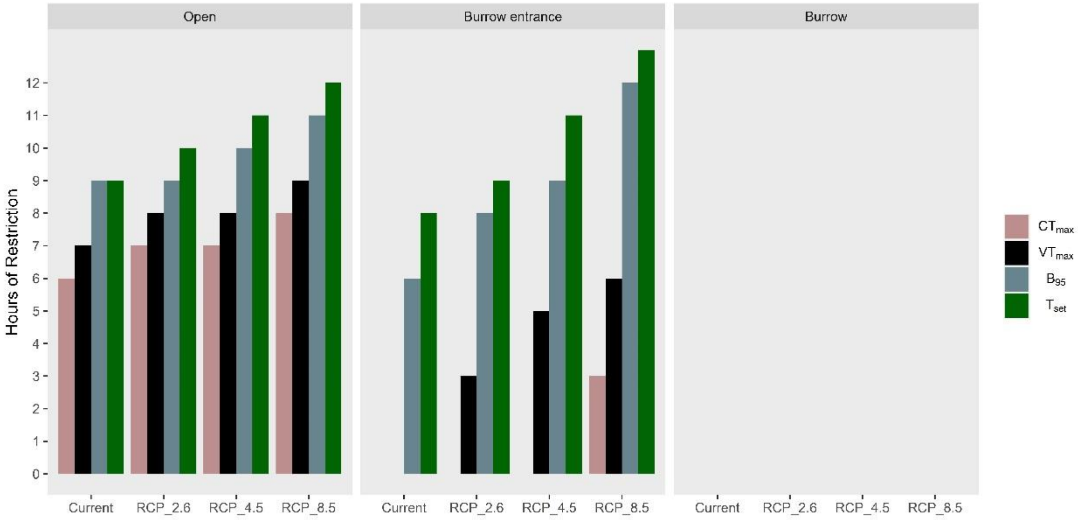

Figure 9: The number of active period (0700 to 2000) hours that *S. hardwickii* are restricted from being in open, burrow entrance and burrow, calculated as hours in which temperatures exceed CT_{max}, VT_{max}, T_{set} and B_{95}.

6. Discussion

In our study on the thermal ecology of *S. hardwickii***,** we integrated various thermal variables to test how this desert ectotherm thermoregulates and how it will respond to rising temperatures. Congruent to our hypothesis, the results of the study suggest a substantial decrease in locomotor performance and an increase in hours for which the lizards are restricted to their burrows by the end of the century.

As expected, mass and SVL of *S. hardwickii* were strongly related. The slope of the regression line was higher than what was quantified in Kutch by Dutta & Jhala, (2007), which indicates that lizards in our study had higher BCI values, an outcome of having higher mass for the same SVL. The average mass and SVL was also higher in our study area. Our sampling sites had an average burrow density of 59 burrows/ha in summer whereas Dutta & Jhala, (2007) reported a density of 42.45 burrows/ha in summer in their study area. Strength of natural selection is higher in areas with higher population densities and it usually favours larger lizards, as it enhances their competitive ability(Calsbeek & Smith, 2007). This might be the reason why lizards are larger in our study area even when our study area is more arid and less productive compared to Kutch.

We found that with a substantial increase in average monthly environmental temperatures from 33.3°C ± 0.2°C in March to 38.9 °C ± 0.2°C in May during the course of study, the average monthly body temperatures did not increase to the same magnitude. This indicates that *S. hardwickii* actively thermoregulates, mainly by using burrows (refugia) to keep their T_b relatively constant. The fact that they thermoregulate using burrows is consistent with other studies on thermoregulating lizards which survive in hot deserts (Burrow et al., 2001; Clusella-Trullas et al., 2011; Ivey et al., 2020; Moore et al., 2018; Wilms et al., 2011). Using the slope of the relationship between T_e open and T_b, we confirmed that *S. hardwickii* is a thermoregulator and not a thermoconformer. In the Linear Mixed Model between T_e open and T_b, inter-individual variability was significant. Hence, it is recommended for further studies to account for inter-individual variability when quantifying variables that explain body temperatures in the wild.

In this study, we found substantial support for the hypothesis that Temperature-Based Activity Estimation (TBAE) can be used to evaluate activity patterns of a large, behaviourally thermoregulating, desert lizard. We used temperatures measured by biophysical models inside burrows and outside in the open to classify activity of the tagged lizards. Since lizards displayed high burrow fidelity, we could easily corroborate our TBAE model with focal animal sampling. Only two states of activity – active (when lizards were out in the open) and inactive (when lizards were inside burrows) were predicted and 99.1% of the estimates were correctly assigned. Davis et al., (2008) similarly predicted activity with 93% agreement between observations and estimates in *Gambelia sila* (Ivey, 2020) where they predicted activity in three microhabitats and 96% agreement between observations and estimates in Gila monsters where they predicted activity in two microhabitats. Moore et al.,(2018) and Al-Sayegh et al., (2017) used TBAE algorithm to predicted the activity pattern of *Liopholis kintorei* and *Uromastyx aegyptius* respectively, but they did not match the predicted activity pattern with observed activity pattern. We found that *S. hardwickii* spends majority of its active season inside burrows. When it is active (0700 hrs to 2000 hrs), it shuttles between its burrow and the open environment where it can perform essential activities like foraging, basking and interacting with other individuals. Even as T_e open increased by 2.5°C from April to May, the monthly activity pattern remained similar. However, proportion of activity decreased in the afternoon and evening when the temperatures were higher, and increased in morning when the temperatures were relatively milder. As the season progressed, the activity pattern of the lizard became more bimodal, which is similar to what was observed in studies with direct observation of *S. hardwickii* (Das et al., 2013; Dutta & Jhala, 2007). Lizards in temperate regions also show a bimodal activity pattern in summer but they are usually more active in the late morning and in the afternoon till early evening(Vicenzi et al., 2019; Vidal et al., 2010). The similarity in activity patterns might be due to the fact that lizards in colder regions have lower thermal preferences compared to lizards in warmer regions. We did not take into account the proportion of time the lizards spent at different burrow depths and the burrow entrance which might be different for the two months (Moore et al., 2018).

We tested the locomotor performance of the species using the speed of the individuals for short sprints at various temperatures between the lizards' VT_{min} and VT_{max}. The temperature at which the lizard performs the best is known as the optimum temperature (T_{opt}). At $T_{opt,}$ the lizard has the highest probability to outrun a predator but the substrate of the habitat has a major impact on a lizards' locomotor performance which might still affect its probability of getting predated (Brandt et al., 2015; Vanhooydonck et al., 2015). Hence, accurate thermoregulation by the lizard to maintain its T_b within B_{95}, which is the temperature range in which the lizard can maintain its speed at or above 95% of the maximum velocity, is critical. The T_{opt} in this case falls in the T_{set} range. This supports the thermal co-adaptation hypothesis which posits that T_{opt} for traits closely linked to fitness, like running performance, should match temperatures preferred or selected by a species (T_{set}; Angilletta et al., 2006). As suggested by Cecchetto et al. (2020), inter-individual variation was accounted for in the GAMM analysis and the variation was significant. Inter-individual variation has been found to be an essential part of life history variation in populations (Nussey et al., 2007) and might indicate species' plasticity. We did not quantify the locomotor performance of the individuals which were observed in the wild. Since inter-individual variation was significant in field T_b, this could have revealed how fitness relates to activity restriction and thermoregulatory accuracy in the natural environment.

Most thermophysiological studies only use CT_{max} as the maximum threshold (Caldwell et al., 2015; Diele-Viegas et al., 2018; Herrando-Pérez et al., 2019). In this study, we used VT_{max}, which is the temperature at which the animal flees to refugia in the wild, as it is ecologically more relevant (Camacho & Rusch, 2017). Lizards prefer to thermoregulate within their T_{set} but that rarely happens throughout the day (Porter et al., 1973). Hence, we added B_{95} to our activity restriction models. We found that during the hottest month, T_b was within B_{95} for 11 hours of the lizard's 13-hour active period from 0700 hrs to 2000 hrs. The T_b fell below B_{95} only between 0700 hrs and 0900 hrs when the temperatures of all microhabitats were below B_{95}.

Evaluation of the biophysical models and T_b during a very hot month of their active season revealed the following patterns: 1) The T_b exceeded the CT_{max} of *S.*

hardwickii for six hours during the mid-day from 1100 to 1700 hrs. 2) Burrows act as an exceptional thermal buffer against extreme temperatures for the lizards throughout the day and even at night when the temperatures in open reach VT_{min}. 3) Lizards used various burrow depths to thermoregulate as their field T_b was always between burrow and burrow entrance temperatures. 4) Lizards usually emerged out of their burrows after 0800 hrs and were mostly in the open until T_b reached T_{set} and until T_e open was below VT_{max} which was approximately at 1100 hrs. After 1100 hrs, when T_e open exceeded VT_{max}, T_b decreased which signals either complete restriction or higher rates of shuttling between open and burrow microhabitats (Cowles & Bogert, 1944). 5) After emergence, the lizards maintained their T_b within B_{95} and slightly below T_{set}, which indicates a fairly high thermoregulatory accuracy. The lizards were restricted to their burrows for 6-9 hours (depending on the variable used) of their active period. Shuttling behaviour might mitigate these restrictions but 6-9 hours of restriction is extremely high (Sinervo et al., 2010) and the lizard might already be restricted to their burrows for more hours than in the past. In addition to shuttling between microhabitats, the lizards might have been thermoregulating using melanopore dispersion which is darkening of skin to absorb more radiation (Sherbrooke et al., 1994) which was observed in *S. hardwickii* in Kutch (Dutta & Jhala, 2007). The lizards might also be thermoregulating in the open by changing their body posture (Muth, 1977). In further studies, biophysical models in the same microhabitat can be used to emulate different postures to account for this.

It is evident that *S. hardwickii* is adapted to extremely hot environments and mitigates the effects of temperatures in the open above its thermal thresholds via behavioural thermoregulation. However, this might lead to evolutionary inertia of thermophysiological traits since individuals with higher thresholds might not get selected (Bogert, 1949; Cowles & Bogert, 1944; Farallo et al., 2018; Logan et al., 2019). Considering this "static thermoregulatory view" (sensu Hertz et al., 1983), we predicted the impacts of rising temperatures on locomotor performance and activity patterns of *S. hardwickii*. A 2.1% decrease in locomotor performance in the best-case scenario (RCP 2.6), a 9.5% decrease in the intermediate-case scenario (RCP 4.5), and a 28.3% decrease in the worst-case scenario (RCP 8.5) by 2100 might have a devastating impact on the species' ability to evade predators and to forage efficiently (Ekner-Grzyb et al., 2013; Husak, 2006). Our activity restriction models predict that as temperatures rise, *S. hardwickii* will continue to lose hours of activity during its active period as environmental temperatures will exceed its T_{set}, B_{95}, VT_{max} and CT_{max} for more number of hours. Burrows will be the only microhabitat available to the species where the temperatures do not exceed their thermal thresholds during these hours. But since we only placed biophysical models deep inside the burrows and at burrow entrances, we could not take into account the change in burrow depths they may choose for thermal refugia at specific hours. During our activity observations, we noticed that lizards use burrow entrances for territory defence and passive foraging. Even in the best-case scenario (RCP 2.6), the temperatures at the burrow entrance will exceed the VT_{max} of the lizard for three hours by 2100 which they currently do not. Hence, this might restrict lizards to deeper parts of the burrow for more hours, further reducing their time to forage and defend territories. Further studies exploring the thermal gradient of the species' burrow are required.

Conservation Implications

Pastoralism is prevalent in areas where *S. hardwickii* is found and the species prefers stunted grasslands modified by cattle (Dutta & Jhala, 2014) but cattle grazing usually overlaps with the species' activity peaks. The presence of cattle forces the lizards to go into their burrows which might result in an increase in hours of restriction. TBAE can be used by managers to monitor the activity of lizards and identify the peaks in activity in order to prevent this overlap. Livestock and *S. hardwickii* compete for similar resources as they are both grazers (Dutta & Jhala, 2007). If grazing intensity is high, the impact of warming induced activity restriction would be more since lizards have to venture far from their burrows and spend longer time foraging. The impact of climatic warming would be lower with more vegetation cover as lizards will spend less time finding food patches. Hence, it is recommended that grazing should be regulated in areas with high abundance of this lizard species. High number of *S. hardwickii* mortalities are also caused by vehicular activity (Kumawat and Purohit, 2020). After identifying the peaks, managers can regulate the traffic in areas with high *S. hardwickii* abundance by imposing speed limits at specific hours.

Dutta & Jhala (2014) found that *S. hardwickii* was practically absent from croplands. This might be because these lizards are usually found in areas with high soil compaction (Ramesh & Ishwar, 2008) as it might help their burrows retain structural integrity. Since burrows are exceptional thermal buffers for the lizards, cropland expansion in areas with *S. hardwickii* populations should be avoided. Further studies on burrowing site selection of the lizard may shed light on this.

7. Bibliography

Al-Sayegh, M. (2020), *Eco-physiological Implications of Conservation of Dhubs (Uromastyx aegyptius) in Kuwait*. Arizona State University, USA

Almazroui, M., Saeed, S., Saeed, F., Islam, M. N., & Ismail, M. (2020). Projections of Precipitation and Temperature over the South Asian Countries in CMIP6. *Earth Systems and Environment*, *4*(2), 297–320.

Altmann, J. (1974). Observational study of behavior: Sampling methods. *Behaviour, 49*(3–4), 227–266.

Angilletta, M., Bennett, A., Guderley, H., Navas, C., Seebacher, F., & Wilson, R. (2006). Coadaptation: A Unifying Principle in Evolutionary Thermal Biology. *Physiological and Biochemical Zoology : PBZ, 79*, 282–294.

Angilletta, M. J., Niewiarowski, P. H., & Navas, C. A. (2002). The evolution of thermal physiology in ectotherms. *Journal of Thermal Biology*, *27*(4), 249–268.

Bakken, G. S. (1992). Measurement and Application of Operative and Standard Operative Temperatures in Ecology. *American Zoologist*, *32*(2), 194–216.

Bakken, G. S., & Angilletta Jr, M. J. (2014). How to avoid errors when quantifying thermal environments. *Functional Ecology*, *28*(1), 96–107.

Bogert, C. M. (1949). Thermoregulation in reptiles, a factor in evolution. *Evolution*, *3*(3), 195–211.

Brandt, R., Galvani, F., & Kohlsdorf, T. (2015). Sprint performance of a generalist lizard running on different substrates: Grip matters. *Journal of Zoology*, *297*(1), 15–21.

Briscoe, N. J., Kearney, M. R., Taylor, C. A., & Wintle, B. A. (2016). Unpacking the mechanisms captured by a correlative species distribution model to improve predictions of climate refugia. *Global Change Biology*, *22*(7), 2425–2439.

Brusch, G. A., Taylor, E. N., & Whitfield, S. M. (2016). Turn up the heat: Thermal tolerances of lizards at La Selva, Costa Rica. *Oecologia*, *180*(2), 325–334.

Burrow, A. L., Kazmaier, R. T., Hellgren, E. C., & Ruthven III, D. C. (2001). Microhabitat selection by Texas horned lizards in southern Texas. *The Journal of Wildlife Management*, 645–652.

Caldwell, A. J., While, G. M., Beeton, N. J., & Wapstra, E. (2015). Potential for thermal tolerance to mediate climate change effects on three members of a cool temperate lizard genus, Niveoscincus. *Journal of Thermal Biology*, *52*, 14–23.

Calsbeek, R., & Smith, T. B. (2007). Probing the adaptive landscape using experimental islands: density-dependent natural selection on lizard body size. *Evolution*, *61*(5), 1052–1061.

Camacho, A., & Rusch, T. W. (2017). Methods and pitfalls of measuring thermal preference and tolerance in lizards. *Journal of Thermal Biology*, *68*(Pt A), 63–72.

Cecchetto, N. R., Medina, S. M., & Ibargüengoytía, N. R. (2020). Running performance with emphasis on low temperatures in a Patagonian lizard, Liolaemus lineomaculatus. *Scientific Reports*, *10*(1), 14732.

Clusella-Trullas, S., Blackburn, T. M., & Chown, S. L. (2011). Climatic predictors of temperature performance curve parameters in ectotherms imply complex responses to climate change. *The American Naturalist*, *177*(6), 738–751.

Cowles, R. B., & Bogert, C. M. (1944). A preliminary study of the thermal requirements of desert reptiles. *Iguana*, *83*, 53.

Das, S. K., Dookia, S., Das, K., & Dutta, S. K. (2013). Ecological observations on the Indian Spiny-tailed Lizard Saara hardwickii (Gray, 1827)(Reptilia: Squamata: Agamidae) in Tal Chhapar Wildlife Sanctuary, Rajasthan, India. *Journal of Threatened Taxa*, *5*(1), 3516–3526.

Davis, J. R., Taylor, E. N., & DeNardo, D. F. (2008). An automated temperature-based option for estimating surface activity and refuge use patterns in free-ranging animals. *Journal of Arid Environments*, *72*(8), 1414–1422.

Davis, J., Taylor, E., & DeNardo, D. (2008). An automated temperature-based option for estimating surface activity and refuge use patterns in free-ranging animals. *Journal of Arid Environments*, *72*(8), 1414–1422.

Deutsch, C. A., Tewksbury, J. J., Huey, R. B., Sheldon, K. S., Ghalambor, C. K., Haak, D. C., & Martin, P. R. (2008). Impacts of climate warming on terrestrial ectotherms across latitude. *Proceedings of the National Academy of Sciences*, *105*(18), 6668–6672.

Diele-Viegas, L. M., Vitt, L. J., Sinervo, B., Colli, G. R., Werneck, F. P., Miles, D. B., Magnusson, W. E., Santos, J. C., Sette, C. M., & Caetano, G. H. (2018). Thermal physiology of amazonian lizards (reptilia: Squamata). *PloS One*, *13*(3), e0192834.

Dutta, S., & Jhala, Y. (2007). Ecological aspects of Indian spiny-tailed lizard Uromastyx hardwickii in Kutch. *Journal of the Bombay Natural History Society*, *104*(3), 255–265.

Dutta, S., & Jhala, Y. (2014). Planning agriculture based on landuse responses of threatened semi-arid grassland species in India. *Biological Conservation*, *175*, 129–139.

Ekner-Grzyb, A., Sajkowska, Z., Dudek, K., Gawałek, M., Skórka, P., & Tryjanowski, P. (2013). Locomotor performance of sand lizards (Lacerta agilis): Effects of predatory pressure and parasite load. *Acta Ethologica*, *16*(3), 173–179.

Farallo, V. R., Wier, R., & Miles, D. B. (2018). The Bogert effect revisited: Salamander regulatory behaviors are differently constrained by time and space. *Ecology and Evolution*, *8*(23), 11522–11532.

Grant, B. W., & Dunham, A. E. (1988). Thermally imposed time constraints on the activity of the desert lizard Sceloporus merriami. *Ecology*, *69*(1), 167–176.

Herrando-Pérez, S., Ferri-Yáñez, F., Monasterio, C., Beukema, W., Gomes, V., Belliure, J., Chown, S. L., Vieites, D. R., & Araújo, M. B. (2019). Intraspecific variation in lizard heat tolerance alters estimates of climate impact. *Journal of Animal Ecology*, *88*(2), 247–257.

Hertz, P. E., Huey, R. B., & Nevo, E. (1983). Homage to Santa Anita: Thermal Sensitivity of Sprint Speed in Agamid Lizards. *Evolution*, *37*(5), 1075–1084. JSTOR.

Hertz, P. E., Huey, R. B., & Stevenson, R. (1993). Evaluating temperature regulation by field-active ectotherms: The fallacy of the inappropriate question. *The American Naturalist*, *142*(5), 796–818.

Huey, R. (1988). Temperature, Physiology, and the Ecology of Reptiles. In *Biology of the Reptilia* (Vol. 12, pp. 387–437).

Huey, R. B., Losos, J. B., & Moritz, C. (2010). Are lizards toast? *Science*, *328*(5980), 832–833.

Husak, J. F. (2006). Does Survival Depend on How Fast You Can Run or How Fast You Do Run? *Functional Ecology*, *20*(6), 1080–1086. JSTOR.

Ivey, K. N., Cornwall, M., Crowell, H., Ghazian, N., Nix, E., Owen, M., Zuliani, M., Lortie, C. J., Westphal, M., & Taylor, E. (2020). Thermal ecology of the federally endangered blunt-nosed leopard lizard (Gambelia sila). *Conservation Physiology*, *8*(1).

Johnson, M. (2005). A New Method of Temporarily Marking Lizards. *Herpetological Review*, *36*.

Kumawat, R., Purohit, A. (2020). Impact and assessment of wildlife mortalities on road due to vehicular movements in Desert National Park, Rajasthan, India. *Asian Journal of Conservation Biology*, (1), 173-177

LABRA, A., & BOZINOVIC, F. (2002). Interplay between pregnancy and physiological thermorégulation in Liolaemus lizards. *Écoscience*, *9*(4), 421–426. JSTOR.

Laspiur, A., Santos, J. C., Medina, S. M., Pizarro, J. E., Sanabria, E. A., Sinervo, B., & Ibargüengoytía, N. R. (2021). Vulnerability to climate change of a microendemic lizard species from the central Andes. *Scientific Reports, 11*(1), 11653.

Logan, M. L., van Berkel, J., & Clusella-Trullas, S. (2019). The Bogert Effect and environmental heterogeneity. *Oecologia*, *191*(4), 817–827.

Lutterschmidt, W. I., & Hutchison, V. H. (1997a). The critical thermal maximum: History and critique. *Canadian Journal of Zoology*, *75*(10), 1561–1574.

Lutterschmidt, W. I., & Hutchison, V. H. (1997b). The critical thermal maximum: Data to support the onset of spasms as the definitive end point. *Canadian Journal of Zoology*, *75*(10), 1553–1560.

Moore, D., Stow, A., & Kearney, M. R. (2018). Under the weather?—The direct effects of climate warming on a threatened desert lizard are mediated by their activity phase and burrow system. *Journal of Animal Ecology*, *87*(3), 660–671.

Muth, A. (1977). Thermoregulatory Postures and Orientation to the Sun: A Mechanistic Evaluation for the Zebra-Tailed Lizard, Callisaurus draconoides. *Copeia*, *1977*(4), 710–720. JSTOR.

Neel, L. K., Logan, M. L., Nicholson, D. J., Miller, C., Chung, A. K., Maayan, I., Degon, Z., DuBois, M., Curlis, J. D., Taylor, Q., Keegan, K. M., McMillan, W. O., Losos, J. B., & Cox, C. L. (2021). Habitat structure mediates vulnerability to climate change through its effects on thermoregulatory behavior. *Biotropica*.

Nussey, D. H., Wilson, A. J., & Brommer, J. E. (2007). The evolutionary ecology of individual phenotypic plasticity in wild populations. *Journal of Evolutionary Biology*, *20*(3), 831–844.

Peig, J., & Green, A. J. (2009). New perspectives for estimating body condition from mass/length data: The scaled mass index as an alternative method. *Oikos*, *118*(12), 1883–1891.

Pianka, E. R. (1986). *Ecology and Natural History of Desert Lizards*. Princeton University Press; JSTOR.

Porter, W., Mitchell, J., Beckman, W., & DeWitt, C. (1973). Behavioral implications of mechanistic ecology. *Oecologia*, *13*(1), 1–54.

Ramesh, M., & Ishwar, N. (2008). *Status and distribution of the Indian spiny-tailed lizard Uromastyx hardwickii in the Thar Desert*. western Rajasthan. Technical Report.

Sherbrooke, W., Castrucci, A., & Hadley, M. (1994). Temperature Effects on in vitro Skin Darkening in the Mountain Spiny Lizard, Sceloporus jarrovi: A Thermoregulatory Adaptation? *Physiological Zoology*, *67*, 659–672.

Sinervo, B., Méndez-de-la-Cruz, F., Miles, D. B., Heulin, B., Bastiaans, E., Villagrán-Santa Cruz, M., Lara-Resendiz, R., Martínez-Méndez, N., Calderón-Espinosa, M. L., Meza-Lázaro, R. N., Gadsden, H., Avila, L. J., Morando, M., De la Riva, I. J., Sepulveda, P. V., Rocha, C. F. D., Ibargüengoytía, N., Puntriano, C. A., Massot, M., … Sites, J. W. (2010). Erosion of Lizard Diversity by Climate Change and Altered Thermal Niches. *Science*, *328*(5980), 894.

Vanhooydonck, B., Measey, J., Edwards, S., Makhubo, B., Tolley, K. A., & Herrel, A. (2015). The effects of substratum on locomotor performance in lacertid lizards. *Biological Journal of the Linnean Society*, *115*(4), 869–881.

Vicenzi, N. P., Ibarguengoytía, N., & Corbalán, V. E. (2019). *Activity patterns and thermoregulatory behavior of the viviparous lizard Phymaturus palluma in Aconcagua Provincial Park, argentine Andes*.

Vidal, M. A., Habit, E., Victoriano, P., González-Gajardo, A., & Ortiz, J. C. (2010). Thermoregulation and activity pattern of the high-mountain lizard Phymaturus palluma (Tropiduridae) in Chile. *Zoologia (Curitiba)*, *27*, 13–18.

Wilms, T., Wagner, P., Shobrak, M., Rödder, D., & Böhme, W. (2011). Living on the edge?–On the thermobiology and activity pattern of the large herbivorous desert lizard Uromastyx aegyptia microlepis Blanford, 1875 at Mahazat as-Sayd Protected Area, Saudi Arabia. *Journal of Arid Environments*, *75*(7), 636–647.