Protection from overheating of simulated *Sceloporus horridus* lizards in a biosphere reserve of seasonally dry tropical forest in central Mexico

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ABSTRACT

In seasonally dry ecosystems, loss of vegetation cover leads to warmer microclimates that can increase lizards' body temperatures to the point of threatening their performance. Preserving vegetation by establishing protected areas may mitigate these effects. We used remote sensing to test these ideas in the Sierra de Huautla Biosphere Reserve (REBIOSH) and surrounding areas. First, we determined whether vegetation cover was higher in the REBIOSH compared to adjacent unprotected areas to the north (NAA) and south (SAA). Then, we used a mechanistic niche model to test whether simulated *Sceloporus horridus* lizards in the REBIOSH experienced a cooler microclimate, higher thermal safety margin, longer foraging duration, and lower basal metabolic rate compared to adjacent unprotected areas. We compared these variables between 1999, when the reserve was declared, and 2020. We found that vegetation cover increased from 1999 to 2020 in all three areas; it was higher in the REBIOSH than in the more anthropized NAA, and was intermediate in the less anthropized SAA in both years. The microclimate temperature decreased from 1999 to 2020 and was lower in the REBIOSH and SAA than in the NAA. Thermal safety margin increased from 1999 to 2020; it was higher in the REBIOSH than in the NAA and intermediate in the SAA. Foraging duration increased from 1999 to 2020 and was similar among the three polygons. Basal metabolic rate decreased from 1999 to 2020 and was higher in the NAA than in the REBIOSH and SAA. Our results suggest that the REBIOSH provides cooler microclimates that increase the thermal safety margin and lower the metabolic rate of this generalist lizard compared to the NAA, and that the REBIOSH could contribute to increased vegetation cover in its surroundings. Besides, protecting original vegetation cover is an important part of climate change mitigation strategies more generally.

1. Introduction

Seasonally dry tropical forests are one of the most seriously threatened ecosystems worldwide (Portillo-Quintero and Sánchez-Azofeifa 2010). By 2004, an average of 66% of seasonally dry tropical forest area in America had been converted to croplands and livestock pastures, and only 29% of Mexican seasonally dry tropical forest area remained as primary forest (Portillo-Quintero and Sánchez-Azofeifa 2010). The loss of canopy cover leads to intense warming, especially in arid ecosystems. On one hand, natural seasonal changes in seasonally dry tropical forests lead to the majority of trees dropping their leaves in the dry season, resulting in a 28% decrease in canopy cover and a 3.8 °C increase in air temperature in two Mexican seasonally dry tropical forests (Siliceo-Cantero et al., 2016). On the other hand, vegetation loss from human activities also decreases canopy cover. For instance, a 44% decrease in vegetation cover due to anthropogenic disturbance increased the mean

soil temperature by 3.4 °C in patches of a Mexican seasonally dry tropical forest (Suazo-Ortuño et al., 2008). These two effects can combine to further compound the naturally hot and dry conditions during the dry season, resulting, for example in 4 °C higher temperatures in anthropogenic pastures than in primary forests in a Costa Rican seasonally dry tropical forest (Klemens et al., 2011).

The body temperature of terrestrial ectotherms like lizards depends on the thermal characteristics of their habitats. Microclimate changes, including anthropogenic and seasonal changes, can therefore affect lizards' body temperatures. For example, mean temperatures of *Sceloporus aeneus* lizards were higher when the shade availability in their refuges was experimentally decreased in hot environments (Rangel-Patiño et al., 2020). In the case of seasonal changes, mean temperatures of *Ctenosaura oaxacana* iguanas were 2.3 °C higher during the dry season than in the rainy season in a Mexican seasonally dry tropical forest (Valenzuela-Ceballos et al., 2015). High body

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temperatures are relevant because they strongly impact lizards' performance. Performance indicators such as growth rate, running speed, and predation success all strongly and suddenly decrease when body temperatures exceed the species' optimal temperature range (reviewed by Huey 1982). In addition, ectotherm metabolism increases positively with body temperature (de Andrade, 2018; due to increased enzyme kinetics), thereby increasing the intake needed to compensate for such a cost of living (Vucic-Pestic et al., 2011) or decreasing selected body temperatures (Gilbert and Miles 2016). Lizards therefore use thermoregulatory behaviors to sustain the interval of body temperatures that allow them to carry out their activities (interval of voluntary thermal tolerances; Camacho and Rusch 2017). In hot microclimates, lizards usually increase their investment in thermoregulatory behaviors as environment temperatures increase. For instance, in natural contexts, *Carlia* spp. lizards increased their investment in thermoregulatory behaviors during the summer when the habitat was hotter than in the winter (Vickers et al., 2011), and *Sceloporus occidentalis* lizards in an arid woodland restricted their activities to shadier microhabitats and higher perch heights than those in a temperate forest (Asbury and Adolph 2007). However, lizards cannot increase their investment in thermoregulatory behaviors indefinitely, since they incur costs in terms of energy, time, predation risk, and investment in other activities such as foraging or reproductive behaviors (Huey and Slatkin 1976). For example, the conversion of a conserved seasonally dry tropical forest to a pasture decreased the time that the tortoise *Gopherus evgoodei* had the necessary body temperatures to carry out its activities such as foraging (Lara-Reséndiz et al., 2022).

The extremes of the interval of voluntary thermal tolerances are the voluntary thermal minimum (VT_{min}) and voluntary thermal maximum (VT_{max}). When lizards' body temperatures exceed VT_{max} they overheat; in the short term, their performance decreases (reviewed by Camacho and Rusch 2017), which in the long term can translate into decreased survival, and ultimately threaten populations (Bestion et al., 2015). For example, *Zootoca vivipara* lizards experienced an accelerated life cycle and lower adult survival in field enclosures that were 2 °C warmer than the mean ambient temperature, which led to the prediction that the population would be locally extinct within 20 years (Bestion et al., 2015). Given the risks of overheating, it is particularly relevant to determine how close a lizard is to ceasing activity to cool down before exceeding its VT_{max}—in other words, the difference between VT_{max} and body temperature. We refer to this variable as the "thermal safety margin", similar to how it is defined by Sunday et al. (2014).

Protected areas, by protecting vegetation cover, should maintain cooler microclimates and thus decrease lizards' risk of overheating compared to unprotected areas. There are several examples of higher mean vegetation cover within protected areas than in unprotected adjacent areas (reviewed by Geldmann et al., 2013 and Laurance et al., 2012, and references therein), including arid ecosystems such as semi-arid savanna (Wasiolka and Blaum 2011) and desert (Al-Sayegh et al., 2020). This leads to the straightforward expectation that higher vegetation cover in protected areas in arid ecosystems generate microclimates that are more conducive to lizard thermoregulation. However, we know of only one empirical study testing this idea, which did not find clear support for it (Al-Sayegh et al., 2020). The daily mean body temperatures of *Uromastyx aegyptia* lizards were similar among protected and unprotected areas of a desert, even though the mean vegetation cover was higher in the protected than in the unprotected areas (Al-Sayegh et al., 2020). To better understand whether and how protected areas provide protection from overheating for the lizard populations inhabiting them, we need studies that compare the effect of protected areas on vegetation cover, and in turn on the microclimate experienced by lizards, at their spatial scale and considering their thermoregulatory behaviors.

In this study, we tested the hypothesis that the Sierra de Huautla Biosphere Reserve (REBIOSH) has habitats with higher vegetation cover and cooler microclimate that provide *Sceloporus horridus* lizards with higher thermal safety margin, foraging duration, and lower metabolic rate compared to its surrounding area. The REBIOSH covers 59,031 ha in south-central Mexico and 60.6% of its area is seasonally dry tropical forest. This region has a marked dry season from November to mid-May (Torres et al., 2009). The hottest months of the dry season challenge lizard thermoregulation and have the lowest ecosystem productivity (i. e., prey availability) (Siliceo-Cantero et al., 2016; Singh and Chaturvedi 2018). *Sceloporus horridus* uses a variety of microhabitats, where they forage with a sit-and-wait strategy and where males court and defend territories in high and conspicuous places from March through June (Bussjaeger 1971; Bustos-Zagal et al., 2013; Castro-Franco et al., 2017). The fact that the most demanding period for lizard's thermoregulation (which requires available shade) is also the period during which *S. horridus* males invest in courtship and territory defense (in the open), sets up a potential trade-off between thermoregulatory and reproductive behaviors during the dry season. This is a particularly biologically important context in which to assess whether the REBIOSH provides cooler microclimates for *S. horridus* thermoregulation than its surroundings.

We used data on climate, vegetation cover, behavior, and thermal biology to simulate the microclimate temperature experienced by simulated *S. horridus* lizards and their thermoregulation in the REBIOSH and in the unprotected area bordering the reserve. We carried out the comparisons considering the conditions when the REBIOSH was declared in 1999 and after 20 years of protection (2020). We addressed five distinct, but related questions. Compared to the unprotected surrounding area: 1) Did the area within the REBIOSH have higher vegetation cover?; 2) Was the simulated microclimate cooler within the REBIOSH?; 3) Was the thermal safety margin higher for simulated *S. horridus* lizards within the REBIOSH (i.e., did they maintain body temperatures farther below the species' VT_{max})?; 4) Did the simulated lizards spend more time foraging within the REBIOSH?; 5) Did the simulated lizards have a lower metabolic rate in the REBIOSH? We expected that the REBIOSH would have habitats with higher vegetation cover and cooler microclimate, as well as simulated lizards with higher thermal safety margins, longer foraging duration, and lower metabolic rate than its unprotected surroundings. We expected these differences to be stronger in 2020, after 20 years of protection of the REBIOSH.

2. Materials and methods

2.1. Study area

The study area included the Sierra de Huautla Biosphere Reserve (REBIOSH) and the unprotected area surrounding it, located mostly in the state of Morelos (Fig. 1a, b; southwest corner at coordinates 18.1713N, 99.6634O and northeast corner at 18.7855N, 98.5264W) between the Trans-Mexican Volcanic Belt and the Sierra Madre Occidental biogeographic provinces.

In the study area, the average monthly rainfall during the core months of the rainy season (July–September) is 169.0 mm (SD = 4.3 mm) and the mean temperature of the hottest months of the dry season (March–May) is 25.7 °C (SD = 1.3 °C) (SMN 2010; Fig. S1). The seasonally dry tropical forest of the REBIOSH has an arboreal stratum 4–10 m tall dominated by the families Fabaceae, Poaceae, Asteraceae, and Burseraceae, and by the species *Conzattia multiflora*, *Lysiloma acapulcense*, *Lysiloma divaricatum*, *Bursera* spp., and *Ceiba* spp. (CONANP 2005). There are also small patches of conifer forests and grasslands (CONANP 2005).

Within the REBIOSH, there are 30 small towns, connected by dirt tracks and paved roads, where there is small-scale farming, ranching, and selective timber extraction. To the north of the REBIOSH, the landscape is relatively flat, and in 2015 there were large areas of pastures and croplands, roads and highways, as well as larger towns and cities (CONABIO 2020). To the south, the landscape is mainly mountainous, and in 2015 there were small areas of croplands, human
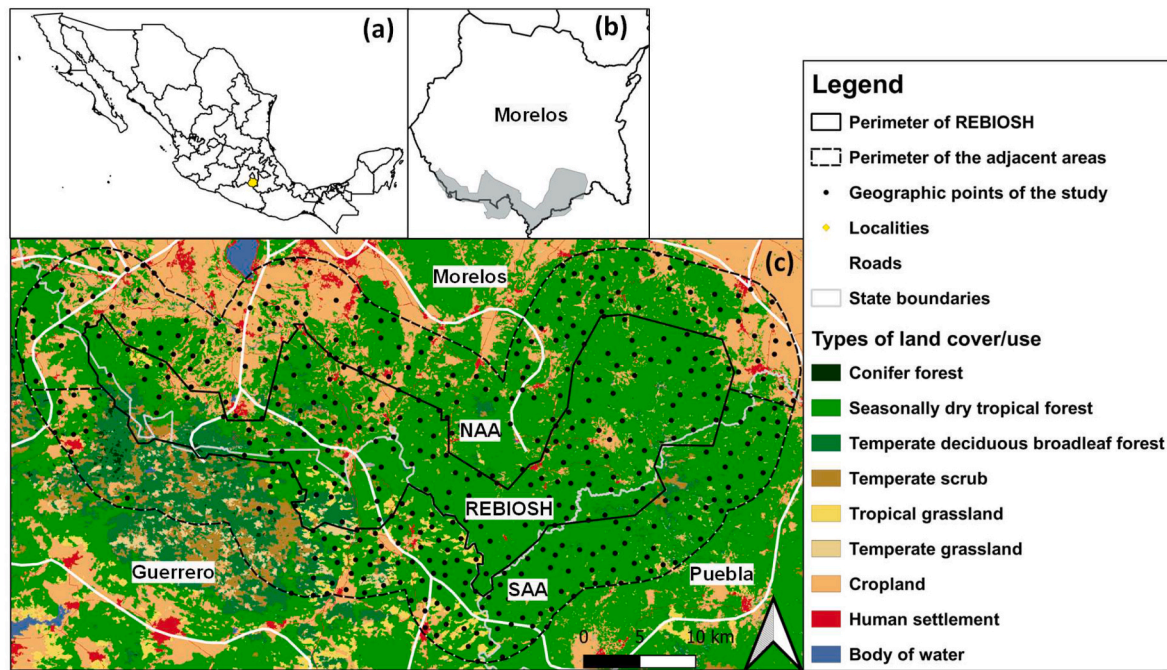
Fig. 1. Maps of the study area. (a) Location of Morelos state in south-central Mexico. (b) Location of the Sierra de Huautla Biosphere Reserve (REBIOSH) in southern Morelos. (c) Map of land use/cover (CONABIO 2020) and sampling points ("simulated home ranges") within the three study polygons: REBIOSH, north adjacent area (NAA), and south adjacent area (SAA). Note that the 150 sampling points within each polygon were restricted to the altitudinal range shared among the three polygons (759–1470 masl).

settlements, and few paved roads (CONABIO 2020). Even before 1999, the area that was eventually declared as the REBIOSH had more favorable conservation status than the surrounding area. This contributed to the declaration of the REBIOSH because in order to qualify to be designated as a biosphere reserve in Mexico, an area must be representative of a determined ecosystem and not significantly disturbed by humans (DOF 2021).

To compare the REBIOSH with its surroundings, we followed the method used by Figueroa et al. (2009) to assess the effectiveness of Mexican protected areas, with some modifications. Using QGIS (v.3.8.0), we divided the area surrounding the REBIOSH into two polygons, one to the north and one to the south, to account for the aforementioned landscape-scale differences. Each of these polygons was 1.1 km wide and had the same area like the REBIOSH polygon (59,076 ha). As sample units, within each polygon, we randomly placed 150 sampling points separated from each other by ≥ 1 km (Fig. 1c). To avoid confounding land-use effects with altitude, the sampling points were restricted to the elevational range shared among the three polygons, 759–1470 masl. We also ensured that points did not fall on irrigated croplands, buildings, greenhouses, or paved roads.

2.2. Study variables

Vegetation cover. We characterized the vegetation cover at each of the 150 sampling points in each polygon using the normalized difference vegetation index (NDVI) * 100 (i.e., converted to percentage). The NDVI has been used previously to characterize vegetation cover in studies of lizard ecology and conservation in arid ecosystems (Furnas et al., 2019). We obtained the rasters of the average NDVI for the hottest trimester of the dry season (March–May) and for the core months of the rainy season (July–September) in 1999 and 2020 at a resolution of 30m from Climate Engine (Huntington et al., 2017). We used the NDVI from the rainy season to compare vegetation cover among polygons because the NDVI is most sensitive during the most productive period in seasonal and semi-arid ecosystems (Guzmán et al., 2019). NDVI from the dry season was an input for the simulations of microclimate, thermal safety margin,

foraging duration, and metabolic rate (see below).

Simulated microclimate. We used the R package NicheMapR (Kearney and Porter 2017; 2020) to simulate the microclimate available to *S. horridus* lizards and to model its thermoregulatory behaviors, body temperature, foraging duration, and metabolic rate at each sampling point. To simulate the microclimate, we used the micro_ncep function of NicheMapR, which integrates the topography, incident solar radiation, and climate of a specified geographical point, during a specified interval of date and time, and at both extremes of a specified interval of perch height and shade percentage (this last calculated based on vegetation cover, leaf area index, and the leaf angle ratio) (Kearney and Porter 2017). There is no information about the home range size of *S. horridus* specifically, but the mean home range size of six *Sceloporus* species for which this information is available (1104.0 m², SD = 1440.5 m²; Table S1) is similar to the 30 m spatial resolution (i.e., 900 m² grid cells) utilized by NicheMapR. Thus, we considered the cell surrounding each sampling point to represent the home range of a single simulated *S. horridus* lizard (hereafter, "simulated home range"). The elevation, slope, and orientation of the terrain of the simulated home range were extracted automatically by NicheMapR from a digital elevation model. We were interested in understanding how microclimate was affected by changes in vegetation cover generated by 20 years of protection in the REBIOSH, rather than temperature differences between the specific years of 1999 and 2020. We therefore decided to separate the effect of vegetation cover from the effect of yearly weather fluctuations by using a single climate dataset for microclimate modeling. Constraints of the NicheMapR program did not allow us to use a composite climate dataset that averages the weather of the three hottest months of the dry season across the 20 year timespan, so we used climate data from a single year to run all microclimate simulations. We chose to use climate data from the year 2017 because it was the warmest year in Mexico since data became available in 1971 (CONAGUA 2017) and therefore represented a worst-case scenario for lizard thermoregulation under hot conditions. We used hour as the temporal scale and averaged the hourly records of microclimate temperature from 9 to 16h, the activity time of *S. horridus* (Bustos-Zagal et al., 2013) for the days of the study period in the dry

season (March–May). We calculated the microclimate at perch heights of both 3 cm and 120 cm since microclimate may be cooler higher above the ground in arid woodlands due to increased wind speed (Asbury and Adolph 2007). Using these perch heights allowed us to capture the daytime microclimates available to the lizards that move vertically to access cooler air temperatures and higher wind speeds (Ortega et al., 2017). NicheMapR can accurately describe the microclimate temperature at perch heights of 5 cm and 120 cm (root mean square error of 3.8 °C and 2.8 °C, respectively; Kearney et al., 2018). To characterize the dry season of the seasonally dry tropical forest in NicheMapR, we set the leaf area index to 1.5 (one-sided green leaf area per unit soil surface area; following Maass et al., 1995) and the albedo to 0.24 (following Barradas and Adem 1992). We set the leaf angle ratio to 0 given that nearly all trees in the seasonally dry tropical forest lose their leaves during the dry season. Finally, we set the minimum shade percentage to 0, and the maximum to the percent vegetation cover of the simulated home range.

Simulated body temperature and thermal safety margin. To simulate the body temperature, NicheMapR integrates into the ectotherm subroutine the microclimate simulated previously and the specified traits of the lizard (Kearney and Porter 2017; 2020; code available at https://github.com/mrke/NicheMapR/blob/master/R/ectoR_devel.R). We set the morphology to a "lizard-like object" of 35g of mass with diurnal activity (Bussjaeger 1971; Bustos-Zagal et al., 2013). As thermoregulatory behaviors, the simulated lizard could change its body orientation relative to direct insolation, move along the specified interval of shade percentage, and climb from 3 cm up to 120 cm perch height to attempt to maintain an average body temperature of 34.2 °C or to avoid body temperatures outside the interval of voluntary thermal tolerances (28.8°C–36.4 °C). There are no published reports of VT_{min} for *S. horridus*, only of its VT_{max} (Lemos-Espinal et al., 1993), so we set its VT_{min} as the average body temperature of *S. horridus* in the field during the dry season (34.2 °C) minus 1SD (5.4 °C) (Bustos-Zagal et al., 2013). NicheMapR can accurately describe the observed body temperature in a seasonally arid shrubland similar to our study ecosystem (root mean square error of 3.9°C; Kearney et al., 2018). We did not allow sheltering in burrows because *S. horridus* is not a fossorial or burrowing species, and males spend much of their time courting and defending their territories in open and conspicuous perches above the ground during the dry season (Bussjaeger 1971). *Sceloporus horridus* has been reported to be active between 9 and 16h during the dry season (Bustos-Zagal et al., 2013). We considered this reported activity time because it reflects the meteorological conditions that challenge the thermoregulation of *S. horridus* while it defends its territory during the dry season, generating a temporal trade-off between thermoregulatory and territorial behaviors. We also carried out simulations considering the daylight hours (from 7 to 19h in our study site) to account for the possibility of bimodal activity. The parameters used in the ectotherm model are in Table S3. We calculated the thermal safety margin for each simulated lizard as the species' VT_{max} minus the body temperature recorded every hour between 9 and 16h or 7–19h for each day of the dry season (March–May).

Foraging duration and metabolic rate. Foraging duration was calculated as the average of the total daylight hours per day when the simulated lizard's body temperature was within the species' voluntary thermal tolerance range (28.8°C–36.4 °C) during the hottest trimester of the dry season (March–May). The code of NicheMapR to calculate the foraging duration is available at https://github.com/mrke/NicheMapR/blob/master/R/trans_behav.R. The basal metabolic rate was calculated based on the allometric relationship of the basal metabolic rate to body mass and body temperature of squamate reptiles, following equation number 2 of (Andrews and Pough 1985). The NicheMapR code to calculate the metabolic rate is available at https://github.com/mrke/NicheMapR/blob/master/R/ectotherm.R. We averaged the sum of the 24 hourly basal metabolic rate records generated each day during the dry season (March–May). The unit of the basal metabolic rate was transformed from consumed mL of O_2 to kJ in order to determine the

daily energy required by the simulated lizards to satisfy their basal metabolic rate under the different simulated conditions. We multiplied the O_2 mL/day consumed by the simulated lizard by 20.08 J/mL O_2 to obtain the kJ/day that the simulated lizards expended to maintain its basal metabolic rate (Benabib and Congdon 1992).

2.3. Statistical analysis

We determined whether parametric models were appropriate using the Shapiro-Wilk test of normality, Levene's test of homoscedasticity, normal quantile-quantile plots, and residuals-versus-fit plots. We compared the percent vegetation cover during the rainy season between 1999 and 2020 using Wilcoxon's rank sum test, and among the REBIOSH, NAA, and SAA using a Kruskal-Wallis test. To test for the interactions between year and polygon, we compared the percent vegetation cover during the rainy season among the REBIOSH, NAA, and SAA in 1999 and 2020 using a Kruskal-Wallis test considering six groups (three polygons in two years) with 150 sampling points each. If the Kruskal-Wallis tests were significant, we conducted *post-hoc* Dunn's tests with Bonferroni correction, and we reported effect size as Cliff's delta for significant comparisons. Cliff's delta ranges from -1 to 1, the number indicates the effect size, and the positive numbers indicate that the first group of the comparison is higher than the second. Whenever comparing among the six year-by-polygon groups, we only interpreted pairwise comparisons that were relevant to our main questions (between years within the same polygon and among polygons within the same year). We compared the difference in vegetation cover between years among polygons using an analysis of variance (residuals were normal and heteroscedastic). If the analysis of variance was significant, we conducted Tukey's *post-hoc* tests, and we reported effect size as Cohen's d for significant comparisons.

We compared the microclimate temperature of simulated home ranges, and the thermal safety margin, daily foraging duration, and daily basal metabolic rate of simulated lizards during the dry season using two-way analysis of variance considering polygon, year, and their interaction. Each group had a sample size of 150 sampling points. Whenever the interaction effect was non-significant, it was removed prior to performing *post-hoc* tests. We conducted Tukey's *post-hoc* tests and reported effect size as Cohen's d for significant comparisons. Since *S. horridus* can be found on the ground, on rocks, and on the trunk of trees and may use those surfaces to thermoregulate, we analyzed the available microclimate temperature at the 3 cm and 120 cm perch heights separately. However, since *S. horridus* frequently forages on the ground, we only analyzed the thermal safety margin, daily foraging duration, and basal metabolic rate at the 3 cm perch height. We did all analyses and constructed all figures in R (R Core Team, 2020). The raw data and R-code required to reproduce the below findings are available to download from (Valencia-Esquivel et al., 2015).

3. Results

3.1. Percent vegetation cover

The mean percent vegetation cover differed between years (Wilcoxon rank sum test, W = 39823, *P*= <0.001) and among polygons (Kruskal-Wallis test, X^2 = 58.548, DF = 2, *P*= <0.001). We found a significant difference in the percent vegetation cover among the six polygon-year combinations (Kruskall-Wallis test X^2 = 315.88, DF = 5, *P*= <0.001). *Post-hoc* Dunn's tests showed that in 1999, the mean percent vegetation cover was higher in the REBIOSH than in the NAA, and intermediate in the SAA (statistically similar to the REBIOSH and NAA; Fig. 2; Table 1). In 2020, the mean percent vegetation cover was lower in the NAA than in the REBIOSH and SAA, and similar between the REBIOSH and SAA (Fig. 2; Table 1). *Post-hoc* Dunn's tests showed that the mean percent vegetation cover was higher in 2020 than in 1999 for each of the three polygons (Fig. 2; Table 1). *Post-hoc* Tukey's tests
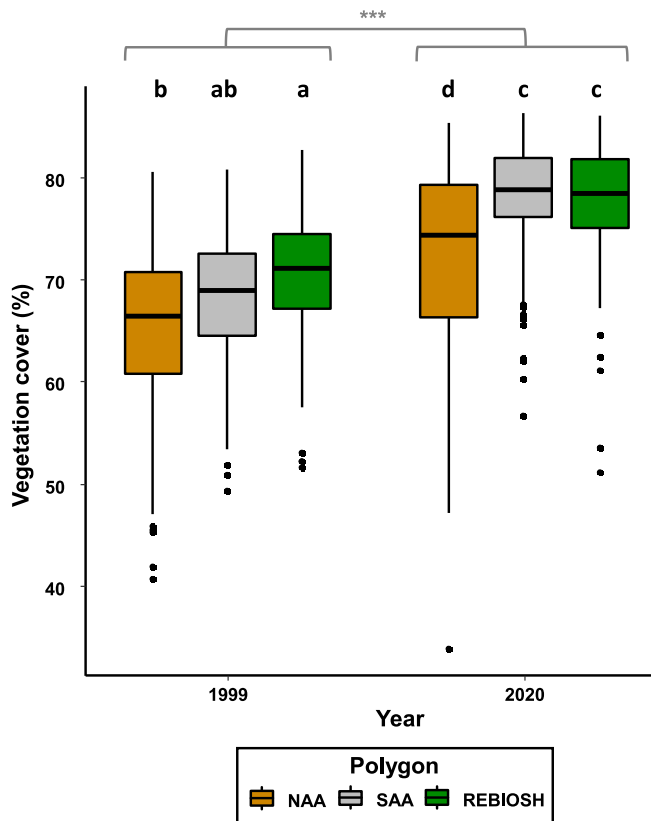
Fig. 2. Vegetation cover (NDVI converted to percentage) within the Sierra de Huautla Biosphere Reserve (REBIOSH) and the unprotected adjacent areas to the north (NAA) and south (SAA) in 1999 and 2020, during the core months of the rainy season (July–September). The color and order of the polygons is shown in the legend. Different letters denote significant differences ($P < 0.05$). Gray brackets denote differences between years (*** indicates a significant difference of $P \leq 0.001$). In the boxplots, the thick black horizontal line denotes the median, the box the interquartile range, the vertical lines 1.5 times the interquartile range, and the points are values outside that range. Each group has a sample size of 150.

Table 1
P-values from *post-hoc* Dunn's test (Bonferroni-adjusted) and Cliff's delta effect size comparing percent vegetation cover among the three polygons (REBIOSH, north adjacent area [NAA], and the south adjacent area [SAA]) in 1999 and 2020, and comparing percent vegetation cover between years in each polygon. *P*-values from *post-hoc* Tukey's test (Bonferroni-adjusted) and Cohen's d effect size comparing the change of percent vegetation cover between years in every polygon. Significant *P*-values are indicated in bold type.

Comparison		Adjusted P	Effect size
Vegetation cover between polygons in each year			
1999 REBIOSH	1999 NAA	**<0.001**	0.372
1999 REBIOSH	1999 SAA	0.517	0.198
1999 NAA	1999 SAA	0.737	−0.208
2020 REBIOSH	2020 NAA	**<0.001**	0.382
2020 REBIOSH	2020 SAA	1.00	−0.026
2020 NAA	2020 SAA	**<0.001**	−0.398
Vegetation cover between years in each polygon			
1999 REBIOSH	2020 REBIOSH	**<0.001**	−0.688
1999 NAA	2020 NAA	**<0.001**	−0.432
1999 SAA	2020 SAA	**<0.001**	−0.762
Difference of the vegetation cover between years among polygons			
1999 vs 2020 REBIOSH	1999 vs 2020 NAA	1.00	0.087
1999 vs 2020 REBIOSH	1999 vs 2020 SAA	0.0716	−0.262
1999 vs 2020 SAA	1999 vs 2020 NAA	**0.0080**	0.349

showed that the difference in mean percent vegetation cover between 1999 and 2020 was similar between the REBIOSH and both adjacent areas, but the SAA gained significantly more vegetation cover than the NAA (Table 1).

3.2. Microclimate temperature

At 3 cm perch height, the mean microclimate temperature of simulated home ranges differed between years ($F_{1,894} = 28.37$, $P = <0.001$) and among polygons ($F_{2,894} = 5.79$, $P = 0.0032$), with no significant interaction effect ($F_{2,894} = 0.10$, $P = 0.9062$). The mean microclimate temperature decreased from 1999 to 2020 in all three polygons (Cohen's d = 0.355; Fig. 3). Considering both years together, the mean microclimate temperature was higher in the NAA than in the REBIOSH and the SAA (NAA-REBIOSH *post-hoc* Tukey's test $P = 0.0043$, Cohen's d = 0.229; NAA-SAA *post-hoc* Tukey's test $P = 0.0224$, Cohen's d = 0.218), and similar between the REBIOSH and SAA (Fig. 3A).

At 120 cm perch height, the mean microclimate temperature of simulated home ranges was different across polygons ($F_{2,894} = 11.108$, $P = <0.001$) but not between years ($F_{1,894} = 0.967$, $P = 0.326$), with no significant interaction effect ($F_{1,894} = 0.003$, $P = 0.997$). Considering both years together, the mean microclimate temperature was higher in the NAA than in the REBIOSH and SAA (NAA-REBIOSH *post-hoc* Tukey's test $P = <0.001$, Cohen's d = 0.385; NAA-SAA *post-hoc* Tukey's test $P = 0.0351$, Cohen's d = 0.203), and similar between the REBIOSH and SAA (Fig. 3B).

3.3. Thermal safety margin

At 3 cm perch height during the reported activity time during the dry season (9–16h), the mean thermal safety margin differed between years
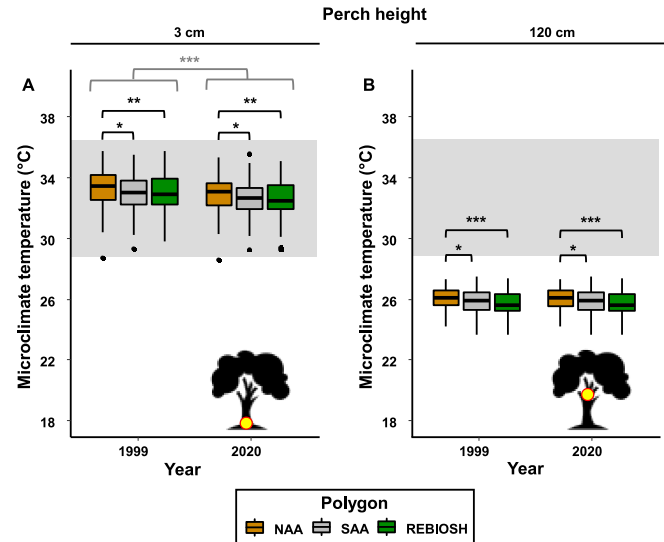

Fig. 3. Microclimate temperature of simulated home ranges within the Sierra de Huautla Biosphere Reserve (REBIOSH) and the unprotected adjacent areas to the north (NAA) and south (SAA) in 1999 and 2020, during the hottest trimester of the dry season (March–May), at 3 (A) or 120 cm (B) perch height. The color and order of the polygons is shown in the legend. Asterisks indicate significant differences between groups connected by brackets (*$P \leq 0.05$, **$P \leq 0.01$, ***$P \leq 0.001$). Gray brackets denote differences between years, and black brackets indicate differences among polygons within each year. Groups not connected by brackets were not significantly different. See text for full statistical results. Each group has a sample size of 150. The shaded region denotes the interval of voluntary thermal tolerances of *S. horridus* (28.8–36.4 °C). In the boxplots, the thick black horizontal line denotes the median, the box the interquartile range, the vertical lines 1.5 times the interquartile range, and the points are values outside that range.

($F_{1,894}$ = 38.218, *P*= <0.001) and among polygons ($F_{2,894}$ = 3.381, *P* = 0.0345), with no significant interaction effect ($F_{1,894}$ = 0.117, *P* = 0.8897). The mean thermal safety margin was higher in 2020 than in 1999 in all three polygons (Cohen's d = 0.413; Fig. 4A). Considering both years together, the mean thermal safety margin was higher in the REBIOSH than in the NAA (*post-hoc* Tukey's test *P* = 0.0398, Cohen's d = 0.199) and intermediate in the SAA (statistically similar to the REBIOSH and NAA; Fig. 4A). The analysis considering the full daylight interval (7–19h) yielded similar results (between years: $F_{1,894}$ = 4.729, *P* = 0.0299; among polygons: $F_{2,894}$ = 4.206, *P* = 0.0152; interaction effect non-significant: $F_{1,894}$ = 0.6811, *P* = 0.5063). As above, the mean thermal safety margin was higher in 2020 than in 1999 in all three polygons (Cohen's d = 0.145) and the thermal safety margin was higher in the REBIOSH than in the NAA (*post-hoc* Tukey's test *P* = 0.0128, Cohen's d = 0.232) and intermediate in the SAA (not statistically distinguishable from the NAA or REBIOSH; figure not shown).

Given that we found differences among polygons in both vegetation cover and thermal safety, we were interested in further exploring whether the thermal safety margin increased with the percent vegetation cover within each polygon and whether the strength of this relationship varied among polygons. Therefore, we performed a multiple linear regression of the thermal safety margin on the percent vegetation cover, the polygon, and their interaction. To simplify the analysis, we considered only the year 2020 since we were most interested in the current conditions. We analyzed the multiple linear regression with a two-way analysis of variance and found that there was a significant interaction effect between predictors ($F_{2,444}$ = 4.439, *P* = 0.0123). Thus, we compared the relationship between the thermal safety margin and percent vegetation cover among polygons with the emmeans package. Thermal safety increased with percent vegetation cover for all three polygons (Fig. S2); the slope of the relationship was significantly higher in the REBIOSH than in the NAA (*post-hoc* Tukey's test *P* = 0.0095; Cohen's d = 0.083), and intermediate in the SAA (statistically similar to the REBIOSH and NAA). Removing one apparent outlier from the NAA (a simulated home range with unexpectedly high thermal safety; See Fig. S2) did not change these overall results (*post-hoc* Tukey's test *P* = 0.0160; Cohen's d = 0.079).

3.5. Foraging duration

The mean daily foraging duration differed between 1999 and 2020 ($F_{1,894}$ = 85.354, *P*= <0.001) but not among polygons ($F_{2,894}$ = 1.088, *P* = 0.3375), with no significant interaction effect ($F_{2,894}$ = 1.387, *P* = 0.2504). The mean foraging duration was higher in 2020 than in 1999 (Cohen's d = 0.616; Fig. 4B) in all three polygons. Considering both years together, mean daily foraging duration was similar among the three polygons (Fig. 4B).

3.6. Basal metabolic rate

The mean daily basal metabolic rate expressed in kJ/d differed between 1999 and 2020 ($F_{1,894}$ = 39.771, *P*= <0.001) and among polygons ($F_{2,894}$ = 4.285, *P* = 0.0141), with no significant interaction effect ($F_{2,894}$ = 1.117, *P* = 0.3279). The mean daily basal metabolic rate was higher in 1999 than in 2020 (Cohen's d = 0.420; Fig. 4B) in all three polygons. Considering both years together, the mean daily basal metabolic rate was higher in the NAA than in the REBIOSH and SAA (NAA-REBIOSH *post-hoc* Tukey's test *P* = 0.0273, Cohen's d = 0.210; NAA-SAA *post-hoc* Tukey's test *P* = 0.0345, Cohen's d = 0.203), and similar between the REBIOSH and SAA (Fig. 4C).

4. Discussion

We found partial support for our hypothesis that the REBIOSH has simulated home ranges with higher vegetation cover and cooler microclimate, and simulated *S. horridus* lizards with higher thermal safety margin, daily foraging duration, and lower daily basal metabolic rate compared to unprotected adjacent areas. The REBIOSH presented simulated home ranges with more vegetation cover and cooler simulated microclimate, and simulated *S. horridus* lizards with higher thermal safety margin and lower daily basal metabolic rate compared to the NAA. The SAA presented simulated home ranges with cooler simulated microclimate and simulated *S. horridus* lizards with lower daily basal metabolic rate than the NAA. Vegetation cover increased over time in all three areas, rather than the REBIOSH only, and microclimate
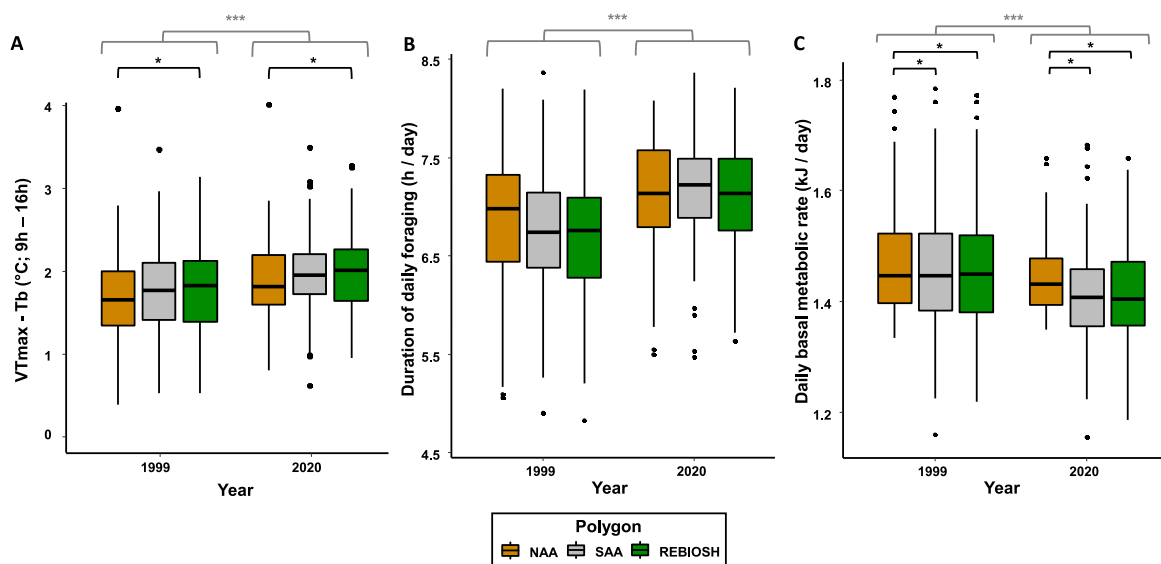

Fig. 4. Thermal safety margin (VT$_{max}$ - T$_b$; A), daily foraging duration (B), and daily basal metabolic rate (C) of simulated lizards within the Sierra de Huautla Biosphere Reserve (REBIOSH) and the unprotected adjacent areas to the north (NAA) and south (SAA) in 1999 and 2020, during the hottest trimester of the dry season (March–May), at 3 cm perch height. The color and order of the polygons is shown in the legend. Asterisks indicate significant differences between groups connected by brackets (*$P \leq 0.05$, **$P \leq 0.01$, ***$P \leq 0.001$). Gray brackets denote differences between years, and black brackets differences among polygons within each year. Groups not connected by brackets were not significantly different. See text for full statistical results. Each group has a sample size of 150. In the boxplots, the thick black horizontal line denotes the median, the box the interquartile range, the vertical lines 1.5 times the interquartile range, and the points are values outside that range.

temperature was higher, thermal safety margin lower, daily foraging duration lower, and daily basal metabolic rate higher in 1999 than in 2020. Thus, our findings suggest that in our study area, *S. horridus* lizards currently experience cooler conditions that allow them to thermoregulate better, reduce their energetic cost of life, and increase their foraging duration compared to when the REBIOSH was declared 20 years ago.

4.1. Vegetation cover

Vegetation cover increased from 1999 to 2020 in the REBIOSH as expected; it also, unexpectedly, increased in the two adjacent areas. Although it was not our initial prediction, increasing vegetation cover in areas surrounding protected areas is a repeated pattern, and the mechanisms behind this trend are the subject of ongoing research (Fuller et al., 2019). It is possible that the vegetation cover of the REBIOSH increased due to its protected status and the implementation of temporary employment opportunities (López-Medellín et al., 2017). Increased vegetation cover within the REBIOSH could augment the production of propagules, pollinators, and/or seed dispersers which may disperse into adjacent areas (sinks; Hansen 2011) and thus increase vegetation cover there through natural succession. It is also possible that larger-scale shifts in conservation attitudes, legislation, and enforcement positively impacted vegetation cover in the region or country. Studies of vegetation cover change over time at larger geographic scales are needed to clarify the mechanisms and scales of this increase in vegetation cover.

The lower vegetation cover in the NAA in both years was probably due to its proximity to tourist developments, cities, and large areas of agricultural fields, all of which were facilitated by its relatively flat terrain (CONANP 2005). In contrast, mountainous terrain has been previously shown to improve conservation status by hampering agriculture and urban activities (Mouillot et al., 2020). Therefore, the REBIOSH and the SAA could share similar percentages of vegetation cover since both are in mountainous terrain. Even though vegetation cover increased in both adjacent areas, this increase was stronger in the SAA than the NAA. It is possible that the REBIOSH influenced this differential increase by acting as a barrier, preventing disturbance from spreading from the NAA to the SAA.

Even though the results of our comparison of vegetation cover among the polygons were clear, NDVI has some limitations in representing the structure of the vegetation and the opportunities it provides for lizard thermoregulation. The vegetation cover estimated using NDVI in the dry season (which we used to simulate microclimates and body temperatures) may be underestimated compared to real vegetation because NDVI considers only active photosynthetic tissue, which is largely reduced during the dry season when woody plants lose their leaves (Singh and Chaturvedi 2018; Guzmán et al., 2019). Even so, NDVI is a realistic and informative marker of vegetation since it correlates with vegetation structure variables such as leaf area index and fractional vegetation cover (Carlson and Ripley 1997) and vegetation function variables such as photosynthetic capacity and net primary production (Pettorelli et al., 2011). Completely excluding dead or non-photosynthetic plant structures using the NDVI could mean that the actual microclimate during the dry season may be cooler than was estimated by our simulation for the three polygons, since real lizards can climb on or take refuge under fallen dead trees or standing leafless trees to thermoregulate. This is partially accounted for in our simulation because the simulated lizards were allowed to ascend to 120 cm perch height to thermoregulate. Also, the NDVI does not differentiate between rain-fed crop fields and native vegetation of the seasonally dry tropical forests during the dry season; however, we determined that it was appropriate to consider these crop fields in our simulations because *S. horridus* does bask and forage there during the dry season (IVE, pers. obs.).

4.2. Microclimate temperature

At 3 cm perch height, simulated lizards experienced cooler microclimates in 2020 compared to 1999 in the entire study area, but at 120 cm perch height, the microclimates were similar between years. This could be due to differences in the interaction between the forest vegetation cover and the atmospheric boundary layer at 3 *versus* 120 cm perch height. The vegetation cover of forest patches buffers the effects of the background environmental conditions, for example by intercepting solar radiation and decreasing wind speed. This buffer is stronger closer to the ground and further from patch borders due to the accumulation of vegetation above and surrounding the point of interest (Ewers and Banks-Leite 2013; Davis et al., 2019). Thus, the cooling of the microclimate at 3 cm perch height from 1999 to 2020 directly mirrored the increase in vegetation cover from 1999 to 2020. Meanwhile, the meteorological conditions at 120 cm were likely more directly affected by background environmental conditions, which are determined by factors that operate on longer time scales, such as topography, soil type, and wind direction (Oliver 2005). The meteorological conditions at 120 cm perch height thus seemed to reflect the local climate more than the more labile microclimate. Finally, our simulation models were deterministic; they did not consider sources of information or randomness of the inputs (as probabilistic models would). Using probabilistic models in future studies could improve our understanding of the biological relevance of vegetation cover change on the temperature of terrestrial ectotherms and their habitats.

Within each year, simulated lizards at both perch heights experienced cooler microclimates on average in the REBIOSH and SAA than in the NAA. This generally followed the vegetation cover differences among polygons, which is expected since higher percentages of vegetation cover generate cooler microclimates (Davis et al., 2019; this study). However, we must consider that although adult lizards use covered sites to exploit their cool microclimates, lizards cannot simply move to areas with increasingly thicker vegetation to avoid the risk of overheating; too much shade may generate environments that are too cold for lizards to sustain their thermal performance (Huey 1982) or the proper development of embryos (Monasterio et al., 2011). Specifically, the performance of lizards increases directly with body temperature up to surpassing its optimal temperature range (Huey 1982) and the embryos of *Psammodromus algirus* take longer to hatch and hatch with poorer body condition at temperatures colder than their optimum. Finer aspects of microclimate dynamics under the canopy could impact lizard thermoregulation and could be explored in future research using more sophisticated modeling tools such as microclimc (Maclean and Klinges 2021).

4.3. Thermal safety margin

The thermal safety margin was higher in 2020 than in 1999 in the entire study area, almost certainly due to the aforementioned increase in vegetation cover and consequent decrease in microclimate temperature. Within each year, considering the reported activity time of *S. horridus* or the daytime hours, the simulated lizards were safer from overheating in the REBIOSH than in the NAA, and intermediate in the SAA (statistically similar to both the REBIOSH and NAA). These results are consistent with previous findings. For example, *S. horridus* lizards had higher mean body temperatures during the dry season of the year in Mexican seasonally tropical dry forests (Bustos-Zagal et al., 2013), and *Uromastyx aegyptia* lizards had higher mean maximum body temperatures during the driest season of the year in disturbed sites with less vegetation cover in the Kuwait desert (Al-Sayegh et al., 2020). These findings demonstrate that thermoregulatory behaviors cannot completely buffer habitat warming during the dry season. The microclimate temperature differed more strongly between polygons than the thermal safety margin. This makes sense given that thermoregulatory lizards like *S. horridus* utilize behavioral thermoregulation to maintain constant body temperatures,

buffering spatial and temporal differences in microclimate temperature (Bustos-Zagal et al., 2013). This finding shows that the thermoregulatory tactics we simulated did partially modulate the effects of microclimatic changes between years and polygons on body temperatures of the simulated lizards.

The buffering capacity of thermoregulatory tactics depends on multiple factors and assumptions, some of which cannot yet be integrated into computational models (Fey et al., 2019). For example, our model assumed that the simulated lizards had the same probability of climbing to thermoregulate in every simulated home range regardless of its vegetation cover. However, territories with lower vegetation cover have fewer bushes and trees to climb, which could make climbing costlier and/or force lizards to utilize other thermoregulatory tactics such as modifying activity times or increasing use of shaded microhabitats. Even though there were simulated home ranges with low vegetation cover in all three polygons, they were more frequent in the NAA, such that the thermal safety margin difference in the NAA could be even stronger than estimated by our models. Indeed, if the vegetation cover of the NAA continues to diminish due to deforestation and fragmentation, the thermal safety margin difference could increase even more, risking in turn the capacity of the landscape north of the REBIOSH to function as a thermal buffer. Another limitation of our model, but a fruitful opportunity for future research, is that we were unable to account for the ecological costs that lizards pay for moving to the shade and climbing to higher perch heights to cool down (Huey and Slatkin 1976). However, there are studies under laboratory conditions that show that thermoregulatory behaviors incur costs on growth, distance moved (Brewster et al., 2013), and travelling time (Basson et al., 2017). Finally, our model did include one of the thermoregulatory tactics used by lizards in hot and arid environments to avoid overheating—a bimodal activity pattern in which lizards are more active in the morning and evening than at midday (Lara-Reséndiz et al., 2014). This occurs in several lizard species that inhabit seasonally dry ecosystems, such as *Phrynosoma goodei* (Lara-Reséndiz et al., 2014) and *Uromastyx aegyptia* (Al-Sayegh et al., 2020) which both avoid the hottest hours at midday by concentrating their activities in the morning and evening. In our simulations, in addition to considering the hours of activity that have been previously reported for this species (9–16h; Bustos-Zagal et al., 2013), we also considered the full daylight interval (7–19h) in order to allow the possibility of a bimodal activity pattern. The thermal safety margin considering the full daylight interval was on average 1 °C higher than when considering the reported activity time, but the differences among polygons were unchanged. These lizards may concentrate their daily activities more frequently in the morning and evening (bimodal activity pattern) in the face of the expected increasingly warmer conditions of their habitats (a result of climate warming). However, such changes in their activity time could increase ecological costs such as interspecific competition, territorial defense, foraging, and predation risk. Field observations of real lizards in dry environments that consider vegetation structure, the thermal conditions of the habitat, the full repertoire of thermoregulatory behaviors, and life history trade-offs will be required to determine how accurately our simulations describe real thermoregulatory ectotherms. Such observations could provide valuable information for designing more complex, flexible, and accurate modeling techniques.

It is also important to consider that different species may respond differently to the same environmental conditions. It is most common to assess environmental quality using species that have low to intermediate stress tolerance (Carignan and Villard 2002). *Sceloporus horridus* is an intermediate heat-tolerant species whose mean body temperature is near the median among 28 lizard species from dry and seasonally dry forests (Table S2). This species could therefore indicate a maximum thermal safety margin for less heat-tolerant species, as well as a minimum thermal safety margin for more heat-tolerant species that inhabit dry or seasonally dry forests.

4.4. Relationship between thermal safety margin and vegetation cover

Thermal safety margin increased with vegetation cover in all three polygons. However, this relationship was stronger in the REBIOSH than the NAA, and intermediate in the SAA (statistically similar to both the REBIOSH and NAA). In general, patches with higher vegetation cover within landscapes with more continuous vegetation cover are more resilient to microclimate warming and have a lower edge effect (Arroyo-Rodríguez et al., 2017). Given that vegetation cover was higher within the simulated home ranges of the REBIOSH than in those of the NAA, the vegetation cover of the former could also be more continuous than in the latter. Therefore, the stronger relationship in the REBIOSH could be the consequence of the vegetation cover being higher within its simulated home ranges and more continuous among them. This emphasizes the importance of habitat connectivity in the planning of protected areas.

4.5. Foraging duration and metabolic rate

We found that simulated lizards were able to dedicate more time of the day to foraging in 2020 than in 1999 and that they foraged a similar number of daily hours among the polygons. The time of thermal restriction (i.e., the time during which an individual must thermoregulate rather than carry out other activities such as foraging) has been previously shown to correlate positively with vegetation loss (Kearney, 2013) and habitat warming (Sinervo et al., 2010). Our results suggest that the lower vegetation cover in 1999 led to higher temperatures, which increased the amount of time that lizards were required to thermoregulate, at the expense of time they could spend feeding. At the same time, we found that the daily basal metabolic rate was higher in the NAA than the REBIOSH and SAA, as well as being higher in 1999 than in 2020. In ectotherms, ingestion efficiency (the energy the animal gains by ingestion minus the energy lost to metabolism) decreases with habitat warming because the metabolic rate increases with increasing body temperature, and can decrease even further if the rate of ingestion cannot increase quickly enough to keep pace with the increased metabolic rate (Rall et al., 2010). Our simulations suggest that lizards in the NAA are subjected to a higher basal metabolic rate, which increases the amount of food they require, but they do not have more time available to forage compared to the REBIOSH and SAA, which likely limits the ability of NAA's lizards to acquire more food to compensate. An insectivorous diet provides 23.276 kJ/g of dry mass (Golley 1961), of which 83% is actually assimilated by *Sceloporus* lizards (19.3 kJ/g; Pough, 1973). Given that the simulated lizards in the NAA, SAA, and REBIOSH consumed 1.44 kJ/d, 1.41 kJ/d, and 1.42 kJ/d in average, respectively, during 2020 conditions; therefore, the lizards in the NAA must consume on average 0.001 more grams of an insectivorous diet than the lizards in the REBIOSH and 0.002 more than in the SAA under 2020 conditions.

4.6. Protected areas as thermal refuges against climate warming

Climate warming could decrease the thermal safety margin of lizards, risking the viability of their populations. Direct effects of climate warming can modify life history traits of lizard populations and threaten their population persistence. For example, *Zootoca vivipara* lizards in field enclosures 2 °C warmer than the mean ambient temperature had an accelerated life cycle and lower adult survival, leading to the prediction of their local extinction in the near future (Bestion et al., 2015). A similar trend was suspected to have occurred as a consequence of climate changes over the past several decades, leading to the local extirpation of several lizard species of *Sceloporus* in Mexico (Sinervo et al. 2010). Sinervo et al. (2010) proposed that the disappearance of previously documented populations between 1975 and 2010 was related to the hours of restriction of activities like foraging, when lizards had to retreat to thermal refuges to avoid overheating. Direct effects of climate warming or temporal costs of thermoregulatory behaviors are unlikely

to decrease sufficiently to compensate for climate warming even if heat tolerance increases through mechanisms such as plasticity or adaptive evolution. For example, acclimation led to a heat tolerance increase of 1.8 °C at most for multiple species of lizards (Clusella-Trullas and Chown 2014) and CT_{max} increased by only 0.51 °C after 16 generations in *Drosophila subobscura* (Mesas et al., 2021). This degree of tolerance is clearly insufficient to cope with the mean temperature increase of 4.2 °C during March–May that is projected by the year 2080 in Morelos, Mexico under business-as-usual climate projections (Bolongaro et al., 2006). Furthermore, directional selection on the adaptive evolution of heat tolerance traits such as physiological increases in CT_{max} could be slowed down by the buffering effect of behavioral thermoregulation (Huey et al., 2003). Given the evident importance and flexibility of behavioral thermoregulation, it is therefore critical to decrease lizards' thermal exposure in their habitats through management activities such as protected areas. Protected areas can provide cooler microclimates which ectotherms may exploit to decrease their risk of overheating in tropical ecosystems (like in this study), and as always, protecting tree biomass and preventing land use change and habitat loss are important strategies to promote biodiversity, ecosystem services, and carbon sequestration and storage (Imorou et al., 2021).

The buffering capacity of habitats in protected areas could decrease if vegetation cover is lost within or adjacent to protected areas. Therefore, we must protect the percentage of vegetation cover of protected areas to ensure that lizards have access to shade where they can avoid stressful temperatures in order to assure the sustainment of their hours of diurnal activity (Kearney 2013). Secondly, we must address the disturbance in the surroundings of protected areas (Laurance et al., 2012). For example, we must control and manage the anthropization in the NAA since disturbance in adjacent areas tends to creep into the edges of protected areas, especially regarding climatic attributes, vegetation cover, and deforestation (Laurance et al., 2012). Finally, although it is important to increase the total area dedicated to protected areas, it is important that this expansion be strategic, protecting the sites that can maintain the most favorable conditions for populations persistence in the face of climate warming scenarios (Prieto-Torres et al., 2021). Our simulations show that in addition to a number of considerations such as biological interactions and existing anthropogenic disturbance (Mora 2017), thermal biology must be taken into account, especially when considering the conservation of ectotherms in hot, dry environments that will only be further stressed as the climate continues to warm. In the case of the REBIOSH, our simulations suggest that it would be highly valuable to extend the protection of the REBIOSH into the SAA. The SAA presented cool microclimate temperatures, similar to those of the REBIOSH, which allowed simulated lizards to spend less energy to fulfill their daily basal metabolic rate than in the NAA. Furthermore, the western portion of the SAA has already been tagged as a priority terrestrial region for conservation, the Sierra Taxco-Huautla (Arriaga et al., 2000), and its eastern portion is part of a proposed protected area, the Mixteca Baja Poblana Biosphere Reserve (Valenzuela-Galván et al., 2013). Our study emphasizes the importance of considering thermal biology of the habitats and native species at the microclimate scale when evaluating the effectiveness of protected areas. A valuable next step would be to test our predictions in the field, as well as to carry out similar simulations using projected conditions under different climate change scenarios to better pinpoint which areas are most likely to continue to have favorable microclimate and prioritize the protection of those areas.

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Data and code

The raw data and R-code required to reproduce the below findings are available to download from https://doi.org/10.17632/882j9btjk9.1 (https://data.mendeley.com/datasets/882j9btjk9).

Declaration of interest

The authors declare that they have no conflicts of interest.

CRediT authorship contribution statement

Israel Valencia-Esquivel: Conceptualization, Formal analysis, Investigation, Writing – original draft, Writing – review & editing, Funding acquisition. **Lynna Marie Kiere:** Conceptualization, Formal analysis, Investigation, Writing – review & editing, Supervision. **Marcela Osorio-Beristain:** Conceptualization, Investigation, Writing – review & editing, Supervision, Funding acquisition, All authors contributed to the interpretation of results.

Data availability

I have shared the documents of our dataset and R-code at the Attach File step and the url link where you can find the dataset: https://data.mendeley.com/datasets/882j9btjk9

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jtherbio.2023.103462.

References

Al-Sayegh, M.T., Abd El-Wahab, R.H., Wright, C.D., DeNardo, D.F., 2020. Impact of anthropogenic disturbance and vegetation composition on ecophysiology and activity of *Uromastyx aegyptia* (Forskål, 1775). J. Arid Environ. 181, 104232.

de Andrade, D.V., 2018. Temperature effects on the metabolism of amphibians and reptiles: caveats and recommendations. In: de Andrade, D.V., Bevier, C.R., de Carvalho, J.E. (Eds.), Amphibian and Reptile Adaptations to the Environment, first ed., pp. 129–154 Brazil.

Andrews, R.M., Pough, F.H., 1985. Metabolism of Squamate reptiles: allometric and ecological relationships. Physiol. Zool. 58, 214–231.

Arriaga, L., Espinoza, J.M., Aguilar, C., Martínez, E., Gómez, L., Loa, E., 2000. Sierras de Taxco-Huautla. RTP-120. In: Regiones terrestres prioritarias de México, first ed. CONANP, México, pp. 469–471. Available from: http://www.conabio.gob.mx/conocimiento/regionalizacion/doctos/Tlistado.html.

Arroyo-Rodríguez, V., Saldaña-Vázquez, R.A., Fahrig, L., Santos, B.A., 2017. Does forest fragmentation cause an increase in forest temperature? Ecol. Res. 32, 81–88.

Asbury, D.A., Adolph, S.C., 2007. Behavioural plasticity in an ecological generalist: microhabitat use by western fence lizards. Evol. Ecol. Res. 9, 801–815.

Basson, C.H., Levy, O., Angilletta, M.J., Clusella-Trullas, S., 2017. Lizards paid a greater opportunity cost to thermoregulate in a less heterogeneous environment. Funct. Ecol. 31, 856–865.

Barradas, V.L., Adem, J., 1992. Albedo model for a tropical dry deciduous forest in western Mexico. Int. J. Biometeorol. 36, 113–117.

Benabib, M., Congdon, J.D., 1992. Metabolic and water-flux rates of free-ranging tropical lizards *Sceloporus variabilis*. Physiol. Zool. 65, 788–802.

Bestion, E., Teyssier, A., Richard, M., Clobert, J., Cote, J., 2015. Live fast, die young: experimental evidence of population extinction risk due to climate change. PLoS Biol. 13, e1002281.

Bolongaro, A., et al., 2006. Análisis de la vulnerabilidad y capacidad de adaptación al cambio climático en los sectores más relevantes del Estado de Morelos. Mexico. Instituto Nacional de Ecología, Universidad Autónoma del Estado de Morelos.

Brewster, C.L., Sikes, R.S., Gifford, M.E., 2013. Quantifying the cost of thermoregulation: thermal and energetic constraints on growth rates in hatchling lizards. Funct. Ecol. 27, 490–497.

Bussjaeger, L.J., 1971. Phylogenetic Significance of the Comparative Ethology of the Spinosus Group of *Sceloporus* (Iguanidae). PhD Thesis. University of Oklahoma.

Bustos-Zagal, M.G., Manjarrez, J., Castro-Franco, R., 2013. Uso de microhábitat y termorregulación en *Sceloporus horridus horridus* (Wiegmann 1939) (Sauria: Phrynosomatidae). Acta Zool. Mexic. 29, 153–163.

Camacho, A., Rusch, T.W., 2017. Methods and pitfalls of measuring thermal preference and tolerance in lizards. J. Therm. Biol. 68, 63–72.

Carignan, V., Villard, M., 2002. Selecting indicator species to monitor ecological integrity: a review. Environ. Monit. Assess. 78, 45–61.

Castro-Franco, R., Bustos-Zagal, M.G., Trujillo-Jiménez, P., 2017. Diet composition of *Sceloporus horridus horridus* (Sauria: Phrynosomatidae) in tropical deciduous forest, Mexico. Acta Zool. Mexic. 33, 443–449.

Clusella-Trullas, S., Chown, S.L., 2014. Lizard thermal trait variation at multiple scales: a review. J. Comp. Physiol. B Biochem. Syst. Environ. 184, 5–21.

CONABIO, 2020. Cobertura del suelo de México a 30 metros, 2015. Available from. http://geoportal.conabio.gob.mx/metadatos/doc/html/nalcmsmx15gw.html.

CONAGUA, 2017. Reporte anual del clima en México. Available from. https://smn.conagua.gob.mx/tools/DATA/Climatología/Diagnóstico Atmosférico/Reporte del Clima en México/Anual2017.pdf.

CONANP, 2005. Programa de conservación y manejo de la Reserva de la Biósfera Sierra de Huautla, first ed. CONANP, México.

Carlson, T.N., Ripley, D.A., 1997. On the relation between NDVI, fractional vegetation cover, and leaf area index. Rem. Sens. Environ. 62, 241–252.

Davis, K.T., Dobrowski, S.Z., Holden, Z.A., Higuera, P.E., Abatzoglou, J.T., 2019. Microclimatic buffering in forests of the future: the role of local water balance. Ecography 42, 1–11.

DOF, 2021. Ley general del equilibrio ecológico y la protección al ambiente. Available from. http://www.diputados.gob.mx/LeyesBiblio/pdf/LGEEPA.pdf.

Ewers, R.M., Banks-Leite, C., 2013. Fragmentation impairs the microclimate buffering effect of tropical forests. PLoS One 8, e58093.

Fey, S.B., et al., 2019. Opportunities for behavioral rescue under rapid environmental change. Global Change Biol. 25, 3110–3120.

Figueroa, F., Sánchez-Cordero, V., Meave, J.A., Trejo, I., 2009. Socioeconomic context of land use and land cover change in Mexican biosphere reserves. Environ. Conserv. 36, 180–191.

Fuller, C., Ondei, S., Brook, B.W., Buettel, J.C., 2019. First, do no harm: a systematic review of deforestation spillovers from protected areas. Global Ecol. Conserv. 18, e00591.

Furnas, B.J., Newton, D.S., Capehart, G.D., Barrows, C.W., 2019. Hierarchical distance sampling to estimate population sizes of common lizards across a desert ecoregion. Ecol. Evol. 9, 3046–3058.

Geldmann, J., Barnes, M., Coad, L., Craigie, I.D., Hockings, M., Burgess, N.D., 2013. Effectiveness of terrestrial protected areas in reducing habitat loss and population declines. Biol. Conserv. 161, 230–238.

Gilbert, A.L., Miles, D.B., 2016. Food, temperature and endurance: effects of food deprivation on the thermal sensitivity of physiological performance. Funct. Ecol. 30, 1790–1799.

Golley, F.B., 1961. Energy values of ecological materials. Ecology 42, 581–584.

Guzmán, J.A., Sanchez-Azofeifa, G.A., Espirito-Santo, M.M., 2019. Remote sensing MODIS and PROBA-V NDVI products differ when compared with observations from phenological towers at four tropical dry forests in the Americas. Rem. Sens. 11, 2316.

Hansen, A., 2011. Contribution of Source-Sink theory to protected area science. In: Liu, J., Hull, V., Morzillo, A.T., Wiens, J.A. (Eds.), Sources, Sinks and Sustainability, first ed. Cambridge university press, pp. 339–360.

Huey, R.B., 1982. Temperature, Physiology, and the ecology of reptiles. In: Gans, Carl, Pough, F.H. (Eds.), Biology of the Reptilia, first ed. Academic Press, New York, pp. 25–74.

Huey, R.B., Slatkin, M., 1976. Cost and benefits of lizard thermoregulation. Q. Rev. Biol. 51, 363–384.

Huey, R.B., Hertz, P.E., Sinervo, B., 2003. Behavioral drive versus behavioral inertia in evolution: a null model approach. Am. Nat. 161, 357–366.

Huntington, J.L., Hegewisch, K.C., Daudert, B., Morton, C.G., Abatzoglou, J.T., McEvoy, D.J., Erickson, T., 2017. Climate engine: cloud computing and visualization of climate and remote sensing data for advanced natural resource monitoring and process understanding. Bull. Am. Meteorol. Soc. 98, 2397–2409.

Imorou, I.T., et al., 2021. Estimation of reference emission and absorption levels in Benin's protected areas. Low Carbon Econ. 12, 117–136.

Kearney, M.R., Porter, W.P., 2017. NicheMapR – an R package for biophysical modelling: the microclimate model. Ecography 40, 664–674.

Kearney, M.R., 2013. Activity restriction and the mechanistic basis for extinctions under climate warming. Ecol. Lett. 16, 1470–1479. https://doi.org/10.1111/ele.12192.

Kearney, M.R., Munns, S.L., Moore, D., Malishev, M., Bull, C.M., 2018. Field tests of a general ectotherm niche model show how water can limit lizard activity and distribution. Ecol. Monogr. 88, 672–693.

Kearney, M.R., Porter, W.P., 2020. NicheMapR – an R package for biophysical modelling: the ectotherm and Dynamic Energy Budget models. Ecography 43, 85–96.

Klemens, J.A., Deacon, N.J., Cavender-Bares, J., 2011. Pasture recolonization by a tropical oak and the regeneration ecology of seasonally dry tropical forests. In: Dirzo, R., Young, H.S., Mooney, H.A., Ceballos, G. (Eds.), Seasonally Dry Tropical Forests: Ecology and Conservation, first ed. Island Press, Washington, USA, pp. 221–238.

Lara-Reséndiz, R.A., Jezkova, T., Rosen, P.C., Méndez-de La Cruz, F.R., 2014. Thermoregulation during the summer season in the goode's horned lizard *Phrynosoma goodei* (Iguania: Phrynosomatidae) in Sonoran desert. Amphibia-Reptilia 35, 161–172.

Lara-Reséndiz, R.A., Rosen, P.C., Sinervo, B., Miles, D.B., Méndez-De La Cruz, F.R., 2022. Habitat thermal quality for *Gopherus evgoodei* in tropical deciduous forest and consequences of habitat modification by buffelgrass. J. Therm. Biol. 104, 103192.

Laurance, W.F., et al., 2012. Averting biodiversity collapse in tropical forest protected areas. Nature 489, 290–293.

Lemos-Espinal, J.A., Ballinger, R.E., Javelly-Gurria, J.M., 1993. Observations on the sensitivity to high temperatures in two lizard species (*Ameiva undulata* and *Sceloporus horridus*) from Zacatepec, Morelos, Mexico. Bull. Md. Herpetol. Soc. 29, 24–29.

López-Medellín, X., Vázquez, L.B., Valenzuela-Galván, D., Wehncke, E., Maldonado-Almanza, B., Durand-Smith, L., 2017. Percepciones de los habitantes de la Reserva de la Biósfera Sierra de Huautla: Hacia el desarrollo de nuevas estrategias de manejo participativo. Interciencia 42, 8–16.

Maass, J.M., Vose, J.M., Swank, W.T., Martínez-Yrízar, A., 1995. Seasonal changes of leaf area index (LAI) in a tropical deciduous forest in west Mexico. For. Ecol. Manag. 74, 171–180.

Maclean, I.M.D., Klinges, D.H., 2021. Microclimc: a mechanistic model of above, below and within-canopy microclimate. Ecol. Model. 451, 109567.

Mesas, A., Jaramillo, A., Castañeda, L.E., 2021. Experimental evolution on heat tolerance and thermal performance curves under contrasting thermal selection in *Drosophila subobscura*. J. Evol. Biol. 34, 767–778.

Monasterio, C., Shoo, L.P., Salvador, A., Siliceo, I., Díaz, J.A., 2011. Thermal constraints on embryonic development as a proximate cause for elevational range limits in two Mediterranean lacertid lizards. Ecography 34, 1030–1039.

Mora, F., 2017. A structural equation modeling approach for formalizing and evaluating ecological integrity in terrestrial ecosystems. Ecol. Inf. 41, 74–90.

Mouillot, D., Velez, L., Maire, E., Masson, A., Hicks, C.C., Moloney, J., Troussellier, M., 2020. Global correlates of terrestrial and marine coverage by protected areas on islands. Nat. Commun. 11, 1–12.

Oliver, J.E. (Ed.), 2005. Encyclopedia of World Climatology, first ed. Springer, New York.

Ortega, Z., Mencía, A., Pérez-mellado, V., 2017. Wind constraints on the thermoregulation of high mountain lizards. Int. J. Biometeorol. 61, 565–573.

Pettorelli, N., Ryan, S., Mueller, T., Bunnefeld, N., Jedrzejewska, B., Lima, M., Kausrud, K., 2011. The normalized difference vegetation index (NDVI): unforeseen successes in animal ecology. Clim. Res. 46, 15–27.

Portillo-Quintero, C.A., Sánchez-Azofeifa, G.A., 2010. Extent and conservation of tropical dry forests in the Americas. Biol. Conserv. 143, 144–155.

Pough, F.H., 1973. Lizard energetics and diet. Ecology 54, 837–844.

Prieto-Torres, D.A., Nuñez Rosas, L.E., Remolina Figueroa, D., Arizmendi, M. del C., 2021. Most Mexican hummingbirds lose under climate and land-use change: long-term conservation implications. Perspect. Ecol. Conserv. 19, 487–499.

R Core Team, 2020. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. Available from. https://www.R-project.org/.

Rall, B.C., Vucic-Pestic, O., Ehnes, R.B., Emmerson, M., Brose, U., 2010. Temperature, predator–prey interaction strength and population stability. Global Change Biol. 16, 2145–2157.

Rangel-Patiño, C.A., Mastachi-Loza, C.A., Eifler, D., García-Morales, C., Ruiz-Gómez, M. de L., 2020. When things get hot: thermoregulation behavior in the lizard *Sceloporus aeneus* at different thermal conditions. J. Therm. Biol. 89, 102572.

Siliceo-Cantero, H.H., García, A., Gao, Y., 2016. Abundance and habitat use of the lizard *Sceloporus utiformis* (Squamata: Phrynosomatidae) during the seasonal transition in a tropical environment. Rev. Mex. Biodivers. 87, 1301–1307.

Sinervo, B., Mendez-de-la-Cruz, F., Miles, B., et al., 2010. Erosion of lizard diversity by climate change and altered thermal niches. Science 328, 894–899. https://doi.org/10.1126/science.1184695.

Singh, J.S., Chaturvedi, R.K., 2018. Introduction. In: Tropical Dry Deciduous Forest: Research Trends and Emerging Features, first ed. Springer, Singapore, pp. 1–12.

SMN, 2010. Normales Climatológicas. Available from. https://smn.conagua.gob.mx/es/informacion-climatologica-por-estado?estado=mor.

Suazo-Ortuño, I., Alvarado-Díaz, J., Martínez-Ramos, M., 2008. Effects of conversion of dry tropical forest to agricultural mosaic on herpetofaunal assemblages. Conserv. Biol. 22, 362–374.

Sunday, J.M., Bates, A.E., Kearney, M.R., Colwell, R.K., Dulvy, N.K., Longino, J.T., Huey, R.B., 2014. Thermal-safety margins and the necessity of thermoregulatory behavior across latitude and elevation. Proc. Natl. Acad. Sci. USA 111, 5610–5615.

Torres, C., Osorio-Beristain, M., Mariano, N.A., Legal, L., 2009. Sex-dependent seasonal feeding activity variations among two species of nymphalidae (lepidoptera) in the mexican tropical dry forest. Ann. Soc. Entomol. Fr. 45, 265–274.

Valencia-Esquivel, J.I., Kiere, L.M., Osorio-Beristain, M., 2022. Protection from overheating of simulated Sceloporus horridus lizards in a biosphere reserve of seasonally dry tropical forest in central Mexico. Mendeley Data v1. https://doi.org/10.17632/882j9btjk9.1. https://data.mendeley.com/datasets/882j9btjk9.

Valenzuela-ceballos, S., Castañeda, G., Rioja-paradela, T., Carrillo-reyes, A., Bastiaans, E., 2015. Variation in the thermal ecology of an endemic iguana from Mexico reduces its vulnerability to global warming. J. Therm. Biol. 48, 56–64.

Valenzuela-Galván, D., Martínez-Garza, C., Orozco-Lugo, C.L., Osorio-Beristain, M., 2013. Estudio previo justificativo para el establecimiento de la "reserva de la biosfera mixteca baja poblana (rebmibap)" puebla, méxico. México city, México.

Vickers, M., Manicom, C., Schwarzkopf, L., 2011. Extending the cost-benefit model of thermoregulation: high-temperature environments. Am. Nat. 177, 452–461.

Vucic-Pestic, O., Ehnes, R.B., Rall, B.C., Brose, U., 2011. Warming up the system: higher predator feeding rates but lower energetic efficiencies. Global Change Biol. 17, 1301–1310.

Wasiolka, B., Blaum, N., 2011. Comparing biodiversity between protected savanna and adjacent non-protected farmland in the southern Kalahari. J. Arid Environ. 75, 836–841.

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