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RESEARCH ARTICLE

Micro and macroclimatic constraints on the activity of a vulnerable tortoise: A mechanistic approach under a thermal niche view

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Abstract

1. Thermal constraints imposed by the environment limit the activity time of ectotherms and have been a central issue in ecophysiology. Assessing these restrictions is key to determining the vulnerability of species to changing thermal niches and developing conservation strategies.
2. We generate an explicit tortoise model of thermal constraints at both micro and macroclimate scales based on thermophysiology parameters and environmental operative temperatures during a biologically significant period. As a study model, we use a vulnerable species of gopher tortoise *Gopherus evgoodei*, whose primary habitat is the tropical dry forests in northwestern Mexico.
3. Our mechanistic model is based on a monitoring of 5 years of environmental operative temperatures (T_e). Here, we use the hours of activity (h_a) and hours of thermal restriction (h_r), calculated from the voluntary temperature range of *G. evgoodei* with respect to T_e, to project and compare the thermal constraints across space and time. In addition, this model was projected using a pessimistic climate change scenario for 2070 (RCP 8.5).
4. The results show that the period of activity of *G. evgoodei*, predicted by h_a and h_r, is limited by the frequency and availability of T_e and differs significantly throughout the year and among years. In addition, under the RCP 8.5 scenario, we predict that h_r will increase considerably and exceed the critical value (3.1 h_r) placing this species as highly vulnerable.
5. We discuss and compare the period of potential activity, thermoregulation strategies, and costs and benefits with other *Gopherus* species. Finally, we identify critical areas throughout its range to develop management strategies for protecting this Mexican endemic tortoise.

KEYWORDS
biophysical environment, climate change, environmental constraints, hours of thermal restriction, Testudinidae, thermal niche, tropical dry forest

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1 | INTRODUCTION

Thermoregulation is key to the survival, performance and fitness of ectotherms, since critical physiological functions (e.g. growth rate, sex determination, locomotion and foraging) are optimized within a narrow range of body temperatures. Therefore, the precision with which organisms regulate their body temperature is related to and limited by the thermal quality of their environments (Vickers & Schwarzkopf, 2016). Thermal constraints on energy and activity-time budgets have been a central issue in reptile ecophysiology (Angilletta, 2001; Grant & Dunham, 1988; Grant & Porter, 1992; Porter & Tracy, 1983). In particular, Dunham (1993) demonstrated that a 2°C variation in air temperature severely constrains the activity time of the lizard *Sceloporus merriami*, reducing energy gain and population growth rate, and therefore can accelerate their extinction (see also Adolph & Porter, 1993; Dunham & Overall, 1994; Huey et al., 2010).

According to Dunham (1993), thermal restrictions imposed by the environment limit the activity of a reptile. For example, on hot days, reptiles use burrows and shelters to avoid exposure to extreme temperatures during the day and reduce potential overheating. If air temperature increases as predicted by current climate models, reptiles will spend longer periods in shelters, reducing critical foraging time, so that the net energy gain becomes insufficient for reproduction. This approach was modelled by Sinervo et al. (2010) in a global study to predict the extinction risk of lizards by climate change. According to Sinervo et al. (2010), reduction in activity time is expressed as hours of restriction (h_r), or hours of forced inactivity, defined as the cumulative hours each day when the environmental operative temperature (T_e) exceeds a thermal threshold [e.g. preferred temperature (T_p) or voluntary maximum temperature (VT_{max})], thus restricting lizard activity in both time and space. Above that threshold, performance declines and the species cannot survive except for a limited period of time, which is further constrained when the maximum critical temperature (CT_{max}) is exceeded. Sites in which activity time has been reduced to 3.85 h_r (as a critical value) per day are the same sites in which lizard populations have become locally extirpated because they are already close to their thermal limits.

Recent studies have been performed using h_r to predict the species geographical distribution (Caetano et al., 2020), determine environmental thermal constraints (Gadsden et al., 2020; Medina et al., 2016) and assess vulnerability to global climate change (Ceia-Hasse et al., 2014; Kubisch et al., 2016; Lara-Reséndiz et al., 2021; Pontes-da-Silva et al., 2018; Sinervo et al., 2018) and other stressors (Tourinho et al., 2021). The use of these eco-physiological models has been widely discussed, where it is desirable to incorporate potential limiting processes (Caetano et al., 2020; Huey et al., 2010; Kearney, 2013). These models are species specific because they are explicitly constructed from the relationship between species physiological variables (e.g. thermal requirements or thermal tolerances) and environmental and biophysical parameters to describe the complexity of its thermal habitat (Buckley et al., 2010; Deutsch et al., 2008; Kearney & Porter, 2009).

Quantifying the heterogeneity of the thermal landscape depends on macroclimatic (e.g. global solar radiation, annual temperature and precipitation) and microclimatic variables of a particular habitat (e.g. T_e, soil type, vegetation type). These factors are integrated with the biophysical and physiological properties of organisms to determine the distribution of available and suitable thermal microclimates (Grant & Porter, 1992). This distribution is defined as the operative thermal environment, and all activities such as thermoregulation, foraging, digestion, mate acquisition, predation and inactivity are constrained to occur within this distribution (Dunham et al., 1989; Grant, 1990; Grant & Dunham, 1988). Therefore, according to Grant and Porter (1992), body temperature and activity times of ectotherms are the result of (a) trade-offs between these resource gains and losses; (b) performance constraints derived from temperature-dependent capacities influencing digestion, locomotion and other vital functions; and (c) the constraint that thermally suitable microclimates are available in sufficient frequency in the ectotherm's home range for activity to occur (see also Angilletta, 2001; Grant, 1990; Porter & Tracy, 1983).

These limitations are especially important for desert tortoises, as the selection of a suboptimal thermal microclimate can lead to hyperthermia and even death by overheating (Hailey & Coulson, 1996; Moulherat et al., 2014; Swingland & Frazier, 1980; Voigt, 1975). In particular, desert tortoises of the genus *Gopherus* experience serious problems when their body temperature exceeds 40°C, which can even be lethal after only a few minutes of exposure (Hutchison et al., 1966; Voigt, 1975). In fact, gopher tortoises spend much of their lives in burrows and other types of shelters to avoid daily and annual thermal extremes (Bailey et al., 1995; Nagy & Medica, 1986; Zimmerman et al., 1994). Despite being herbivorous, they spend little time active on the surface. For example, tortoises in the Sonoran and Mojave deserts hibernate over 100 days per year (Averill-Murray et al., 2002), although there are records of more than 200 days (Bailey et al., 1995). In addition, *Gopherus* tortoises spend considerable time inside burrows during their activity season (late spring, summer and fall). In total, they spend 98.3% of 'inactivity' per year in a burrow (Nagy & Medica, 1986). Therefore, only 1.7% of the year involves surface activity (153 hr/year), in which a substantial proportion of time is devoted to foraging (Marlow, 1979; Nagy & Medica, 1986). Thus, they can be considered as the most elusive animals of the desert.

The tortoise, *Gopherus evgoodei*, is a recently recognized diurnal species that inhabits tropical dry forests (TDFs) in northwestern Mexico (Edwards, Karl, et al., 2016). Because of the cooler thermal environments that characterize TDFs, *G. evgoodei* has one of the lowest active body temperatures among tortoises (T_b; Lara-Reséndiz et al., 2022; Sinervo et al., 2017). In contrast, other species in the genus that inhabit desert environments have higher field active body temperatures, for example, *G. morafkai* and *G. agassizii*. In addition, the distribution of *G. morafkai* abuts that of *G. evgoodei*. Thus, differences in body temperatures between desert and forest tortoises may reflect heterogeneity in thermal opportunity.

In this study, our main objective was twofold. The first goal is to generate an explicit model of thermal constraints at both micro and macroclimatic scales integrating thermal biology parameters and environmental operative temperatures across multiple years for *G. evgoodei*. The second aim is to project our model on the entire geographical distribution and in a climate change scenario. This approach is key to determining the vulnerability of the species, orienting conservation efforts through management of wildlife habitats and reducing the negative impacts of climate warming changes on tropical species. In particular, we ask when are tortoises expected to be active, where are thermal opportunities optimal and what is the duration of time that tortoises may be active? We next examine how these constraints vary throughout its distribution range and under a pessimistic climate change scenario (2070-RCP8.5). Last, we determine to what extent are the patterns of tortoise activity explained by the thermal constraints? To answer these questions, we first gathered data on environmental operative temperatures during a biologically significant period (5 years) and the thermal requirements of *G. evgoodei* (Lara-Reséndiz et al., 2022) to measure thermal restrictions during daily and seasonal activity. Finally, we model the hours of activity and thermal restriction to project them throughout its geographical distribution according to the protocols described above.

2 | MATERIALS AND METHODS

2.1 | Study system

Gopherus evgoodei (Testudinidae) is a recently described species that is considered a vulnerable species by the International Union for Conservation of Nature (Edwards et al., 2018). However, the tortoise does not have protection by the Mexican government (Edwards et al., 2018). A previous study of the thermal biology of *G. evgoodei* determined that its average T_b is 29.4 ± 3.2°C (min–max: 25.3–35.1°C) and the setpoint range (T_{set}; sensus Hertz et al., 1993) was 27.1–31.6°C (Lara-Reséndiz et al., 2022; Sinervo et al., 2017). It is an herbivorous species that reaches a carapace length between 250 and 300 mm (Edwards, Karl, et al., 2016; Van Devender et al., 2002). Its primary habitat includes TDFs and thorn scrub in southern Sonora-Chihuahua and northern Sinaloa, Mexico (Edwards, Karl, et al., 2016). Unlike the habitats of its sister species (*G. agassizii* and *G. morafkai*), the TDF environment experiences marked seasonality providing a well-developed forest canopy that attains a height of 12 m. The understorey environment is a warm, humid and shady microhabitat, which serves as a thermal refuge during the middle of the year (Lara-Resendiz, In Press). The vegetation is composed of tropical species including *Bursera* spp., *Ipomea arborescens*, *Lysiloma divaricatum*, *Handroanthus impetiginosa*, *Haematoxylum brasiletto*, and many other trees and large shrub species (Robichaux & Yetman, 2000). In addition, *G. evgoodei* shares this habitat with other representative tropical reptiles (e.g. *Rhinoclemmys pulcherrima*, *Anolis nebulosus*, *Heloderma horridum exasperatum*, *Ctenosaura macrolopha*, *Boa sigma*, *Micrurus distans*, *Drymarchon melanurus* and *Leptophis diplotropis*, Bury et al., 2002; Schwalbe & Lowe, 2000).

TDFs in Mexico are a major biodiversity hotspots (Myers et al., 2000). TDFs are under a rising threat of habitat fragmentation, where dense continuous forests are being cleared for both livestock and agriculture (Trejo & Dirzo, 2000). The climate of TDF is characterized by a main rainy season in the summer (July to September–November) and a secondary one in the winter (December to January). Due to this bi-seasonal pattern of rains, periods of drought rarely extend beyond one season, so rains provide water and food in the hottest part of summer. The dry season begins in late January until the beginning of the summer rains, although it can be extended up to 8 months (November to June). Mean annual air temperature is 21–22°C with 10 and 41°C as minimum and maximum temperature and freezing temperatures are rare.

2.2 | Environmental operative temperature (T_e)

As part of the Mexico Tortoise Project, a long-term study of available T_e for *G. evgoodei* has been conducted at the Sierra de Alamos-Rio Cuchujaqui Reserve in Sonora, Mexico between 2012 and 2017 (Lara-Resendiz, In Press; Lara-Reséndiz et al., 2022; Rosen, 2014). This protected natural area is recognized by the UNESCO's Man and the Biosphere Program. At this site, *G. evgoodei*'s habitat consists of rocky outcrops and crags and the vegetation is primarily tropical plant species (described above). We monitored a preserved TDF site within the reserve (26.97°N and 108.94°W; elevation 550 m). Precipitation at an elevation of 400–600 m varies between 620 and 700 mm/year (Bury et al., 2002).

Environmental operative temperature models were constructed to mimic the size and shape of the *G. evgoodei* shell. Each model was built using a copper sheet (thickness: 0.66 mm), cut, bent, riveted and sealed with solder and silicone. The size of each model was as follows: 250–300 mm length, 200–220 mm width and 150–170 mm height. These domed, hollow and waterproof models were painted using leaf-green colour (Rustoleum™ Spray Paint) to approximate *Gopherus* reflectivity. These models were previously described and calibrated (see Lara-Resendiz, In Press; Lara-Reséndiz et al., 2022; Rosen, 2014). This methodology has been widely used in tortoises (Bakken & Angilletta, 2014; Dzialowski & O'Connor, 2004; O'Connor et al., 2000; Spotila et al., 2014; Zimmerman et al., 1994).

Environmental operative temperature was monitored using six models with temperature data loggers (Hobo® Pro v2) that recorded temperature every 30 min for 24 hr from October 2012 to September 2017. To prevent the sensor from touching the walls of the model, each sensor was suspended in the middle of the interior of the model. All the models were sealed with silicone and screws to avoid the entry of water and wind once the data logger was inserted in the shell. The models were previously calibrated, with a highly significant linear correlation between the tortoise temperature (T_b) and T_e ($r = 0.94$, $n = 623$, $p < 0.001$; $T_b = 6.875 + [0.783 * T_e]$; see details in Lara-Resendiz, In Press). Therefore, we assume that the copper models accurately measured the T_e available for *G. evgoodei* under field conditions.

The selection of study sites and the location of the models were based on the observation of tortoises during previous fieldwork

(Rosen, 2014) with the purpose characterizing in detail the thermal landscape available to *G. evgoodei*. All models were placed directly on the substrate and distributed in typical microhabitats including a variety of potential microclimates with different levels of solar exposure, soil conditions and vegetation, but always located in the vicinity of tortoise refuges or resting areas and never in open areas (Rosen, 2014; Zimmerman et al., 1994). According to observations obtained from fieldwork and literature, the peak period of activity of *G. evgoodei* occurs during the months of May and October and is mainly diurnal (Edwards, Karl, et al., 2016; Lara-Reséndiz et al., 2022; Rosen, 2014). Permits to place the models were granted by the Área de Protección de Flora y Fauna Sierra de Álamos-Río Cuchujaqui (CONANP) and the landowners. The data on thermal physiology of *G. evgoodei*, used as inputs for the ecophysiological models, were obtained from previous publications (see Lara-Resendiz, In Press; Lara-Reséndiz et al., 2022; Rosen, 2014); therefore, this study did not require ethical approval.

2.3 | Hours of activity (h_a) and hours of restriction (h_r)

To obtain a general function based on the relationship between h_a and h_r, daily maximum, mean and minimum air temperature data (T_{max}, T_{mean}, T_{min}) were obtained from a meteorological station near Alamos (www.conagua.gob.mx). The function *RichHobo* of R package Mapinguari was used to estimate a generalized logistic regression model (Richards growth curve) between h_a and $T_{min} - VT_{min}$ (minimum voluntary temperature: lower 5% of body temperature recorded in the field) and h_r and $T_{max} - VT_{max}$ (maximum voluntary temperature: 95% of body temperature in the field), respectively (Caetano et al., 2020; Sinervo et al., 2018). Where average h_r across the days of the activity season (May–October) is computed integrating the thermal threshold (voluntary temperature range; 25.3–35.1°C; Lara-Reséndiz et al., 2022) and T_e data each day by hours. Here, to calculate h_a and h_r, we only use T_e from May to October and from dawn till dusk according to the seasonal and daily activity time of *G. evgoodei*. In our model, h_r has a value of 1 for $T_e > 35.11°C$ or 0 for $T_e \leq 35.1°C$ and h_a has a value of 1 when $T_e > 25.31°C$ or 0 for $T_e \leq 25.3°C$. Because h_a was calculated from the low threshold (25.3°C) to obtain the total number of h_a, the difference between $h_a - h_r$ per day was obtained. The equation of h_a and h_r in the code was:

$$h_a = \mathrm{Asym}/\left(\left(1 + \mathrm{M}^{*}\exp\left(-\mathrm{K}^{*}\left(T_{min} - VT_{min} - [\mathrm{Infl}]\right)\right)^{\wedge}(1/\mathrm{M})\right)\right)$$
$$\text{and } h_r = \mathrm{Asym}/\left(\left(1 + \mathrm{M}^{*}\exp\left(-\mathrm{K}^{*}\left(T_{max} - VT_{max} - [\mathrm{Infl}]\right)\right)^{\wedge}(1/\mathrm{M})\right)\right),$$

where Asym is the asymptote, M is the shape parameter, K is the slope and Infl is the inflection point.

2.4 | Species distributional records and ecophysiological layers (present and future)

Data for the geographical distribution of *G. evgoodei* were obtained from a variety of sources: Global Biodiversity Information Facility (GBIF, 2021), Madrean Discovery (www.madreandiscovery.org), our prior field sampling (Lara-Resendiz, In Press; Lara-Reséndiz et al., 2022; Rosen, 2014; Sinervo et al., 2017) and the literature (Edwards, Karl, et al., 2016; Edwards, Vaughn, et al., 2016). Localities with points having uncertain localities, identification or otherwise unusable locality descriptors were removed from the dataset. This geographical information was used to crop surfaces automatically in the function *EcophysRaster* of R package Mapinguari (Caetano et al., 2019; Caetano et al., 2020). A 1.5° projection margin was considered from the most extreme points of presence to cut the climatic surfaces and create the ecophysiological layers (h_a and h_r). These layers were constructed based on the hours of activity (h_a) and hours of restriction (h_r) over the whole year. Here, the approach of Sinervo et al. (2010) was applied using the Mapinguari R package (Caetano et al., 2020), which incorporates the extrapolation of biological processes, in this case, thermal physiology (voluntary thermal range) and two important climatic variables for tortoises: (a) maximum air temperature (T_{max}) and (b) minimum air temperature (T_{min}). We obtained these variables from WorldClim (http://www.worldclim.org) at a spatial resolution of 30 arc s (~1 km, Hijmans et al., 2005). We simulated the daily variation in temperature by making a sine wave between maximum and minimum temperature at each cell considering the voluntary temperature thresholds (VT_{min}: 25.3°C and VT_{max}: 35.1°C) of *G. evgoodei* (see Sinervo et al., 2010; also see Caetano et al., 2019; Caetano et al., 2020). Both h_a and h_r were projected for the year 2070 under a pessimistic climate change forecast (RCP8.5). These were computed using T_{max} and T_{min} variables from the Max Planck Institute (MPI-ESM-LR). This model has been validated for its ability to predict contemporary climate change during the control period (Anav et al., 2013) and used in a wide range of reptiles (Lara-Reséndiz et al., 2021; Pontes-da-Silva et al., 2018; Sinervo et al., 2017; Sinervo et al., 2018). We adopted a metric of critical hours of restriction for *G. evgoodei* using the 95% percentile of present-day h_r values, as in the model developed by Sinervo et al. (2010). If a site was predicted to exceed its present critical h_r value, we assumed it would be at risk of extirpation.

Finally, a one-way ANOVA or ranks (Kruskal–Wallis *H* test) to compare thermal constraints by year and activity season was used based on the data conforming to the statistical assumptions. SigmaPlot version 11 (Systat Software) and R software (R Core Team, 2021) were used for statistical analysis and graphing. We built the maps with our ecophysiological layers using QGIS (QGIS.org, 2021). Figures and tables in the text show mean ± standard deviation, sample size (*n*) and temperature range (min − max).

3 | RESULTS

3.1 | Microclimate constraints: Environmental operative temperature, h_a and h_r

The maximum average T_e in the canopy was in April (31.9 ± 12.3°C; 11.5–72.1°C), May (37.0 ± 13.5°C; 12.9–71.8°C), June (39.0 ± 11.8°C; 10.5–72.9°C) and July (30.9 ± 6.3°C; 16.62–66.8°C), while August, September and October maintained constant average temperatures (28.29 ± 4.1, 29.4 ± 6.2 and 28.7 ± 8.7°C; 10.7–69.5°C) and the average temperature was lower in the remaining months (between 20.7 ± 7.6 and 26.7 ± 9.4°C; 3.5–69.5°C). Figure 1 shows T_e throughout the year and day, while Figure 2 shows the T_e levels with respect to the voluntary temperature of *G. evgoodei* in a contour plot. The months that maintained the highest percentage of T_e within their range were June, July, August, September and October between 37.1 and 66.4% and the rest of the months between 11.3 and 30.2% (Figure 3a). Regarding $T_e > 35.1$°C were during June (40.8%), May (36.6%), April (23.7%) and October (20%), while the rest of the months were between 2.6% and 15.9%. The highest percentages of $T_e < 25.3$°C were from November to March (62.5%–85.5%). On the other hand, concerning the time, the highest percentages of T_e within the voluntary range were between 15:00 and 23:00 hr (48.5%–80.7%; Figure 3b); while the lowest hours of potential activity were between 07:00 and 10:00 hr (47%–60.2%) and between 00:00 and 06:00 hr (35.7%–45.7%). These last periods registered the highest percentages of T_e outside the voluntary range (Figure 3b).

Hours of activity and restriction for *G. evgoodei* in Alamos, Sonora are presented in Figure 4. In addition, we related h_a and h_r with environmental temperatures (T_{min}, T_{mean} and T_{max}) to predict environmental signal drives on the activity patterns of *G. evgoodei* (Supplementary Material). The equations for h_a and h_r are:

$$h_a = (7.434)/((1 + (31.971)^* \exp(-(2.088)^* (T_{min} - VT_{min} - [-4.267])))\hat{}(1/(31.971))) \text{ and}$$

$$h_r = (10.035)/((1 + (43.567)^* \exp(-(7.296)^* (T_{max} - VT_{max} - [6.3782])))\hat{}(1/(43.567))).$$

The comparison of h_a and h_r between years and months is shown in Figure 5. Hours of activity between years were significantly different (H_4 = 118.25; $p < 0.001$). The groups identified by Dunn's method are shown in Figure 5. In 2014 and 2015, the lowest values were recorded (4.3 ± 2.8 and 5.2 ± 3.3 h_a; Figure 5a) while the highest values were in 2013, 2017 and 2016 (6.4 ± 2.5 and 8.5 ± 1.9 h_a, respectively). Also, h_a was differed among months (H_6 = 430.87; $p < 0.001$; Figure 5), the lowest values occurred between April and June (2.9 ± 2.4 and 4.3 ± 1.9 h_a), while the highest values occurred between July and October (5.6 ± 2.3 and 10.2 ± 2.3 h_a; Figure 5b). On the other hand, h_r was statistically different between years (H_4 = 95.193; $p < 0.001$) the lowest values were in 2013 and 2016 (2.9 ± 2.4 and 3.5 ± 2.5 h_r), while the highest values were in 2014, 2015 and 2017 (5.3 ± 4.4 and 7.4 ± 3.0 h_r; Figure 5c). Regarding the months, the lowest average h_r was between July and October (0.9 ± 1.4 and 4.8 ± 1.92 h_r), while between April and June the highest h_r occurred (6.7 ± 2.5 and 9.7 ± 2.3 h_r; Figure 5d).

3.2 | Macroclimate constraints: h_a and h_r (present and future)

Hours of activity and restriction across the entire distribution of *G. evgoodei* are presented in Figure 6a,b. Here, we use a polygon of potential distribution of *G. evgoodei* (Lara-Resendiz, unpublished data) to delimit h_a and h_r values within its range. Throughout the distribution, h_a varied between 1.8 and 12.3 (Figure 6a). In particular, the southern part of the distribution (Sonora, Chihuahua and Sinaloa) presented the highest values (>8 h_a), while in the central part of the distribution there were intermediate values (6–8 h_a) and in the northern part were the lowest values (<6 h_a). On the other hand, the h_r varied from 0 to 4 (Figure 6b). In particular, in the northwestern area, there was a higher frequency of high values (>5 h_r), while in the rest of the range there were lower values (<4 h_r).

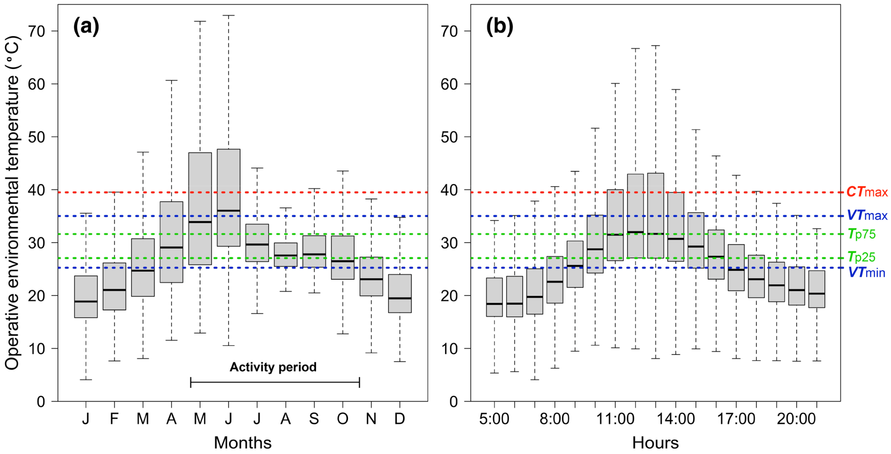

FIGURE 1 Environmental operative temperature values (T_e) for *Gopherus evgoodei* during the active period in Alamos, Sonora. (a) Monthly T_e throughout the year and (b) from 05:00 to 22:00 hr during May to October. Voluntary (VT_{min} – VT_{max}) and preferred (T_{p25}-T_{p75}) temperature range of *G. evgoodei* are indicated by the blue and green dotted lines. Critical maxima temperature of *G. agassizii* (CT_{max} = 39.5°C; Brattstrom, 1965) by the red dotted line and represents the risk of overheating. The boxplots show the median (black line), first and third quartiles (box), and 95% confidence intervals (whiskers) excluding outliers.

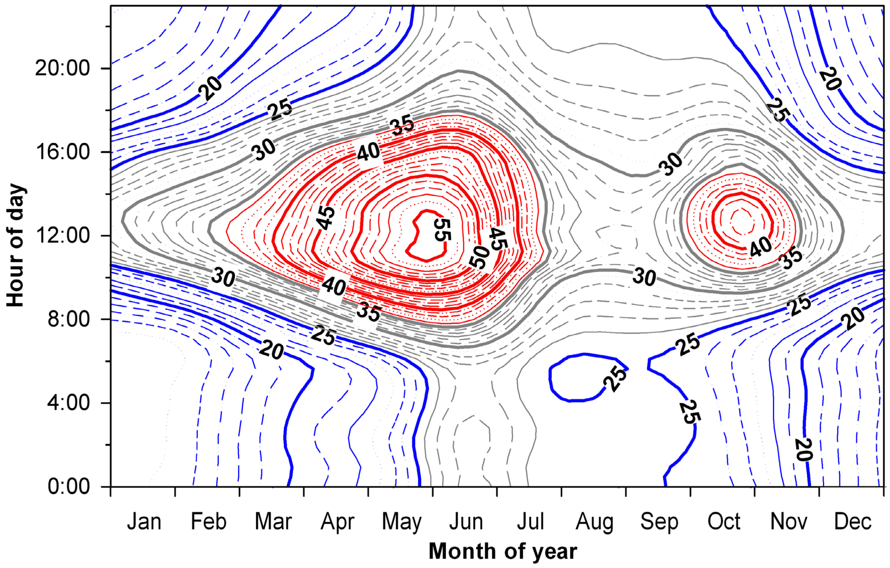

FIGURE 2 Contour plot of average environmental operative temperature (T_e) available throughout the day and year for *Gopherus evgoodei* in Alamos, Sonora. $T_e < 27.09°C$ (blue), $\geq 27.1 \leq 31.6°C$ (grey) and $>31.61°C$ (red).

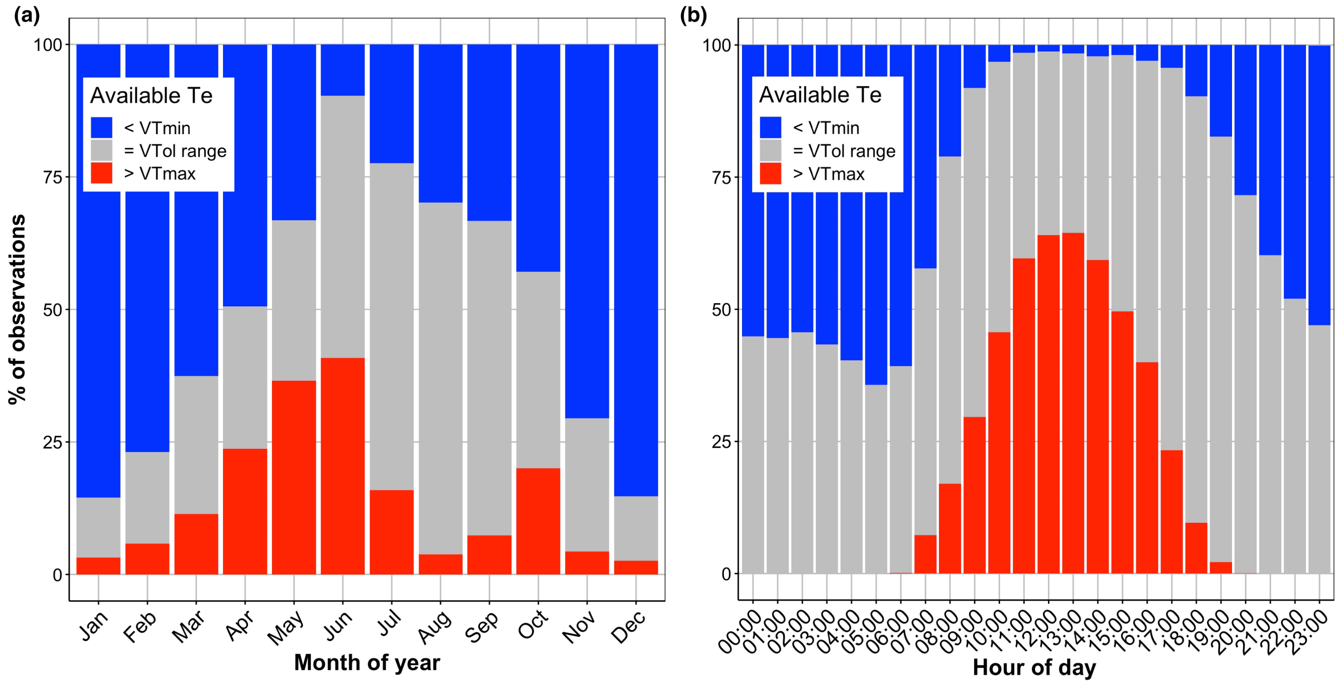

FIGURE 3 Frequency distribution of environmental operative temperature (T_e) available for *Gopherus evgoodei* in Alamos, Sonora. $T_e < 25.3°C$ (blue), $\geq 25.3 \leq 35.1°C$ (grey) and $>35.1°C$ (red). (a) T_e throughout the year and (b) throughout the day during activity season (May–October).

Otherwise, h_a and h_r predicted for 2070 under RCP8.5 were consistently higher than present (Figure 6c,d). With respect to h_a, the sites with the highest activity (>10 hr) increased and the sites with the lowest activity (<5 hr) practically disappeared. This change is most evident in the western and central distribution (Figure 6c). The pattern of h_a in the present versus the future scenario shows an increase (Figure 7a), since the curve of h_a in the present starts from 4 to 12 hr, while in the future it starts from 6 to 12 hr of activity. Similarly, the h_r increased in the future scenario and was manifested throughout the entire distribution of *G. evgoodei* (Figure 6d). The curves of h_r in the present and future (Figure 7b) show an increasing trend. The maximum h_r in the present reached up to 4 hr; however, for the future, they reached up to ~8 hr of restriction. In our model, the critical value of present-day h_r using the 95% percentile of h_r values was 3.1 hr (Figure 7b).

4 | DISCUSSION

In this 5-year ecophysiological study, we mapped the environmental operative temperatures of the available microclimates experienced by *G. evgoodei* within the TDF with biomimetic models. Based on

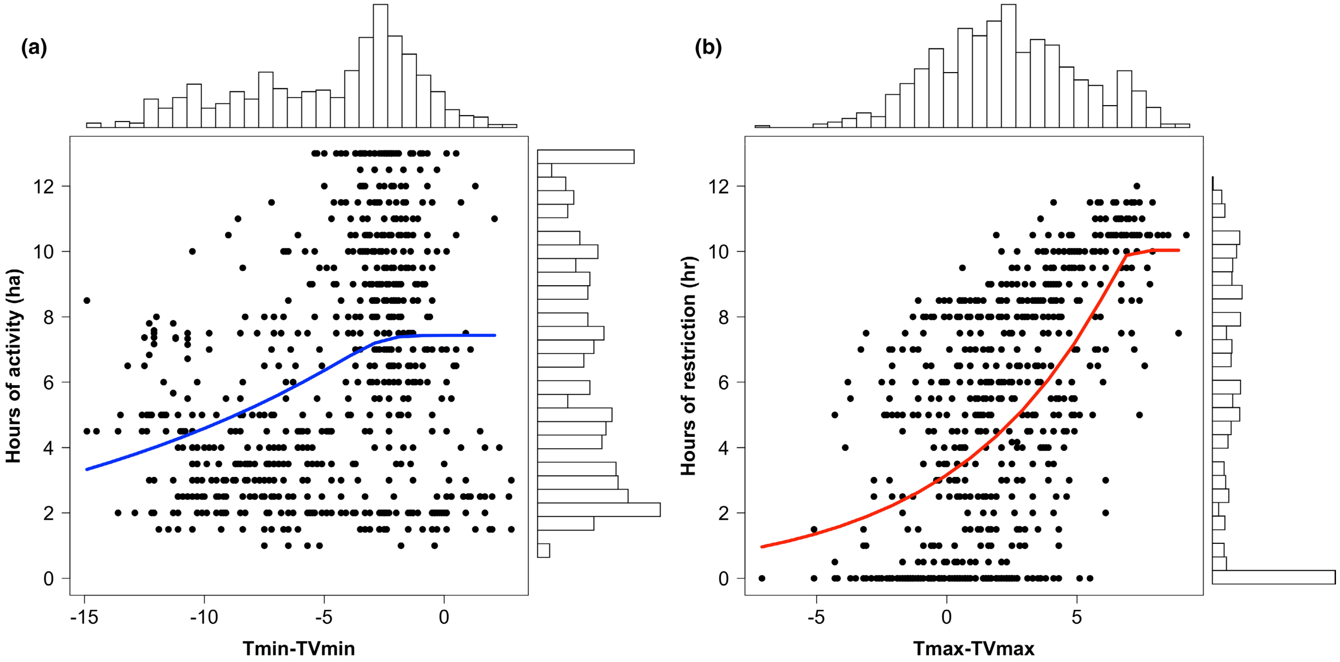

FIGURE 4 Relationship between (a) hours of activity (h_a) and T_{min} – VT_{min} [daily minimum air temperature – minimum voluntary temperature (25.3°C)] and (b) hours of restriction (h_r) and T_{max} – VT_{max} [daily maximum air temperature – maximum voluntary temperature (35.1°C)] of *Gopherus evgoodei* in Alamos, Sonora. h_a and h_r were calculated using environmental operative temperature (T_e) from May to October and from 05:00 to 22:00 hr according to its seasonal and daily activity period. The fitted Richard's growth equations are in the text. Histograms show density.

their thermal thresholds, we predicted the physiological suitability of habitats at a spatiotemporal scale. The results show that the period of activity of *G. evgoodei*, estimated using h_a and h_r, is limited by the frequency and availability of T_e and differs significantly throughout the year and among years. Below, we first discuss and compare the period of potential activity, thermoregulation strategies, and costs and benefits with other *Gopherus* species. Second, we discuss the thermal constraints throughout its distribution. Third, we relate our h_a and h_r results to potential threats that alter their thermal niche. This information is relevant for the establishment and development of conservation strategies for this vulnerable species.

According to Grant and Dunham (1988), many of the behavioural patterns of reptiles can be fully or partially explained by the patterns of temperature availability. Our results support the effect of temperature on the potential activity of *G. evgoodei*. During the dry season in the TDF, the trees lose their leaves and allows sunlight to pass through the canopy. As a result, thermal conditions at ground level are warm and dry, which decreases the proportion of adequate T_e. However, after the first summer rains, the forest canopy recovers, sunlight is mostly intercepted by the canopy, and the understorey becomes shady, warm and humid. In addition, the habitat has high plant productivity, yielding high food availability for tortoises (Robichaux & Yetman, 2000). During this wet season, the understorey exhibits T_e adequate for the activity of *G. evgoodei*, which increases the activity ranges of the tortoises.

Gopherus evgoodei exhibits a passive or thermoformer behaviour with respect to environmental conditions (Lara-Reséndiz et al., 2022; Sinervo et al., 2017). As in other tropical species, understorey tortoises maintain their temperature by moving between 'cold' and warm zones, which implies a lower cost in thermoregulation (Huey & Slatkin, 1976). Furthermore, the average activity temperature of *G. evgoodei* (29.4°C) is similar to other tropical tortoises, but lower than other *Gopherus* species (~3.7°C; Lara-Reséndiz et al., 2022). Apart from its thermoconformity strategy and its low T_b, our model predicts a bimodal activity pattern from April to late May and from October to November, while from early June to late September the pattern could be unimodal (Figure 2). According to this bimodal period, tortoises that are active between 11:00 and 15:00 hr have a high risk of overheating (>50%; Figure 2), while outside this period the risk decreases. Therefore, the narrowness of the activity window for *G. evgoodei* (Figures 2 and 3) supports that these tortoises are severely limited by the reduced availability of favourable T_e at this site.

The environmental T_e of *G. evgoodei* in TDF is strikingly different from that experienced by *G. agassizii* in Mojave Desert (Zimmerman et al., 1994) or *G. morafkai* in the Sonoran Desert (Rosen, 2014). According to the thermal map by Zimmerman et al. (1994) (their Figure 3), the time spent by *G. agassizii* on the surface was constrained by high temperatures during midday. This is consistent with our results, however, Zimmerman et al.'s (1994) thermal map suggests a unimodal pattern of T_e (>40°C) from late June to late September, which is opposite to the bimodal pattern of T_e in the TDF (mid-March–mid-July and early October–early November; Figure 2). The difference in activity patterns is a result of the buffering of extreme T_e by the canopy cover resulting in a near homogeneous thermal landscape, which favours thermoconformity. In

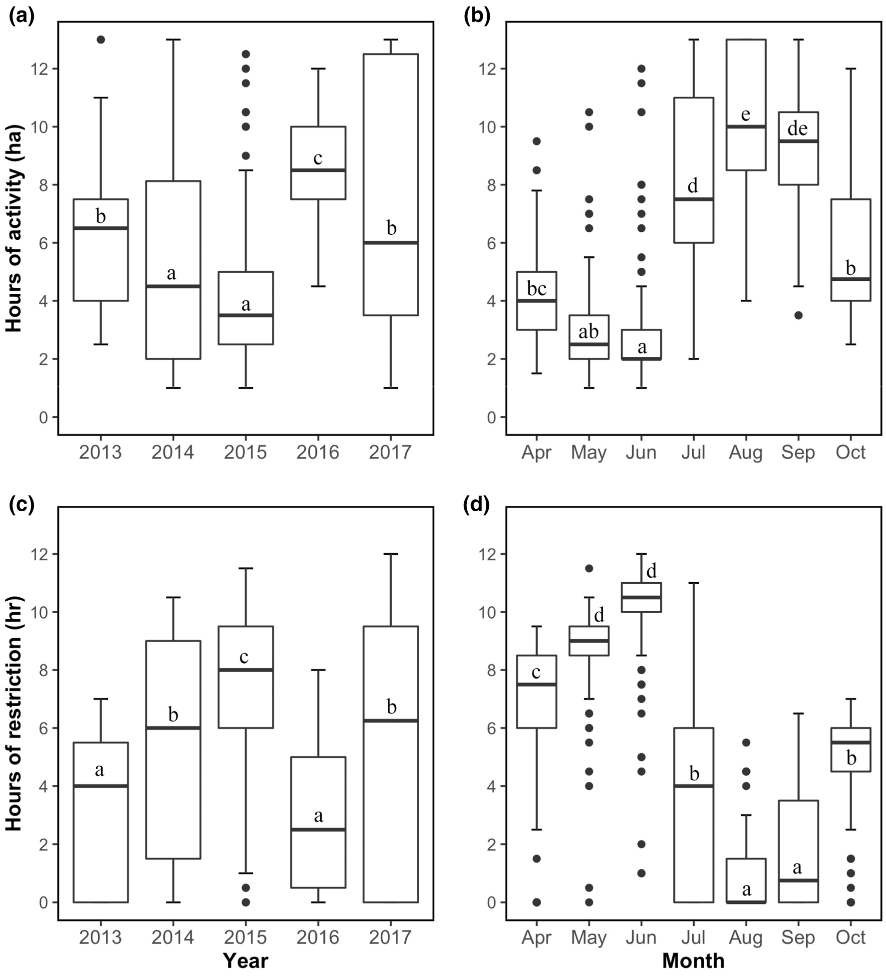

FIGURE 5 Hours of activity (h_a) and hours of restriction (h_r) throughout the years 2013–2017 (a and c) and the months (b and d; activity season) for *Gopherus evgoodei* in Alamos, Sonora. h_a and h_r were calculated using environmental operative temperature (T_e) from May to October and from 05:00 to 22:00 hr according to *G. evgoodei*'s seasonal and daily activity period. Same letters identify same statistical groups using the post-hoc method of Dunn. The boxplots show the median (black line), first and third quartiles (box), 95% confidence intervals (whiskers), and outliers (black points).

contrast, tortoises in the Mojave and the Sonoran Desert require behavioural thermoregulation to maintain T_b below lethal levels (Spotila et al., 2014). It is evident that this result emphasizes the relationship of vegetation with physiological or life-history traits by tropical tortoises. Therefore, habitat modification will have adverse effects on the thermal quality of tortoise's habitat, which results in higher energetic costs, a reduction in spatial and seasonal accessibility and/or availability of adequate microhabitats, and constraining activity times due to hours of thermal restriction.

With regard to climate change, the alteration of the thermal environment can result in a local extinction for this species. On the one hand, a possible advantage of low T_b is that it gives a wide safety margin before overheating (Hailey & Coulson, 1996), there is a margin of over 7.7°C between mean CT_{max} and mean T_e (warming tolerance index; Deutsch et al., 2008) and 3.3°C between VT_{max} and mean T_e. The increase of h_a in the future climate change scenario could be considered a positive effect to *G. evgoodei*; however, the critical threshold of h_r (3.1 hr) is exceeded in practically the entire range (Figure 6d). Sinervo et al. (2010) mention for lizards that if the h_r exceeds the critical value of 3.85 hr, the risk of local extirpation of a species can be as high as 100%. In our analysis using a pessimistic climate change scenario, few populations will remain given the h_r critical threshold. Figure 6d identifies critical areas to develop management strategies for protecting *G. evgoodei* in Mexico from climate warming and other threats because surface temperatures could become lethal in the medium term.

It is clear that *G. evgoodei* faces different thermal challenges throughout its range that could be buffered by thermoregulatory behaviour (Kearney et al., 2009). For example, tortoises escape temperature extremes by retreating to their burrows, which stay cooler in the summer than outside temperatures (~8°C difference between T_b in burrow and T_b on the surface; Zimmerman et al., 1994). Despite this, climate models for northwestern Mexico indicate that towards the end of the 21st century, days with extreme temperatures will increase, the average summer temperature will increase between 3 and 6°C, it is expected that in this area there will be a decrease in the availability of water, including the discharge of streams and the frequency of rains, affecting the relative humidity and the humidity of the soil with prolonged periods of drought (Garfin et al., 2013), which will affect the vegetation cover in the tropical forests (Álvarez-Yépiz, 2020; Bojórquez et al., 2019). In this sense, low food availability and strong thermal constraints on activity could explain slow growth and delayed maturity of lizards (Tinkle & Ballinger, 1972). Here, our ecophysiological model was based on information from thermal niche variables and other environmental variables such as humidity or solar radiation were not considered. As a consequence, the use of different variables derived from nesting ecology, burrow selection, ontogeny shifts in thermal tolerance and demography

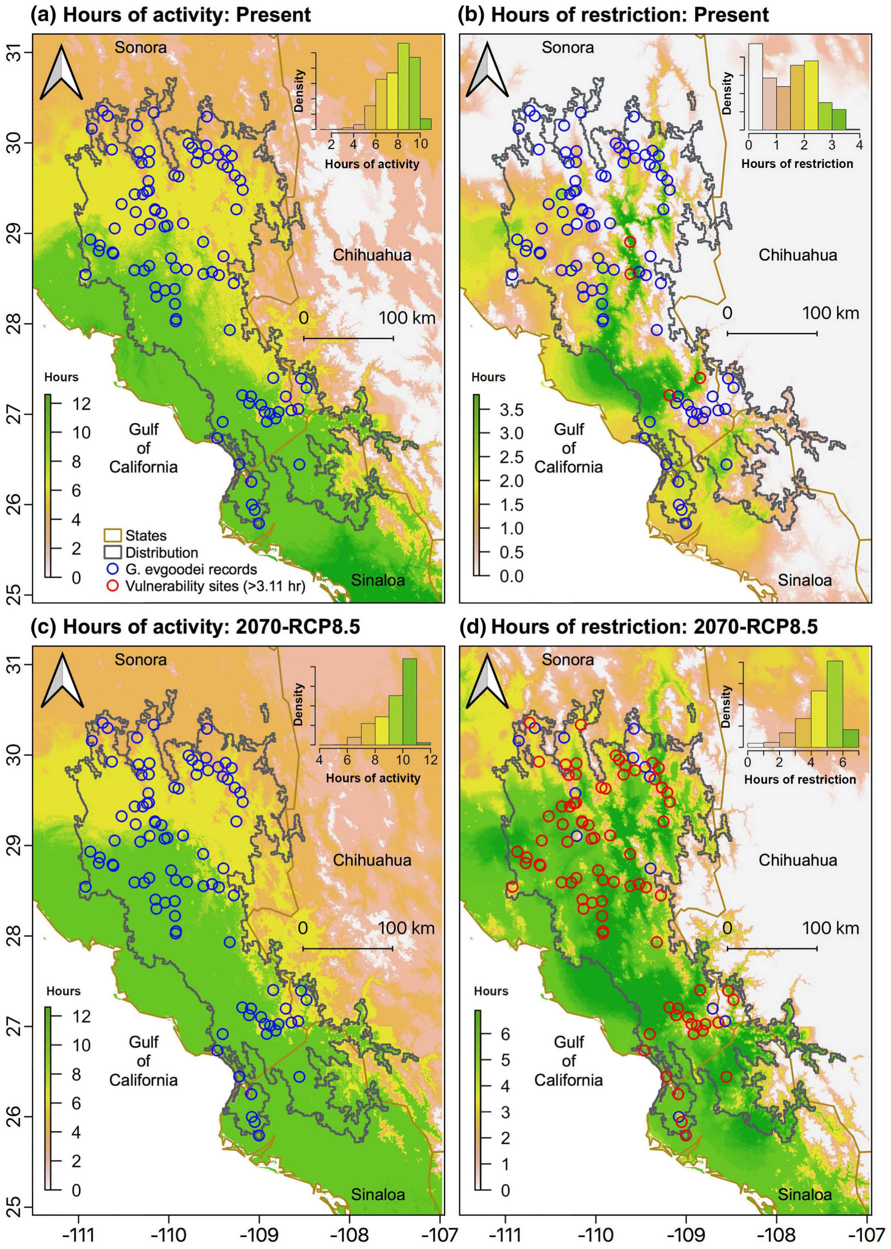

FIGURE 6 (a) Hours of activity (h_a) and (b) hours of restriction (h_r) across the known distribution of *Gopherus evgoodei*. (c and d) show h_a and h_r for 2070 under a pessimistic climate change forecast (RCP8.5). h_a and h_r were calculated using the Senoid method considering the whole year. Histograms show density within the potential distribution. Blue dots show the known distribution filtered at a distance of 10 km. Red dots show sites that exceed the 3.1 h_r threshold.

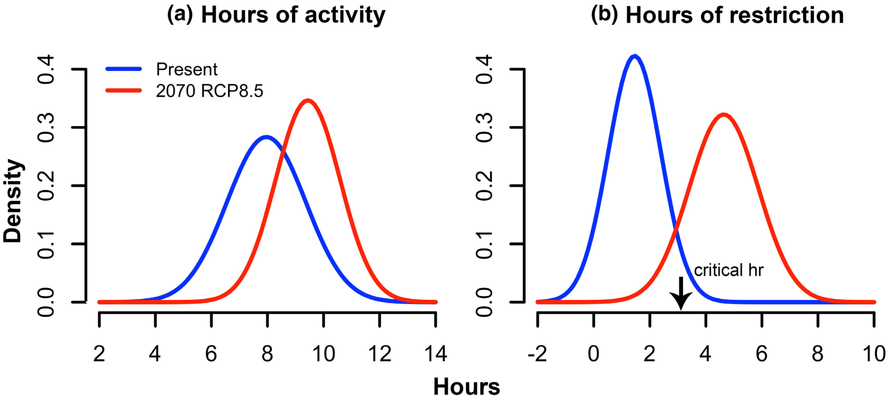

FIGURE 7 Hours of activity (h_a) and restriction (h_r) of *Gopherus evgoodei* for present-day (blue) and 2070 RCP8.5 (red). Arrow indicates the h_r critical calculated from 95% quantile for present-day h_r (3.1 h).

could increase the predictability of the estimated changes observed in our analysis (Kearney, 2013).

As pointed out by Grant and Porter (1992), the daily and seasonal biophysical constraints on activity time affect: (a) individual daily thermoregulatory behaviour; (b) seasonal potential for growth, storage and reproduction; (c) trophic interactions among species; and (d) species distribution limits (also see Dunham, 1993; Dunham & Overall, 1994). Here, we provide an estimate of variation in temperature availability to delineate constraints on daily and seasonal activity time impinging on this tortoise. The scope of this study does not allow us to affirm the effects of warming climate on the population dynamics of this species (e.g. survival, reproductive success or dispersal), but several predictions can be made. In principle, increasing thermal restriction time would further reduce the time available for *G. evgoodei* for foraging and social interactions. It could cause imbalances in their water, energy, and electrolyte budgets and storage levels (Duda et al., 1999). On the other hand, tortoises could modify their thermoregulatory behaviour, selecting higher T_b that can relax the restriction time, but with higher evaporation and overheating rates (Huey & Slatkin, 1976). Because *G. evgoodei* is an herbivorous species, voluntary selection of shelters or perches with high temperatures would maximize the efficiency of the digestion, reproduction and growth processes (Adolph & Porter, 1993). Our model supports that, due to the increase in h_a under a pessimistic climate change scenario, tortoises can extend activity time into twilight or dusk and increase foraging, the number of copulations, and complete their biological activities when the thermal quality allows it. This premise of extending the activity time towards scotophase as a response to climate change has been documented in other reptiles considered exclusively 'diurnal' (Arenas-Moreno et al., 2021; Lara-Resendiz, 2020). Testing these hypotheses and their costs and benefits requires additional field and laboratory studies to define thermal restrictions in locomotion, resource processing capacity, energy budgets, foraging and biotic interactions.

Finally, desert tortoises have adapted to unpredictable periodic climatic conditions (Duda et al., 1999). Although droughts in tropical communities rarely extend beyond one season, our data demonstrate that environmental constraints (h_a and h_r) varies among years. According to available data for *G. agassizii* in the south-central Mojave Desert during a drought year, average monthly temperatures during the spring are slightly warmer, whereas temperatures during the productive year are generally cooler. Also, the productive year has, on average, a warmer autumn than the drought year, as temperatures remain above normal from August through November (Duda et al., 1999). Faced with extreme disturbance events, behavioural modifications have been documented in ectotherms, for example, gopher tortoises avoid leaving their burrow, even during a full year of drought (Duda et al., 1999) or lizards that decreased or modified their activity patterns (Ballinger, 1981; Westphal et al., 2016). These environmental constraints represent a challenge to meet their energy demands over prolonged periods; therefore, we are currently conducting studies of inter-year variation of rainfall and productivity on parameters such as effective surface activity time and 'inactivity' within burrows, home ranges and mobility in response to thermal variation and will make our conclusions more general to future managements and conservation plans.

AUTHOR CONTRIBUTIONS

Philip C. Rosen, Barry Sinervo, Donald B. Miles and Rafael A. Lara-Reséndiz conceived the ideas and designed the study; Rafael A. Lara-Reséndiz and Philip C. Rosen, conducted the fieldwork, developed the methodology and analysed the data; Rafael A. Lara-Reséndiz wrote the manuscript; Donald B. Miles and Barry Sinervo provided editorial advice; Philip C. Rosen, Barry Sinervo, Donald B. Miles and Rafael A. Lara-Reséndiz contributed funding.

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CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

DATA AVAILABILITY STATEMENT

Data deposited in the Dryad Digital Repository https://doi.org/10.5061/dryad.rv15dv49h (Lara-Resendiz et al., 2022).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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