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Hot, dry, and salty: The present and future of an Extremophile model lizard from Argentina

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ABSTRACT

Global warming poses a threat to lizard populations by raising ambient temperatures above historical norms and reducing thermoregulation opportunities. Whereas the reptile fauna of desert systems is relatively well studied, the lizard fauna of saline environments has not received much attention and—to our knowledge—thermal ecology and the effects of global warming on lizards from saline environments have not been yet addressed. This pioneer study investigates the thermal ecology, locomotor performance and potential effects of climate warming on *Liolaemus ditadai*, a lizard endemic to one of the largest salt flats on Earth. We sampled L. *ditadai* using traps and active searches along its known distribution, as well as in other areas within Salinas Grandes and Salinas de Ambargasta, where the species had not been previously recorded. Using ensemble models (GAM, MARS, RandomForest), we modeled climatically suitable habitats for *L. ditadai* in the present and under a pessimistic future scenario (SSP585, 2070). *L. ditadai* emerges as an efficient thermoregulator, tolerating temperatures near its upper thermal limits. Our ecophysiological model suggests that available activity hours predict its distribution, and the projected temperature increase due to global climate change should minimally impact its persistence or may even have a positive effect on suitable thermal habitat. However, this theoretical increase in habitat could be linked to the distribution of halophilous scrub in the future. Our surveys reveal widespread distribution along the borders of Salinas Grandes and Salinas de Ambargasta, suggesting a potential presence along the entire border of both salt plains wherever halophytic vegetation exists. Optimistic model results, extended distribution, and no evidence of flood-related adverse effects offer insights into assessing the conservation status of *L. ditadai*, making it and the Salinas Grandes system suitable models for studying lizard ecophysiology in largely unknown saline environments.

1. Introduction

Ectothermic organisms rely on external sources of heat to achieve body temperatures that allow them to engage in prolonged activity (Huey, 1982; Huey and Slatkin, 1976). Temperature and availability of basking sites and refuges vary among habitat types and climatic regions. Habitats with sparse, low vegetation, such as those found in deserts, often have high and variable temperatures, low availability of refuges, but abundant basking sites. Conversely, tropical forests have high and stable temperatures, high availability of refuges, but low availability of basking sites (Tewksbury et al., 2008).

Lizards have evolved to thrive in extreme environments like deserts,

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taking advantage of their low-cost lifestyle, making a more efficient use of food (Bennett and Nagy, 1977; Nagy et al., 1999) and maintaining an homeostatic equilibrium through different strategies, such as reducing water loss through evaporation (Chew and Dammann, 1961) using their urinary bladders as physiological reservoirs (Davis and DeNardo, 2007) or relying on antidiuretic hormones (Cooper, 2017). In addition, desert lizards may use specialized structures, such as salt glands to excrete excess of electrolytes (Hazard, 2001; Schmidt-Nielsen, 1963).

Deserts typically occur in a belt around 30° latitude, where hot and dry conditions are produced by Hadley cells in the transition between tropics and temperate areas (Whitford and Duval, 2020). In South America, the transition between the tropics and temperate regions occurs as semi-arid forest and woodlands, instead of deserts (Morello and Adamoli, 1968; Prado, 1993). This transition, located in an area shared between Argentina, Paraguay, Bolivia and Brazil is known as the Chaco (or Great Chaco). Some areas in the Chaco still experience extreme conditions, with some of the highest temperature records for South America (air temperatures >50 °C) and rainfall as low as 300 mm per year (Reati et al., 2010). In these arid and salty areas of central-western Argentina, species of the *Liolaemus anomalus* group—the "salty" group—stand out (Abdala and Juárez Heredia, 2013; Morando et al., 2021).

Liolaemus ditadai is an endemic lizard belonging to the *L. anomalus* group that inhabits halophytic vegetation found within the salt flats of the Salinas Grandes System. Although in the region some other lizard species can occur, like *Aurivela longicauda*, *Liolaemus chacoensis*, *L. darwinii* and *Teius teyou*, *L. ditadai* is practically the only species of lizard present deeper in the salt flat (Abdala, 2007; Cei, 1983, but see Pelegrin et al., 2020a). In fact, Pelegrin et al. (2020b) reported that the species can tolerate even more extreme conditions, where vegetation is absent. Published records for the species are restricted to the northern region of Salinas Grandes (Abdala, 2007; Abdala and Juárez Heredia, 2013; Cei, 1983), northern Salinas de Ambargasta (Avila et al., 2015), and a location East of Salinas Grandes (Pelegrin et al., 2020b). Abdala (2007) reported a new record in southeastern Santiago del Estero province, near the saline lake of Mar Chiquita, consisting of a single, poorly preserved museum specimen; therefore, this record should be taken with caution (Abdala and Juárez Heredia, 2013; Avila et al., 2015).

There is scant data on the natural history and population status of *L. ditadai*. The narrow area with halophytic vegetation in the border of the salt flats where *L. ditadai* occurs, is occasionally affected by flooding events. The specialized ecology of the species is likely responsible for the limited number of records since its description in 1983 (Abdala, 2007). The scarcity of occurrence records has resulted in the categorization of *L. ditadai* as threatened in 2012 (Abdala et al., 2012). However, the lack of research on the species' autology led to its categorization as Data Deficient by IUCN (Pelegrin and Abdala, 2017).

The predicted rise in global temperatures may reduce lizard activity by increasing the hours when ambient temperatures exceed preferred temperatures (Sinervo et al., 2010). Given the high temperatures and scarce rainfall, the harsh conditions in the Salinas Grandes system can be compared to those found in deserts environments worldwide (Nicholson, 1998). Whereas the reptile fauna of desert systems is relatively well studied (Disi, 2011; Pianka, 1985, 2017; Tejero-Cicuéndez et al., 2022), the lizard fauna of saline environments has not received much attention and—to our knowledge—thermal ecology and the effects of global warming on lizards have not been addressed in these systems until the present days. *Lioalemus ditadai* can be an excellent model to study the ecology and the effects of climate change in lizards from these particular systems, where high levels of salt are added to the extreme conditions of typical deserts.

Our hypothesis is that the species may be constrained in its ability to maintain its body temperature in the range of its optimal physiological performance due to the high temperatures and low vegetation cover in the Salinas Grandes system, thus making it vulnerable to increasing temperatures. We predict that: 1) Given the disjunct distribution of *L. ditadai* in Salinas Grandes and Salinas de Ambargasta, this species will be widely distributed in both salt flats, provided that short halophytic vegetation is present; 2) Due to the high environmental temperatures this species will have high thermal parameters (body and preferred temperatures), good locomotor performance at high temperatures and be an effective thermoregulator; 3) An increase in global temperatures will reduce the hours of activity of *L. ditadai*, thus negatively affecting the persistence of the lizard's populations.

The objectives for this study are: 1) to determine the current distribution of *L. ditadai* in the Salinas Grandes system; 2) to describe its thermal ecology; and 3) to assess the potential effects of climate change on the species distribution by using ecophysiological models.

2. Material and methods

2.1. Fieldwork and field body temperature

The study was carried out in the Salinas Grandes System, the largest salt flat in Argentina, located in the driest portion of the Chaco. It consists of two major salt flats, Salinas Grandes (~8800 km^2; 29° 56′S, 65° 07′W) and Salinas de Ambargasta (~6300 km^2; (29° 10′S, 64° 24′W), which are separated by a barely perceptible barrier called Alto de Mancilla (Gutiérrez et al., 2017). The landscape in this environment is characterized by salt crusts, shallow temporary ponds and lakes, and short and sparse halophytic shrubs. A Dry Chaco forest surrounds the salt flats, also forming vegetation islands (Cabido et al., 1994, 2018).

Lizard samplings took place in both salt flats, along the border between the provinces of Córdoba and Santiago del Estero, Argentina, using a combination of drift-fence pitfall traps and active searching.

We conducted fieldwork in several locations from October 2015 to April 2022 (see Supplementary Table 1). Trap arrays were installed in three of the sampled locations (Lucio V. Mansilla, Las Cañas, and Las Toscas). Other locations were also visited to capture specimens or just to confirm the presence of *L. ditadai* in different areas of the Salinas Grandes System.

Captures with traps were made using arrays of drift fences with pitfall traps along a 1-km transect, one for each selected location. Each transect was set across a vegetation gradient between the typical Dry Chaco forest and the salt plain. We installed 25 drift-fence pitfall trap arrays along each transect, separating each trap array 40 m from each other. For this study, we only used data from trap arrays located in the salt plain (12 traps from each transect). Each array consisted of four 20 L buckets with three 6 m plastic drift fences arranged in a Y shape. We placed one bucket at the central part of the "Y" and three at the end of each fence (Pelegrin et al., 2017). We checked the traps daily before noon to avoid lizards dying from overheating. Active searches were conducted from 08:00 to 20:00 h, which corresponds to the activity period of the lizards based on our previous observations. We captured lizards using fishing rods affixed with nooses or by hand. To avoid recaptures, all individuals were marked by removing the distal phalange of the second toe of the right forelimb. Also, active captures were made in different areas, and never where traps were located.

For every lizard captured actively, we recorded its body temperature (T_b) along with substrate temperature (T_s) at the site of capture, and air temperature (T_a; measured 5 cm above the substrate) using a digital thermometer (CEM DT-610B, precision of ±0.1 °C). We also recorded the microhabitat type (bare ground, under shrubs, under logs), exposure to sunlight (sun, shade, or filtered light), time and date of capture, sex (male, female, juvenile, unsexed), snout-vent length (SVL, in mm), mass (g), and GPS location. We used the T_b data only from active lizards captured within 20 s. T_b was not measured in individuals captured in traps. All lizards were brought to the laboratory to measure the thermal physiological traits.

We used regression analysis to determine the relationship between T_b and T_a or T_s. Mean ± standard error, sample size (n), and temperature range are presented in all tables and figures. All statistical analyses were performed using the R statistical environment (R Core Team, 2021).

2.2. Thermal preference, critical thermal limits, and the thermal sensitivity of performance

We determined the preferred temperature (T_p) of each individual using a thermal gradient. The gradient was a 160 x 100 × 40 cm (width, length, and height) wooden box that was divided into eight tracks, each containing a substrate of sandy soil measuring 2–3 cm in depth. Solid wood boards separated the tracks to prevent behavioral interference from adjacent lizards. We placed 75 W incandescent light bulbs 20 cm above the substrate at one end of the box, while cold packs were positioned at the opposite end to generate a thermal gradient ranging from 20 to 50 °C. From 07:00 to 19:00 h, we allowed lizards to move freely in the thermal gradient, which contained ten small dishes (1.5 cm diameter) of water. We recorded T_b every minute starting at 9:00 h using ultra-thin (36 ga) T-type thermocouples (OMEGA 5SC-TT-T-36-72) attached with medical tape to the lizards' bellies and connected to an 8-Channel USB Data Acquisition Module (Cardona-Botero et al., 2020).

We considered T_p to be the body temperature selected by a lizard in the absence of biotic and abiotic restrictions. We calculated T_p as the average value of the readings. We also computed the interquartile range (IQR) of temperatures recorded in the gradient, which is defined as the lower (percentile 25%) and upper (percentile 75%) T_p (T_{p25} and T_{p75}, T_{set} *sensus* Hertz et al., 1993). In addition, we computed the lower and upper voluntary thermal range (VT_{min} and VT_{max}) defined as the 5% and 95% percentiles of T_p (Camacho and Rusch, 2017).

After measuring T_p, we determined the thermal sensitivity of sprint speed in 16 adult individuals of *L. ditadai*. To perform locomotor performance trials, we used a racetrack 0.20 m wide and 1 m long. Additionally, lines were drawn on the floor at intervals of 25 cm to facilitate the estimation of sprint speed. Lizards were held at each of six randomized temperatures spanning their critical thermal limits (19, 23, 27, 31, 35, and 39 °C ± 1.5 °C in all cases) for a period of 30 min before measuring sprint performance. We used an 80 W spotlight bulb or ice packs to attain the desired body temperature. We recorded sprint trials using a SJCAM® 7 Star digital camera at 1080 pixels and shutter speed of 120 fps. For each lizard, we conducted three trials at the same temperature, with at least 2 h of rest between runs at different temperatures. We only kept the maximum sprint speed (V_{max}) from the trials over a 25 cm section of the track, using frame-by-frame analysis with Tracker v5.1.5 (Brown and Cox, 2009). To stimulate the lizards to run, we tapped the substrate behind them or gently tapped their tails. Whenever a lizard reversed while running down the track or did not run, the trial was excluded from the analysis. To estimate thermal performance curves (TPCs), we used the best-fit calculated model based on the typical shape of TPC, which is left-skewed with a rapid decline after the optimum, using the Akaike information criterion. We included CT_{min} and CT_{max} data to anchor the endpoints of the TPC (Gilbert and Miles, 2017; Méndez-Galeano et al., 2020), setting sprint speeds to 0 for these endpoints. We applied generalized additive mixed models (GAMM, Zajitschek et al., 2012) using the SVL (mm) as a covariate within the *gamm* function in the MGCV package. The TPC was generated by plotting the residuals of the best GAMM model using ggplot2 and grid packages in R (R Core Team, 2021). We obtained the thermal optimum for performance (T_{opt}), which is the body temperature at which sprint speed is maximal, and the range of temperatures that are ≥80% of the optimal capacity (B80) from TPC. To assess the effect of T_b on V_{max}, we built a linear mixed model (LMM) with Gaussian errors. We performed a post-hoc pairwise comparison test (Tukey) between levels for the temperature effect. We also assessed the effect of size on V_{max} through linear regression analysis with SVL (mm) and mass (g) as predictor variables.

We estimated the critical thermal minimum (CT_{min}) and the critical thermal maximum (CT_{max}) by cooling down or heating up the individuals until they lose their righting response (Bauwens et al., 1995). Cooling and heating rates were about a degree per minute and were obtained by placing the individuals in a plastic container with ice packs (for CT_{min}) or under a lightbulb (for CT_{max}). CT_{min} and CT_{max} trials were separated by a day. Lizard behavior was carefully observed for signals of distress, and their righting response was checked several times per minute. Following the CT_{min} trial, we allowed the lizards to recover by placing them in the thermal gradient for 1 h. After CT_{max} trials, we promptly placed the lizards in a bath of cool water up to their necks to prevent any physiological damage and returned them to their container.

Throughout the experiments, we housed the lizards individually in plastic containers with soil and wooden sticks and provided *ad libitum* water while preventing them from feeding. The containers were maintained at approximately 25 °C. We conducted laboratory experiments within two or three days following capture and released lizards at their capture site after completing the experiments.

2.3. Operative environmental temperatures

We recorded operative environmental temperatures (T_e) for *L. ditadai* on Salinas Grandes during three periods: from January 2017 to March 2018, from August to December 2019 and from December 2020 to October 2021. To approximate *Liolaemus* reflectivity, size, and shape, we used 10-cm long and 2-cm wide polyvinylchloride (PVC) tubes (Dzialowski, 2005; Lara-Reséndiz et al., 2015), painted with 33% reflective gray spray paint (Astudillo et al., 2019; Brizio et al., 2021) connected to dataloggers (Onset HOBO Pro v2 2x External Temperature Data Logger) programmed to record the temperature every 30 min. These models have been validated against body temperatures for small lizards and are widely used and discussed (Bakken and Angilletta, 2014; Dzialowski, 2005; Sinervo et al., 2010). We sealed the models with silicone to prevent the entry of water and air and to affix the sensor, thereby preventing it from touching the PVC walls of the model.

We selected model locations based on previous field observations of *L. ditadai* to accurately characterize the thermal landscape available to the species. We placed the models directly on the substrate and distributed them across microhabitats with varying solar exposure angles, soil conditions, and vegetation cover, which were subjectively determined. Previous observations indicate that *L. ditadai* is diurnal and active mainly between November and May, with activity occurring from 8:00 to 20:00 h (Pelegrin and Abdala, 2017; Pelegrin et al., 2020b).

2.4. Thermoregulation indices

To assess thermoregulation accuracy (d_b) and habitat thermal quality (d_e), we used T_b, T_p, and T_e data. If T_b or $T_e < T_p$ IQR, then $d_b = T_b - T_{p25}$ and $d_e = T_e - T_{p25}$. If T_b or $T_e > T_p$ IQR, then $d_b = T_b - T_{p75}$ and $d_e = T_e - T_{p75}$. If T_b or T_e values were within the T_p IQR, d_b and d_e were considered equal to zero. High values of d_b and d_e indicate low accuracy and low thermal quality, while values equal to or near zero indicate high accuracy of thermoregulation and represent ideal thermal environments. We calculated the effectiveness of temperature regulation (E; Hertz et al., 1993) using the mean values of d_b and d_e as: $E = 1 - \left(\frac{d_b}{d_e}\right)$. E ranges from 0 to 1, when $E = 0$ the organism does not thermoregulate, while E values near 1 indicates that the organism thermoregulates carefully (Hertz et al., 1993).

2.5. Species distributional records, ecophysiological predictors and mechanistic niche modeling

We obtained geographical distribution records of *L. ditadai* from various sources, including Global Biodiversity Information Facility (GBIF, 2021), our own field records, and records from published literature (Abdala and Juárez Heredia, 2013; Avila et al., 2015; Cei, 1983; Pelegrin et al., 2020a, 2020b). Records with dubious identification or locality were excluded. To reduce bias from agglomerated points, we filtered out duplicated records at a resolution of 1 × 1 km using the *cleanpoints* function from the R package Mapinguari v0.4.1 (Caetano et al., 2020). We then cropped climatic surfaces using the *Raster* function and applied a projected margin of 1° from the most extreme presence points. This margin was used to cut the climate surfaces and create the ecophysiological layers (hours of activity: h_a, hours of restriction: h_r, and performance), ensuring accuracy with the distribution records.

We generated layers for availability of activity hours (h_a) and forced hours of inactivity due to high environmental temperatures (hours of restriction, h_r), Here, the approach of Sinervo et al. (2010) was applied using the Senoid functionality within the *EcophysRaster* function of the Mapinguari v0.4.1 R package. Details to this method are presented in Sinervo et al. (2010), and an updated version is outlined in Caetano et al. (2020). This method integrates the extrapolation of biological processes, specifically thermal physiology factors like voluntary thermal limits (VT_{min} and VT_{max}), alongside two crucial climatic parameters for reptiles: maximum air temperature (T_{max}) and minimum air temperature (T_{min}). We obtained T_{max} and T_{min} data from WorldClim version 2 (http://www.worldclim.org) at a spatial resolution of 30 arc-seconds (~1 km; Fick and Hijmans, 2017). The Senoid method was chosen over the Richards method, which uses field-recorded operating temperatures (T_e), due to several advantages such as greater simplicity in the estimation of layers, requiring less computational power, and presenting greater ease of extrapolation to future conditions without sacrificing predictive accuracy compared to the Richards method (Caetano et al., 2020). On the other hand, the latter presents the risk of overfitting to the data used to train it (Caetano et al., 2020). We simulated daily temperature variations by creating a sine wave between T_{max} and T_{min} for each geographic cell, considering the voluntary thermal range. To derive h_a, representing the daily available time for activity when T_{max} fell within this range, we determined h_a as follows: when $T_{min} \geq VT_{min}$, $h_a = 1$; otherwise, $h_a = 0$. Conversely, we estimated h_r as the time when T_{max} exceeded the maximum thermal threshold for activity (VT_{max}; Camacho and Rusch, 2017; Lara-Reséndiz et al., 2021). Hence, when $T_{max} \geq VT_{max}$, $h_r = 1$; otherwise, $h_r = 0$. We utilized the low threshold to compute the overall h_a, we calculated the difference between h_a and h_r per day. Both h_a and h_r were projected for the year 2070 under a pessimistic climate change forecast (SSP585 from MPI-ESM-LR; see below).

We also created a performance layer using the Thermal Performance Curves (TPC) generated with the *EcoPhysRaster* and *PerfFUN* functions in the Mapinguari v0.4.1 R package. This function used the data from TPC (as described above) to create a performance function and projected it onto the geographic space using the T_{max} layer. This allowed us to identify the best and worst sites for the performance of *L. ditadai* at spatial scale.

The modeling included, as the final input, bioclimatic variables from WorldClim version 2 as predictors in the species distribution models (SDM), along with the ecophysiological layers (h_a, h_r, and performance). This hybrid approach utilized predictors with correlation values lower than 0.85 ($r < 0.85$), which were h_a, Bio2, Bio4, Bio9, Bio13, and Bio14.

We constructed SDMs for both present and future climate scenarios (SSP585 for 2070) using the sdm R package (Naimi and Araújo, 2016). Climate data from the Max Planck Institute's global circulation model (MPI-ESM-LR; CMIP6) were employed at a resolution of 30 s (~1 km2; Hijmans et al., 2005). The MPI-ESM-LR model's accuracy in predicting recent climate change during the control period has been established (Anav et al., 2013), and it has been extensively utilized in reptilian studies (Altamirano-Benavides et al., 2019; Lara-Reséndiz et al., 2021; Pontes-da-Silva et al., 2018; Sinervo et al., 2018). The SSP585 scenario represents a high-emissions model with minimal reduction in greenhouse gas emissions.

We developed SDMs using three algorithms—generalized linear modeling (GLM), multivariate adaptive regression splines (MARS), and Random Forest (RF)—with 1000 pseudo-absence background points (Barbet-Massin et al., 2012). Pseudo-absence data was randomly generated within a 0.4-degree radius of lizard presence records (n = 81) using QGIS 3.8. We trained the models on a random sample of 80% of the presence data and tested the remaining 20%. To assess model performance, we calculated several measurements, including the area under the receiver operating characteristic (ROC) curve (AUC) and the true skill statistic (TSS, Allouche et al., 2006) for each algorithm. We used the R package sdm for model selection (GLM, MARS, and RF), retaining models with AUC >0.8 and TSS >0.76, and the presence-absence method (PA) (Ahmad et al., 2020; Hao et al., 2020; Naimi et al., 2014). We used the average threshold of the best models calculated in the sdm package (training sensitivity = specificity) as the cutoff value to convert environmental suitability models into binary maps.

With the previously described hybrid SDMs, we evaluated the impact of climate change on the geographical distribution of *L. ditadai*. We estimated the percentage change in the potential habitable area with the following equation: %change = [(S1 – S0)/S0] * 100, where S0 is the suitable area for a species based on the current climate scenario and S1 is the suitable area for a species given future climatic conditions (Lara-Reséndiz et al., 2021). We then compared suitable areas generated for the future climate scenario (SSP585 for 2070) to the currently suitable areas to predict the persistence (stable), extinction (contraction), and colonization (expansion) of *L. ditadai*. We conducted these analyses in QGIS3.8 (QGIS Development Team, 2021).

3. Results

We sampled 125 individuals of *L. ditadai*, 46 in pitfall traps and 79 by active searching. All individuals were found associated with halophytic shrubs, primarily *Allenrolfea vaginata* and *Heterostachys ritteriana*. Our sample comprised 15 males, 22 females, 52 juveniles, and 36 unsexed adults. It is worth noting that not every recorded individual was captured and consequently, these individuals remained unsexed. These records were used for SDMs.

Trap arrays flooded on two occasions in January and February 2016, remaining covered by water for about a week. After the water evaporated, *L. ditadai* resumed its activity, especially neonates that became frequent in pitfall traps. We recorded L. *ditadai* individuals spanning from its type locality in the north to the southernmost point, encompassing the entire eastern border. In Salinas de Ambargasta, we found populations of *L. ditadai* in the three locations sampled, in the South and Southeast of the salt plain.

3.1. Body temperatures, preferences, and thermal tolerances

The mean field T_b was 33.9 ± 3.1 °C (n = 33 adults, 4 juveniles, range 25.5–40 °C; see Supplementary Table 1). The mean T_s and mean T_a at the time of capture were 35.1 ± 6.7 °C (range 21.6–49.5 °C) and 32.3 ± 4.3 °C (range 23.7–39.9 °C), respectively. Linear regression analysis revealed a significant positive relationship between T_b and T_s (Fig. 1A) ($T_b = 27.09 + 0.196T_s$, $r^2 = 0.154$, $p = 0.009$, $n = 37$) and between T_b and T_a (Fig. 1B) ($T_b = 21.51 + 0.390T_a$, $r^2 = 0.271$, $p = 0.001$, $n = 36$).

The mean T_p was 36.6 °C ± 2.28 °C (n = 29, range: 30.0–42.6 °C). The T_p IQR (T_{set}) was 35.9–38.1 °C (Fig. 2). Among the T_b values, 16% were within, 73% were below, and 11% were above the T_p range (Fig. 3A). The voluntary thermal range (VT_{min} – VT_{max}) determined through laboratory observations, was 31.8–40 °C. The mean CT_{min} was 8.0 ± 2.0 °C (n = 33, range: 4.0–14.8 °C), while the mean CT_{max} was 43.8 ± 1.5 °C (n = 25, range: 41.1–46.5 °C).

3.2. Thermal performance curve

The thermal performance curve of *L. ditadai* indicates that sprint speed increases with body temperature (Fig. 4). The thermal optimum

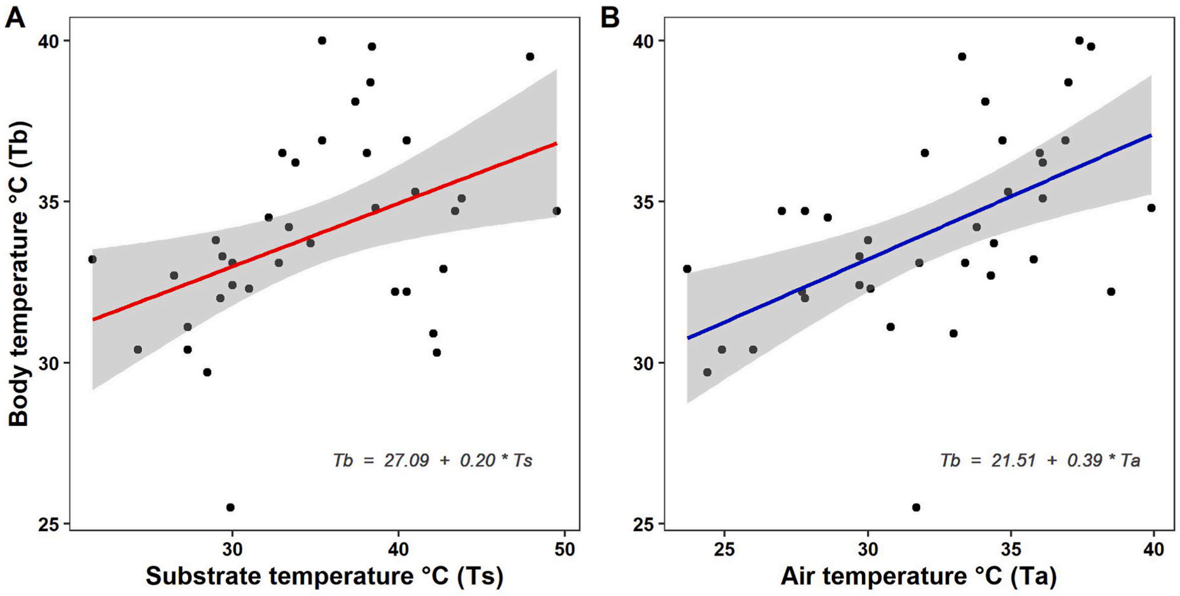

Fig. 1. Relationship among field body (T_b), substrate (T_s; A), and air (T_a; B) temperatures of *Liolaemus ditadai* in the Salinas Grandes system.

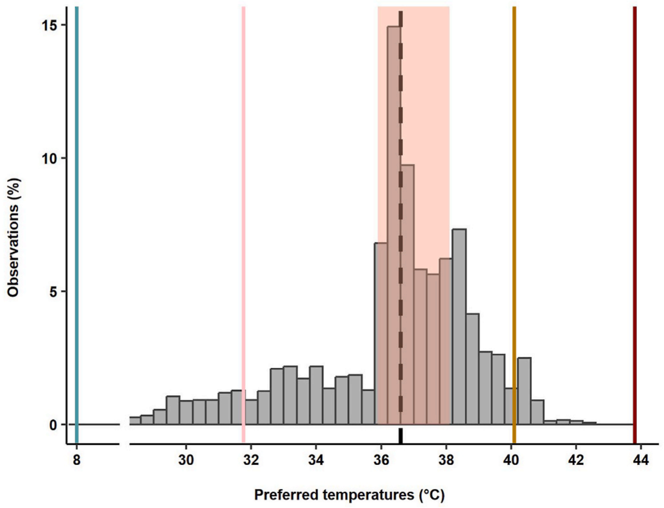

Fig. 2. Distribution of preferred temperatures (T_p) of *Liolaemus ditadai*. The red-shaded area shows the range of T_p (35.9–38.1 °C) and the dashed line shows mean T_p (36.6 °C). The minimum (VT_{min}) and maximum (VT_{max}) voluntary temperatures, and the critical thermal maximum (CT_{max}) are indicated with blue, yellow, and red solid lines, respectively. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

for performance (T_{opt}) was 30.2 °C, and the maximum speed was 2.14 m/s, with a *B80* of 22.7–37.2 °C. There was no significant relationship between the SVL and sprint speed (Linear regression: $r^2 = 0.0018$, $p = 0.791$, $n = 42$), nor between weight and sprint speed (Linear regression: $r^2 = 0.0125$, $p = 0.486$, $n = 42$). Significant differences were found between the treatments with the lowest temperatures (19 and 23 °C), which showed lower performance values (mean 0.98 ± 0.11–1.14 ± 0.20 m/s), and the rest of the treatments (27, 31, 35, and 39 °C) with had higher performance values (mean 1.48 ± 0.13–1.54 ± 0.18 m/s; LMM: $F_{5,28} = 5.25$, $p = 0.0015$) (Fig. 4).

3.3. Operative environmental temperatures and thermoregulation indices

The mean T_e throughout the year was 27.75 ± 10.96 °C, ranging −6.29–67.18 °C. During the annual activity period of *L. ditadai* (November–May), the mean T_e was 31.19 ± 10.07 °C, with a range of −0.12–67.18 °C. T_e varied significantly across hours of the day and months of the year, but in both cases, it showed a unimodal pattern (Fig. 5; Supplementary Figs. 1 and 2).

We found significant differences between the T_e of the models placed on bare ground ($T_{e\text{-sun}}$) and under vegetation ($T_{e\text{-shade}}$) ($F_{1,12} = 1814.05$, $p < 0.0001$). $T_{e\text{-sun}}$ was about 4.5 °C higher than $T_{e\text{-shade}}$ ($T_{e\text{-sun}} = 33.5 \pm 11.02$ °C, 1.83–67.18 °C and $T_{e\text{-shade}} = 28.87 \pm 8.39$ °C; −0.12–61.27 °C). The T_e hourly records (between 08:00 and 20:00 h) showed significant differences between microhabitats ($T_{e\text{-shade}}$ and $T_{e\text{-sun}}$) ($F_{1,12} = 39.25$, $p < 0.0001$). The average $T_{e\text{-shade}}$ never exceeded the T_p range (35.9–38.1 °C), while $T_{e\text{-sun}}$ only exceeded T_p between 13:00 and 16:00 h (Fig. 5A and B). The highest T_e was recorded in November, December, January, and February, in models placed in both shade and sun (Fig. 5C and D, raw data in Table S3).

The thermal quality of the environment (d_e) was 8.72 ± 6.27 °C, while thermoregulation accuracy (d_b) of *L. ditadai* was 2.87 ± 2.2 °C (n = 37). The thermoregulatory efficiency index (E) was $E = 0.67$.

3.4. Ecophysiological predictors and models (present and future)

According to the ecophysiological model of *L. ditadai*, there were no hours of restriction in either the present or the 2070 scenario, so we did not include h_r in our modeling. Both h_a and locomotor performance increased significantly in the future scenario (h_a: Mann-Whitney test: $U = 0.000$, $p < 0.001$; performance: $U = 185.0$ $p < 0.001$, Fig. 6). The h_a and performance layers for the present and 2070 scenarios are available in Supplementary Fig. 3, and the values based on the occurrence records can be found in Supplementary Table 2. The SDMs for *L. ditadai*, based on the ecophysiological model and current environmental conditions, covered an area of 11,270 km^2, of which 5656 km^2 were exclusively within the Salinas Grandes system (see Supplementary Fig. 4). In the future scenario, suitable habitats increased by 26.6 % (14,271 km^2), with a 12.1% increase within the Salinas Grandes System (6340 km^2; see Supplementary Fig. 4). We used a binary prediction model to evaluate the change in habitat suitability of *L. ditadai*, using a threshold value - average TSS = 0.76, where probability values equal to or above the threshold were considered suitable areas. The model predicted 3515 km^2 of newly suitable areas for colonization, 4241 km^2 unchanged, and a contraction of 1416 km^2 by 2070 (see Supplementary Fig. 5B). The

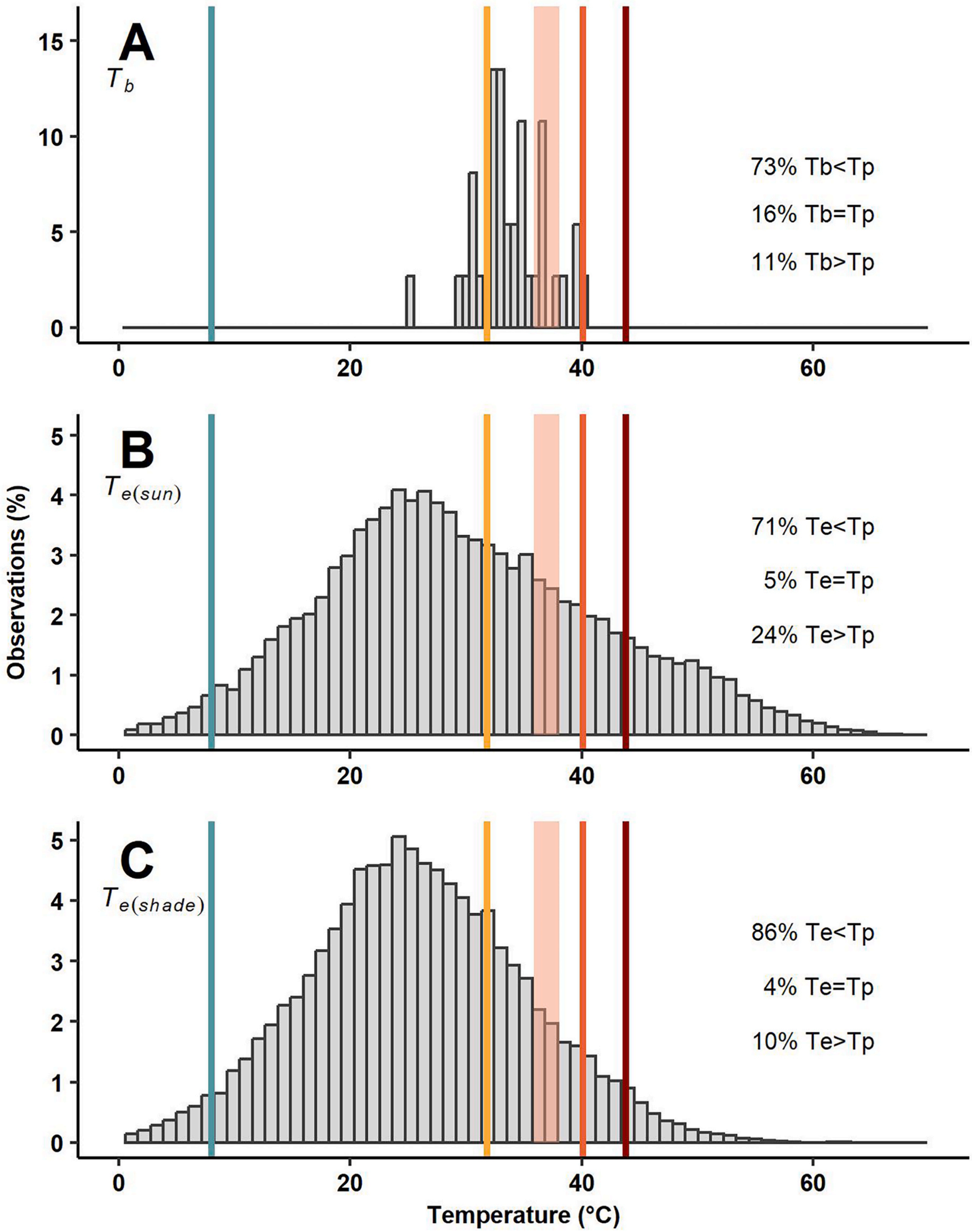

Fig. 3. Distribution of body (T_b, A) and operative (T_e) temperatures for two environments (sun, B and shade, C) for *Liolaemus ditadai*. The red-shaded area indicates the preferred temperature range (35.9–38.1 °C). The minimum (VT_{min}) and maximum (VT_{max}) voluntary temperatures and the minimal critical (CT_{min}) and maximum critical (CT_{max}) are indicated with pink, yellow, light blue and red solid lines, respectively. Percentage of T_b and T_e that are higher, lower and within the interval of T_p for L. *ditadai* is indicated. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

predictor importance results are presented in Supplementary Fig. 6.

4. Discussion

Our surveys revealed that *L. ditadai* is distributed along the entire northern and eastern borders of Salinas Grandes and in the south and southeastern borders of Salinas de Ambargasta, as long as the typical halophytic vegetation is present, significantly extending the known distribution of the species, which was previously considered the most restricted (Abdala, 2007; Avila et al., 2015). It has also been reported that the species is threatened by the flooding of its habitat during the rainy season (Abdala, 2007; Abdala and Juárez Heredia, 2013). Our records indicate that flooding events do not occur in the entire distribution area of the species, nor in every year, and that individuals (even

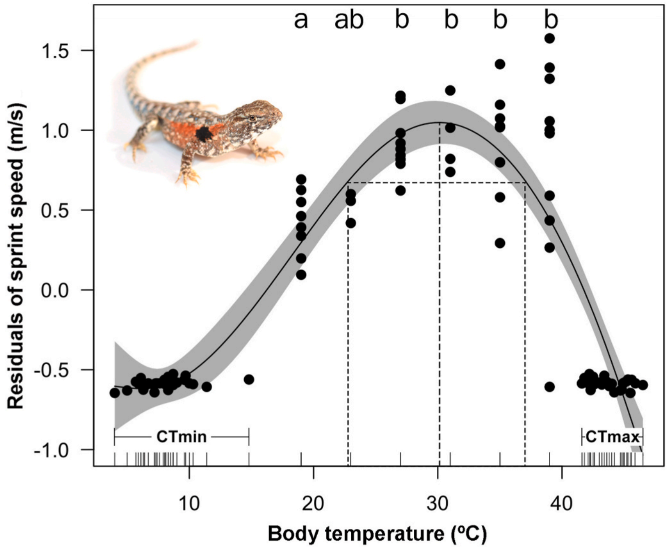

Fig. 4. Thermal performance curve (TPC) of *Liolaemus ditadai.* Black points represent the residuals of sprint speed values for individual tests at different body temperatures (19, 23, 27, 31, 35, and 39 °C). Critical thermal minimum ($CT_{\min}$) and maximum ($CT_{\max}$) individual values are indicated. Dashed lines indicate T_{opt} (30.2 °C) and B_{80} (22.7–37.2 °C). Different letters indicate significant differences using the post-hoc method of Tuckey at $\alpha = 0.05$.

neonates) are not affected by these events, demonstrating its adaptation to the hot, dry, and salty environment of Salinas Grandes.

Many *Liolaemus* species have adapted to extreme conditions of aridity and heat (Brizio et al., 2021; Gómez Alés et al., 2018; Labra et al., 2001; Laspiur et al., 2021; Moreno Azócar et al., 2013; and others), such as *L. ditadai* and other species from the *L. anomalus* group, which are typically endemic to arid and salty environments with little vegetation cover, high temperatures, and low thermal quality (Abdala and Juárez Heredia, 2013).

In *Liolaemus* species, T_b and T_p are often closely related to environmental temperatures (Ibargüengoytía et al., 2021; Medina et al., 2012; Rodríguez-Serrano et al., 2009). For instance, some species inhabiting hot desert and semidesert environments exhibit $T_b > 34$ °C (Medina et al., 2009, 2012), such as *L. scapularis* (35.7 °C; Salva et al., 2021), *L. laurenti* (35.9 °C; Medina et al., 2012), and *L. cuyanus* (37.5 °C; Moreno Azócar et al., 2013). Therefore, the mean T_b of L. *ditadai* (34.3 °C) is expected given the relatively high mean T_e (31.19 ± 10.07 °C) recorded during its annual activity period (November–May). Moreover, *L. ditadai*'s T_b is comparable to that of sympatric species *L. chacoensis* (32.8–33.4 °C; Astudillo et al., 2019; Cruz et al., 2014) and *L. darwinii* (32.8 °C; Villavicencio et al., 2010). Likewise, *L. ditadai*'s T_p (36.6 °C) falls within the known range for the genus (32.67–37.4 °C; Medina et al., 2009; Moreno Azócar et al., 2013; Valdez Ovallez et al., 2022).

Low thermal sensitivity and wide T_{opt} ranges can be advantageous in environments with significant temperature variations (Valdez Ovallez et al., 2022). *L. ditadai* has a wide range of T_{opt} for sprint speed (Fig. 4) which may be an adaptive response to its preferred habitats in the Salinas Grandes system, where sparse halophytic shrubs dominate. When approached by researchers, *L. ditadai* individuals quickly moved among shrubs and even performed short runs when escaping into areas with no vegetation cover. A broad range of body temperatures optimal for sprint runs is essential for avoiding predators in open areas with scarce vegetation (Brizio et al., 2021; Miles et al., 2001). Thus, high sprint performance can be linked to an escape strategy (Brizio et al., 2021; Cabezas-Cartes et al., 2014; Gómez Alés et al., 2018).

The achievement of a high level of thermoregulation accuracy (d_b = 2.87 ± 2.2 °C), despite 84% of T_b values falling outside the preferred temperature range, can be explained because most of these (82%) are within the range of voluntary temperatures (Fig. 3A). This is particularly important in the Salinas Grandes habitat, where the vegetation structure offers limited opportunities for thermoregulation, as evidenced by the low thermal quality of microhabitats (d_e = 8.72 ± 6.27 °C). Furthermore, a high proportion of measured T_e values fall outside the range of T_p for both microhabitat types (96% in microhabitats with vegetation cover and 95% in microhabitats without vegetation cover), indicating the need for active thermoregulation. Again, the low thermal sensitivity of performance could be an adaptation to the low thermal quality of the environment and the large number of operating temperatures that are below most T_bs and $VT_{\min}$. (Fig. 3B and C), especially the T_es of microhabitats with vegetation (Fig. 5A and B). Other *Liolaemus* species from desert and saline environments, such as *L. nigroroseus, L. fabiani*, and *L. cuyumhue*, also exhibit high levels of accuracy and effectiveness in thermoregulation (Brizio et al., 2021; Labra et al., 2001). In such environments, the limited availability of thermally favorable microhabitats increases the costs of thermoregulation (Huey and Slatkin, 1976; Lara-Resendiz et al., 2014; Pérez-Delgadillo et al., 2021; Vickers et al., 2011). Thus, the role of vegetation in these environments could be essential, allowing *L. ditadai* to maintain body temperatures and achieve maximum performance yields, even at times of the day where the T_e of environments without vegetation exceed the 40 °C, reaching higher values than its $CT_{\max}$ (Figs. 3 and 5). Studies focused on habitat selection/occupancy in this species could be useful to determine the role of vegetation in these environments.

The increase of global temperatures has led to the accelerated decline and local extinction of numerous lizard populations (Sinervo et al., 2010). It is expected that lizards from tropical forests, typically thermoconformers, are more threatened by global warming than lizards from temperate regions (Huey et al., 2009). Additionally, some studies also support the idea that ectotherms inhabiting thermally heterogeneous environments exhibit higher physiological tolerance to warming, representing lower vulnerability to global climate change than those inhabiting homogeneous environments (Tewksbury et al., 2008). These predictions have been widely tested—and in general corroborated—in South America, (e.g., Cabezas-Cartes et al., 2019; Diele-Viegas et al., 2018; Guerra-Correa et al., 2020; Laspiur et al., 2021; Pontes-da-Silva et al., 2018; but see Minoli et al., 2019). However, hot desert lizards are exposed to low-quality environments (d_e) and extreme temperatures, which could impose a restriction in scenarios of climate warming, as projected for *Uromastyx* lizards in the African and Arabian deserts (Kechnebbou et al., 2021). Our models for *L. ditadai*, which were built using abiotic and ecophysiological predictors, showed that h_a was the most critical predictor (27%; see Supplementary Fig. 6) confirming previous findings (Caetano et al., 2020). In the case of this salt plain lizard, even under a pessimistic scenario (from 2.42 °C to 5.64 °C for SSP585), the increase of environmental temperature would increase suitable habitats by 12–27% (Fig. 6; Supplementary Figs. 4 and 5), resulting in a positive effect.

To our knowledge, no other studies have addressed the thermal ecology, performance, and ecophysiological modeling of lizards in saline environments. Evolutionarily, seven *Liolaemus* species from the *L. anomalus* group, along with others from different clades, inhabit salt plains and lakes, providing an opportunity to assess their adaptive strategies in saline environments from a phylogenetic perspective. These studies serve as the starting point to understand the interplay between thermoregulation and the osmotic budget. Research on saline loading effects in desert lizards shows alterations in behaviors and decreased preferred temperatures (da Silveira Scarpellini et al., 2015; Dupré and Crawford Jr, 1985; Nagy, 1972), indicating challenges in maintaining a positive osmotic budget for *Liolaemus ditadai.* High values for T_p, T_e, and $CT_{\max}$, combined with low d_e in a region as saline as Salinas Grandes suggest that *L. ditadai* may be maintaining its osmotic balance through an unknown mechanism. No studies are currently available on the adaptations for excreting excess salts in any *Liolaemus* species. This presents an intriguing research opportunity to explore how lizards manage

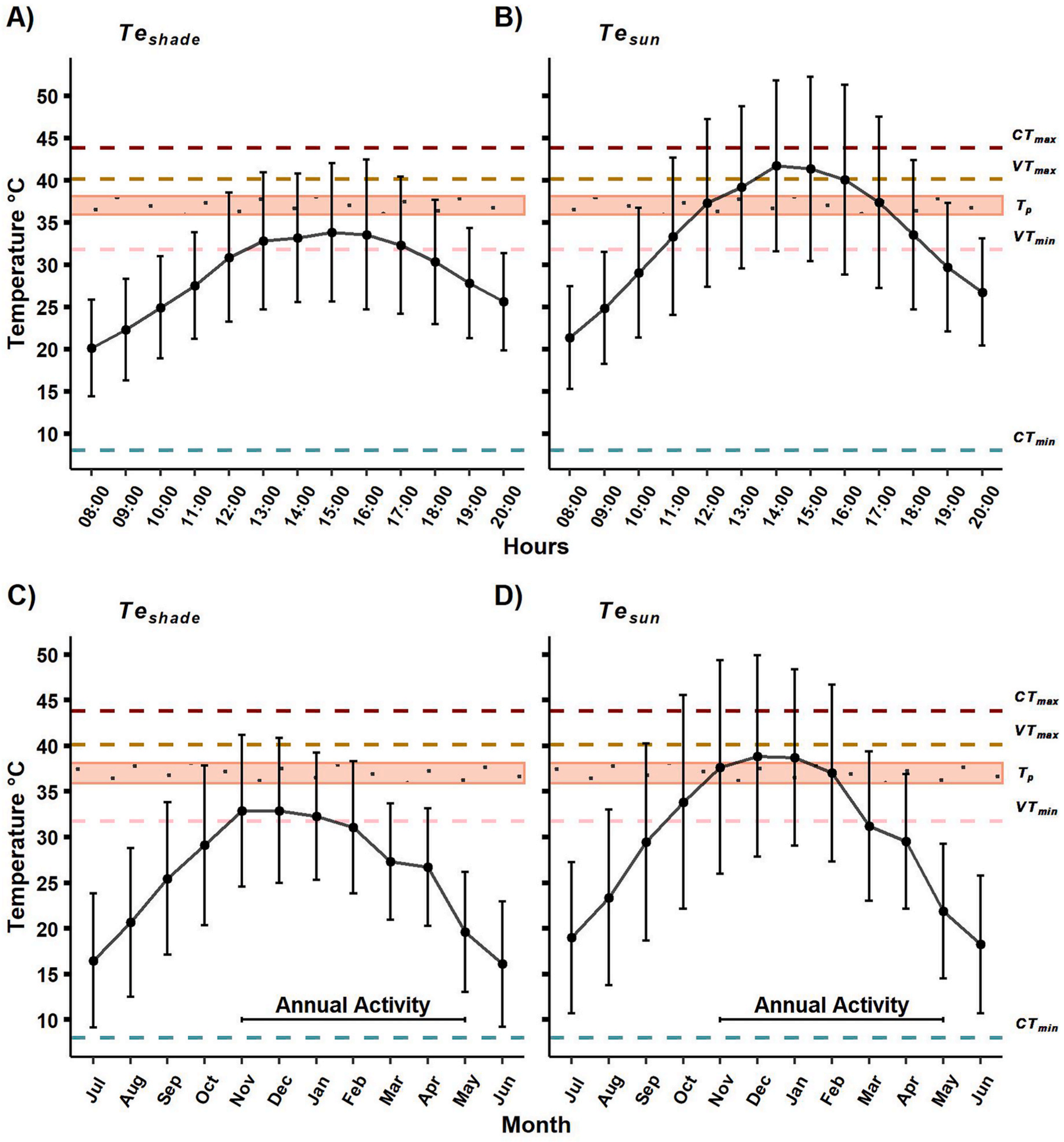

Fig. 5. Operative temperature (T_e) for *Liolaemus ditadai* in two conditions (shade and sun) during a day (A–B) and throughout the year (C–D). A and B include T_e from 8:00 to 20:00 h for the activity period of *L. ditadai* (November–May). C and D shows T_e from 8:00 to 20:00 h for all months of the year. Mean and standard deviation are shown. The red-shaded area is the preferred temperature range (T_p; 35.9–38.1 °C). The pink and yellow dashed lines indicate the minimum (VT_{min}) and maximum (VT_{max}) voluntary temperatures of *L. ditadai*. The light blue and red dashed lines indicate the minimal critical (CT_{min}) and maximum critical temperature (CT_{max}) temperatures. The annual activity period of *L. ditadai* in shown in C and D. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

excess ions in saline environments.

In conclusion, *L. ditadai* emerges as an efficient thermoregulator, tolerating temperatures near its upper thermal limits. Our ecophysiological model suggests that available activity hours predict its distribution, and the projected temperature increase due to global climate change should minimally impact its persistence or may even have a positive effect on suitable thermal habitat. However, this theoretical increase in habitat could be linked to the distribution of halophilous scrub in the future. Our surveys reveal widespread distribution along the borders of Salinas Grandes and Salinas de Ambargasta, suggesting a potential presence along the entire border of both salt plains wherever halophytic vegetation exists. Optimistic model results, extended distribution, and no evidence of flood-related adverse effects offer insights into assessing the conservation status of *L. ditadai*, making it and the Salinas Grandes system suitable models for studying lizard ecophysiology in largely unknown saline environments.

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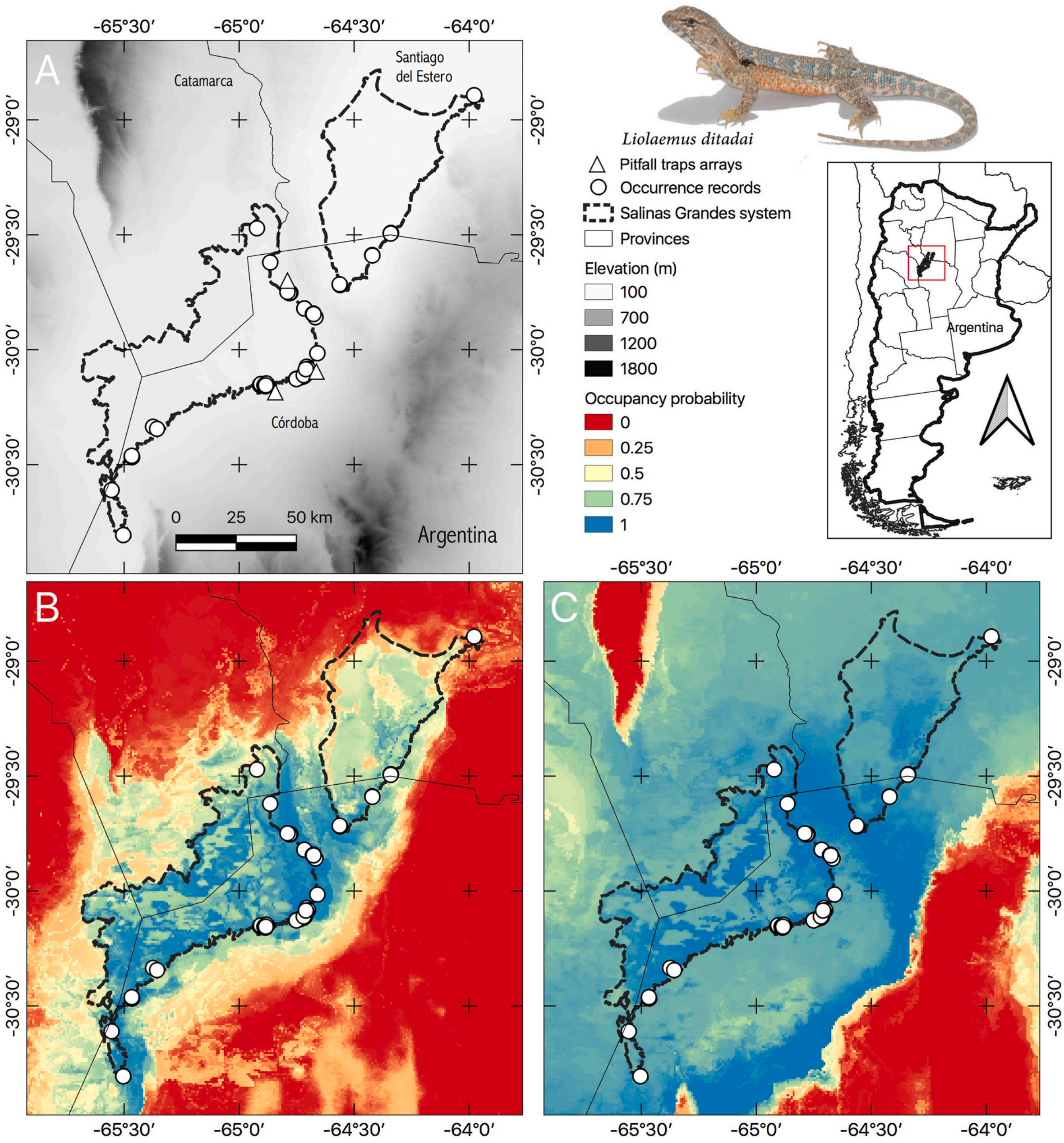

Fig. 6. Occurrence records of *Liolaemus ditadai* (A). Current habitat suitability (B) and projected suitability for 2070 under SSP585 (C). Color legend depicts occupancy probability from red (0-unsuitable areas) to blue (1-suitable areas). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

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CRediT authorship contribution statement

Rafael A. Lara-Reséndiz: Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **José M. Sánchez:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Romina S. Paez:** Writing – review & editing, Methodology, Investigation, Data curation. **Suelem Muniz-Leão:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Data curation, Conceptualization. **Guarino R. Colli:** Writing – review & editing, Writing – original draft, Software, Resources, Funding acquisition, Data curation. **Donald B. Miles:** Writing – review & editing, Writing – original draft, Resources, Funding acquisition, Conceptualization. **Barry Sinervo:** Investigation, Funding acquisition, Conceptualization. **Nicolás Pelegrin:** Writing – review & editing, Writing – original draft, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization.

Declaration of competing interest

The authors declare that they have no conflict of interest.

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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.2024.103917.

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