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THERMAL BIOLOGY OF ZOO-HOUSED *CHELONOIDIS CHILENSIS*: DETERMINING THE ACTIVITY PATTERN AND ESTIMATING SELECTED AND CRITICAL MAXIMUM TEMPERATURE

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Abstract.—**Ectothermic animals depend on environmental temperature to regulate their body temperature. The Chaco Tortoise (*Chelonoidis chilensis*) is widespread in South America; however, populations are threatened mainly because of the pet trade. We described the activity pattern of *C. chilensis* relative to environmental temperature under semi-natural conditions in a zoo enclosure. We also estimated thermal parameters under controlled laboratory conditions: selected temperature (T_{sel}) and critical maximum temperature (CT_{max}) between sex and size indicators. In the enclosure, 81% of the observations were from inactive tortoises and 19% from active tortoises. Tortoises were active over a wide thermal range (12.0°–38.0° C) and T_{sel} was 34.4° ± 0.3° C (mean ± standard error), with no significant differences among sizes or between sexes. Heavier tortoises spent significantly more time at the lowest temperature than lighter ones. The range of CT_{max} was 36.3°–42.0° C and this parameter was inversely related to tortoise length but did not differ between sexes. The results suggest a wide thermal range in *C. chilensis*, dependence of thermal behavior on body size but not on sex, and a wider range of body temperatures in smaller individuals than in larger ones. Knowing the parameters that influence thermoregulation contributes to the improvement of management strategies under semi-natural conditions, which, in turn, can be extrapolated to wild populations.**

Key Words.—body temperature; Chaco Tortoise; thermoregulation

INTRODUCTION

The Chaco Tortoise (*Chelonoidis chilensis*, Testudinidae; Fig. 1) is a desert-dwelling species that is widespread in South America (Cabrera 2015; Ruete and Leynaud 2015). Although we still lack demographic evidence of a population decline, *C. chilensis* is likely severely impacted by habitat degradation, poaching, and illegal pet trade (Chébez 2009; Prado et al. 2012). Although the species has been considered threatened in a recent review (Stanford et al. 2020), illegal trade continues and the actual trade volume and its effect on populations of the species is still unknown (Prado et al. 2012; Farioli 2015). Consequently, zoos and protected areas in Argentina annually receive hundreds of tortoises that have been seized or abandoned (López et al. 2010). In recent years, scientific research focusing on animal populations kept in zoos has been incorporated in projects for the conservation of different species (Rawski et al. 2018; Chusyd et al. 2018; Eguizabal et al. 2019; Prystupczuk et al. 2019; Rose et al. 2019). Indeed, zoo environments are useful for the study of species whose behavior is difficult to observe in the wild, as is the case of the *C. chilensis*. Surprisingly, although this species is a common pet, recent biological studies are relatively scarce (Ruete and Leynaud 2015; Sánchez et al. 2015).

Behavioral studies can provide valuable information for guiding management practices of animals in semi-natural conditions and under human care, such as zoo populations (Bassett and Buchanan-Smith 2007; Hosey et al. 2013; Prystupczuk et al. 2019), to increase survival rates and improve their living conditions in confinement. Ectotherms have several strategies for regulating their body temperatures (Huey 1982;

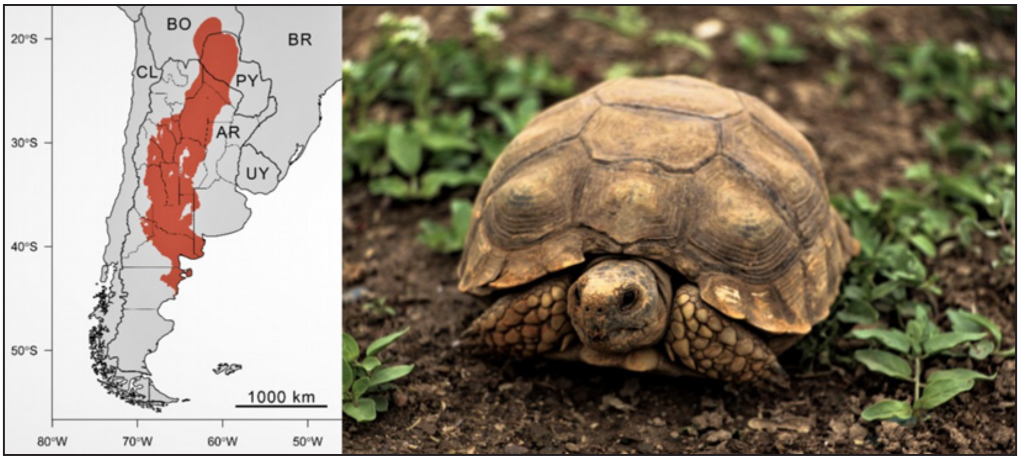

Figure 1. Distribution area of Chaco Tortoises (*Chelonoidis chilensis*) in South America (BO: Bolivia, AR: Argentine, UY: Uruguay, PY: Paraguay, CL: Chile, BR: Brazil; Ruete and Leynaud 2015) and a tortoise at the Córdoba Zoo, Argentina (Photographed by Gerardo C. Leynaud).

Sturbaum 1982), ranging from precise behavioral thermoregulation to passive thermoconformity (Huey 1982; Edwards and Blouin-Demers 2007; Molina and Leynaud 2017). Body temperature (T_b) is perhaps the most important ecophysiological variable affecting the performance of ectotherms, which in turn influences behavior and physiology (Huey 1982; Angilletta et al. 2002; Harlow et al. 2010; Alés et al. 2017). In addition, during daylight hours, solar radiation is often a major contributor to overall energy balance (Snyder et al. 2019). When ectotherms are naturally exposed to a wide range of temperatures, the relative performance of the organism can be described according to some important ecological characters: (1) thermal optimum (T_o), which reflects the body temperature at which an ectotherm has a maximum performance; (2) critical thermal minimum (CT_{min}), the lowest body temperature that allows activity; (3) critical thermal maximum (CT_{max}), the highest body temperature at which activity is allowed; and (4) performance breadth, i.e., the range of body temperatures at which an ectotherm can be active (Huey 1982).

Experimental investigations of the optimal body temperature and activity patterns of captive tortoises are limited and outdated (Perrin and Campbell 1981; Hailey and Loveridge 1998). In addition, it is important to determine the thermoregulatory behavior of tortoises with the ultimate purpose of enhancing its welfare under human care and protecting its populations. Environmental temperature (T_e) is an important variable in determining T_b and tortoise activity is commonly described as a function of T_b; therefore, we assume that the activity of a tortoise can be described in relation to T_e. In addition, thermoregulatory behavior can be evaluated under controlled laboratory conditions using a thermal gradient along which the animals can move to achieve their selected temperature (T_{sel}; Edwards and Blouin-Demers 2007; Tamplin 2009). The selected temperature is expected to optimize performance of a specific behavioral or physiological task (Cecchetto and Naretto 2015). On the other hand, under controlled conditions, it is also possible to find the critical temperatures, for example CT_{max}. In testudines, CT_{max} can be estimated by monitoring thermoregulatory salivation, one of the first physiological stress responses to high temperatures that tortoises commonly exhibit (Cloudsley-Thompson 1974; Douglass and Layne 1978).

Sex and body size can influence thermoregulation performance in ectotherms. Among attributes of individuals, the surface-to-volume ratio has been found to affect heat exchange (McMaster and Downs 2013) and sex may influence behavior (Bulté and Blouin-Demers 2010). Indeed, the energy needed and interactions both with the environment and with other individuals differ between sexes (Seebacher et al. 1999). Therefore, the underlying thermal requirements are different (Huey and Pianka 2007), and this may affect individual responses to the same management strategies implemented for the conservation of ectotherms.

The purpose of our study was to evaluate attributes of *C. chilensis* tortoise related to thermoregulation and variation in environmental temperature, with the aim of improving management strategies under semi-controlled conditions. First, we described the activity patterns of *C. chilensis* in the zoo enclosure relative to environmental temperature using behavior indicators. We then estimated body temperature parameters (T_{sel}, CT_{max}) of differently sized individuals of both sexes under controlled laboratory conditions.

Materials and Methods

We conducted our study at Córdoba Zoo, in Córdoba, Argentina (31°25’S, 64°10’W), in two stages: one conducted under semi-natural conditions of the zoo enclosure where individuals of *C. chilensis* are housed, and another observational stage under controlled laboratory conditions at the Center for Applied Zoology (located inside the zoo). According to the Köppen climate classification, Córdoba city is characterized by a subtropical climate with dry winters (Cwa). In January, the average maximum temperature is 31.1° C and the average minimum is 18.1° C. In July, the coldest month, the average temperatures are 18.6° C maximum and 5.5° C minimum. Rainfall is seasonal and concentrated in summer (November to March), with an annual average of 800 mm (https://www.smn.gob.ar/).

First stage: enclosure conditions.—We collected data from a population of 46 *C. chilensis* tortoises housed in an enclosure of Córdoba Zoo. The population was composed of seized or abandoned individuals from the central area of the country. The enclosure was 12 m long × 6 m wide and was fenced in the areas exposed to visitors with a stone wall and glass on one side, and woven wire on the other (Fig. 2). The enclosure had a circular cement sprue (approximately 50 cm in diameter) in the center and shelters provided by shrubs and fallen trunks arranged in different areas of the enclosure. Tortoises were fed green zucchini, apples, carrots, corn, beetroot, pears, and tomatoes daily (Tracchia 2018) that were placed on the ground in randomly changing positions by the keeper assigned by the zoo.

Figure 2. Enclosure area of Chaco Tortoises (*Chelonoidis chilensis*) in the Córdoba Zoo (Cordoba, Argentina). The active and inactive behavior of tortoises were recorded between 0900 and 1600 from December 2015 to May 2016. (Photographed by Gerardo C. Leynaud).

From December 2015 to May 2016 (the period of maximum activity of *C. chilensis* in the wild: Cabrera 2015), we placed four digital thermometers (Thermochron iButton. DS 1921G) to record the temperature hourly from 0900 to 1600. We defined the period to record temperature by preliminary observations of the same population made 30 d before the study. For the placement of the data loggers, we divided the enclosure into four equal quadrants (6 × 3 m) and we placed the data logger in the center of each quadrant. We recorded the behavior of *C. chilensis* tortoises using scan sampling (Altmann 1974), once per week for 6 mo (120 sampling events; observations were not made on 9 d due to weather conditions). Sampling of the behaviors of the turtle population consisted of a visual scan that lasted approximately 10 min, which was repeated once every hour from 0900 to 1600. We classified behavior as active or inactive, as proposed by Kazmaier et al. (2001) for Texas Tortoises (*Gopherus berlandieri*) in wild populations. Active behavior corresponded to tortoises performing at least one of the following behaviors: locomotion, foraging, feeding, mating, or being agonistic or alert, whereas inactive behavior corresponded to the tortoise resting or hiding (Table 1). We estimated the activity pattern using a curve of active behaviors plotted against T_e. Because we made observations at the population level and the animals were not individually marked, we did not take into account individual attributes such as body size and sex.

Second stage: observational laboratory study.—Following the first stage of behavior recording in the enclosure, we selected 17 individuals representing both sexes and a broad range of body sizes. We transported these tortoises to the laboratory 48 h before the start of the trial for acclimation to laboratory conditions (Huey 1974). Transfer of the animals took < 10 min. For sex determination, we evaluated plastron concavity, as suggested by Douglass and Layne (1978). We recorded the carapace curve length (CCL; tape measurement) and body weight using a spring scale (Pesola, Zurich, Switzerland) with a precision of ± 20.0 g).

Estimation of T_{sel}.—According to the protocol described for reptiles by Cloudsley-Thompson (1974) and Cecchetto and Naretto (2015), before the trials we placed the individuals in a rectangular box (terrarium) in groups of four or five tortoises for a minimum of 3 d for habituation purposes. We maintained temperatures at 19.0°–22.0° C, and we supplied water and food daily. We placed tortoises in an open-top terrarium (230 cm long, 50 cm wide, 30 cm high), with no interference

Table 1. Ethogram showing behaviors recorded on a mixed-sex and mixed-age population of the Chaco Tortoise (*Chelonoidis chilensis*) in the Córdoba Zoo, Argentina, from December 2015 to May 2016. Behaviors described in Lovich (1990), Ruby and Niblick (1994) and Schneider et al. (2010).

Behavioral category		Description
Active	Alert	*Immobile*, head out of the shell, neck fully stretched and eyes open, looking at a fixed point.
	Agonism	*Pursuit*: walking or running in close pursuit of another turtle, moving behind or alongside it. *Biting*: rapid opening and closing movement of the jaws of a turtle directed towards another turtle in close proximity. *Fear*: in response to the above behavior, the receiving turtle hides its head inside its shell and/or moves away from the biter. *Yawning*: opens its mouth wide and keeps it open for a few seconds.
	Feeding	*Biting food*: reaching with the mouth, biting, and pulling back to extract food from the source. *Chewing food*: involves opening and closing movements of the jaw and tongue with food inside the mouth, followed by swallowing the food. *Drinking*: begins with a leaning posture and then immersion of the head or nares in the liquid.
	Locomotion	*Slow walking*: making slow alternating movements of the limbs. Very slow steps. *Normal walking*: alternating movement of the limbs making steps at a faster pace than slow walking. *Fast walking or running*: movement at an accelerated speed. *Climbing*: at least one leg on an object higher than the surface.
	Reproduction	*Courtship*: the male performs movements, in front and by the side of the female alternating with moments when he remains motionless. Sometimes nibbling on the carapace or legs may occur. *Mounting*: the male rests his plastron on the carapace of a female, standing on his hind limbs and using his forelimbs to grasp the carapace of his mate. *Head movement*: during mating, the female performs a lateral, side-to-side movement of the head and neck. *Avoidance*: the female turns on its axis trying to avoid the male copulation behavior or forcing the male to dismount. *Copulation*: male performs copulatory movements accompanied by a characteristic sound, with the neck stretched out and keeping the head horizontal. *Digging*: alternating movement of the hind limbs to remove soil.
Inactive	Resting	*Resting*: motionless, limbs and neck only partially stretched or, plastron resting on the ground with limbs relaxed, eyes open. Sleeping: motionless, plastron resting on the ground, limbs outside or inside the shell, eyes closed or head retracted inside the shell.
	Hiding	*Immobile*, located directly under vegetation, trunks or other elements that provide shelter, with the head and limbs inside or outside the shell. When a turtle was not found during the scan, it was assumed to be hidden.

from the outside environment. Using a line of three overhead infrared lamps (250 W), we made a gradient of progressively increasing temperatures spanning 22.0°–46.0° C. For practical purposes, we delimited four sections determined by four temperature ranges along the gradient, S1(22.0°–30.0° C); S2 (31.0°–37.0° C); S3 (38.0°–45.0° C), and S4 (≥ 46.0° C). Each sector was immediately adjacent to the next. We used cloacal temperature as an indicator of body temperature (Edwards and Blouin-Demers 2007), which we measured using a digital thermometer (± 0.01° C) and catheter thermocouples we placed approximately 2.0

cm inside the cloaca. Observations always started and finished at the same time (0900–1400) and the period between the first and last tortoises measured was 23 d.

We used nine males and eight females for the trials. We put tortoises in the lowest temperature sector of the terrarium where they could move freely. They were allowed to habituate for 30 min (Ben-Ezra et al. 2008) and we did not include the temperature data we obtained during this period in analyses. After this period, we recorded body temperature and the sector where the tortoise was found every 10 min for 4 h. We estimated T_{sel} for each individual as the central 50% of the observations of body temperature (Medina et al. 2011; Cecchetto and Naretto 2015).

Estimation of CT_{max}.—We used the temperature at which salivation occurred as an estimate of the critical temperature, as this approach is less stressful to animals than many other endpoints commonly used to ascertain CT_{max}. The individuals involved were those used to determine T_{sel}. We exposed the tortoises to a temperature of 45.0° C (Cloudsley-Thompson 1974) using two infrared lights of 250 W each, in an open-top terrarium (50 cm long, 50 cm wide, 30 cm high). All tortoises started with the T_{sel}, which was the same for all individuals. We measured cloacal temperature every minute until salivation was evident (Cloudsley-Thompson 1974; Douglass and Layne 1978). After each trial, we placed tortoises in cold water (Hutchison et al. 1966) until their body temperature returned to the initial value at the start of the trial.

Statistical analysis.—For the first stage under enclosure conditions, we described the activity pattern of *C. chilensis* relative to environmental temperatures. We fit Analysis of Variance (ANOVA) models for thermal parameters (T_{sel}, CT_{max}) using log-CCL as a covariate and sex as a fixed effect. We used CCL instead of body weight in the models because there is high collinearity between these variables and CCL had a better fit. We compared frequency of observations in sectors of the thermal gradient between sexes and among body size classes using a Chi-square Test. The body size classes based on weight percentiles were: Small, 400–1,000 g (n = 6); Medium, 1,000–1,450 g (n = 6); Large, 1,450–3,000 g (n = 5). The significance level for all test was α = 0.05. The assumptions of normality and homogeneity of variance for parametric procedures were checked using Shapiro–Wilk's and Levene's tests, respectively, and data met these assumptions. We used INFOSTAT, 2020 version (Di Rienzo et al. 2020) for all statistical analyses.

RESULTS

The population consisted of 27 females, 17 males, and two individuals of unidentified sex (see Appendix Table). In the zoo enclosure, mean environmental temperature was 24.0° ± 0.5° C (Mean ± standard error), ranging between 5.0° C and 38.0° C (n = 165 records). Of all the observations (n = 165 observation intervals, 7,590 total observations of individual tortoises recorded), 81% were from inactive tortoises (6,124 observations) and 19% from active tortoises (1,466 observations). Minimum and maximum temperatures at which tortoises were active were 12.0° C (one active tortoise) and 38.0° C (one active tortoise), respectively. We observed 50% of the active behavior between 25.0° C and 32.0 °C (Fig. 3).

Mean T_{sel} of 17 *Chelonoidis chilensis* was 34.4° ± 0.3° C (range, 33.5°–35.1° C). Neither sex ($F_{1,14}$ = 0.20; *P* = 0.664) nor log-CCL ($F_{1,14}$ = 1.33; *P* = 0.269)

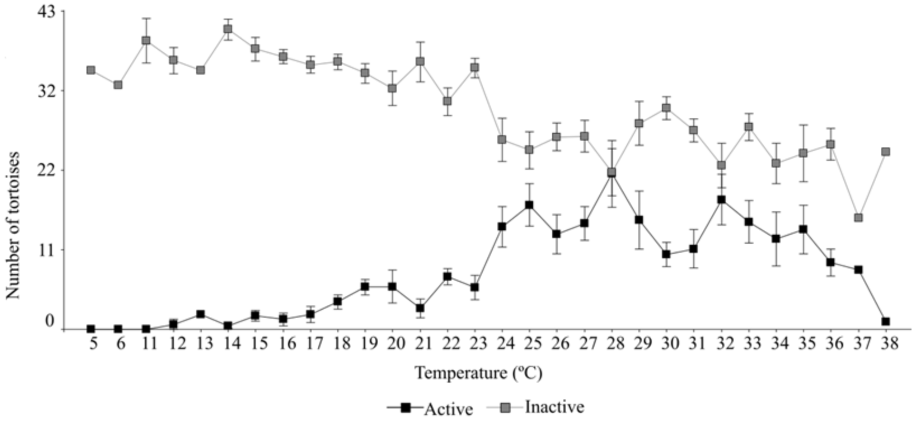

FIGURE 3. Activity pattern of Chaco Tortoises (*Chelonoidis chilensis*) relative to environmental temperature under semi-controlled conditions in the zoo enclosure, Cordoba, Argentina. Behaviors were recorded from December 2015 to May 2016. Mean numbers (± standard error) of observations of individuals that represented active/inactive behaviors at a given temperature are shown in relation to the environmental temperature, as proposed by Kazmaier et al. (2001).

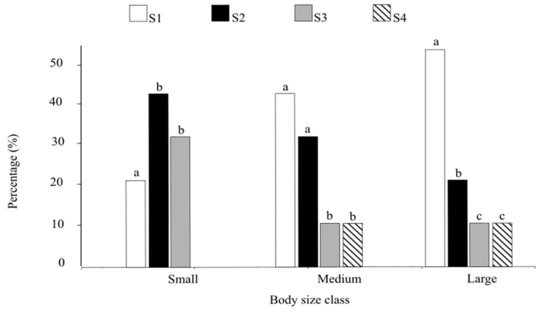

Figure 4. Terrarium with different temperatures ranges in four sections: S1 (22.0°–30.0° C); S2 (31.0°–37.0° C); S3 (38.0°–45.0° C); and S4 (≥ 46.0° C). Each Chaco Tortoise (*Chelonoidis chilensis*) was put inside the terrarium in the lowest temperature section, where they could move freely. After 30 min of habituation, the section where the tortoise was found was recorded every 10 min over 4 h (different letters within body size class in the figure are significantly different at $P < 0.05$).

were significantly related to T_{sel}. Overall, we observed tortoises significantly more frequently in the two cooler sectors of S1 and S2 ($X^2 = 87.88$; df = 3; $P < 0.010$), with no significant differences between males and females ($X^2 = 1.66$; df = 3; $P = 0.650$). We observed tortoises in the medium and large body size classes significantly less frequently in the hottest (S3 and S4) sectors than those in the smallest size class ($X^2 = 66.87$; df = 3; $P < 0.050$; Fig. 4).

The model for log-CCL and sex revealed that CT_{max} is log-CCL dependent ($F_{1,14} = 5.86$; $P = 0.030$; slope = -11.33) but not sex dependent ($F_{1,14} = 0.31$; $P = 0.584$). The range of CT_{max} was between 36.3° C and 42.0° C, with the highest CT_{max} values found in smaller and lighter individuals. The mean time to reach this temperature was 19.0 ± 1.7 min, with no significant differences in the log-CCL ($F_{1,14} = 0.06$; $P = 0.813$) or sex ($F_{1,14} = 1.06$; $P = 0.321$) models. No interaction effect was found between sex and body size ($F_{1,14} = 0.18$; $P = 0.680$).

Discussion

This study provides the first estimation of thermal parameters of the Chaco Tortoise *Chelonoidis chilensis*. Our results show that this tortoise is active at temperature ranges reported for many other tortoise species. For example, Red Foot Tortoises (*Chelonoidis carbonaria*) becoming active at values above 20° C and ceased at temperatures below 20.0° C (Noss et al. 2013). Similarly, Kleinmann`s Tortoises (*Testudo kleinmanni*), a Middle Eastern tortoise of desert and arid regions, was inactive at temperature values below 17.0° C (Lambert 1981; Geffen and Menderlssohn 1989) and Mediterranean Spur-Thighead Tortoises (*Testudo graeca*), another inhabitant of desert and arid regions, became inactive at values below 13.0° C (Cloudsley-Thompson 1974). At the other end of the temperature spectrum, activity of *C. chilensis* decreased above 38.0° C (this study), and *C. carbonaria* became inactive at above 37.0° C (Noss et al. 2013). Other species, like Speke`s Hinge-Back Tortoises (*Kinixys spekii*), a tortoise from the African savannah, are inactive above 29.0° C (Hailey and Coulson 1996) and *T. graeca* (Lambert 1981) and *T. kleinmanni* (Geffen and Menderlssohn 1989) above 28.0° C. Extreme records were obtained for the Desert Tortoise (*Gopherus agassizii*) from Mexico and the USA, which can have active behaviors at up to 45.0° C (Averill-Murray et al. 2002).

According to historical records, the thermal tolerance range of *C. chilensis* could influence its geographic distribution in the wild and its plasticity to respond to increased temperatures related to climate change (Ruete and Leynaud 2015). The broad performance breadth of *C. chilensis* reflects the environmental variability and thermal heterogeneity found throughout its geographical distribution (from southeastern Bolivia and Paraguay to northern Patagonia; Ruete and Leynaud 2015). *Chelonoidis chilensis* is specifically found in the Dry Chaco ecoregion in the wild, with mean temperatures between 18.0° C and 23.0° C, a maximum temperature above 47.0º C, and wide daily thermal fluctuations associated with a great seasonal climate variation (Morello et al. 2012).

In the zoo enclosure, we were unable to determine the environmental maximum temperature that makes *C. chilensis* completely inactive because we did not measure activity above 38.0° C; this information was gathered in the laboratory. Under thermal stress conditions, the first thermoregulatory responses in testudines often involve adjustments in behavior (Huey 1982). When this is insufficient, they can employ physiological mechanisms to keep the body temperature under lethal limits (Huey 1982). In the laboratory, when we exposed the animals to 45.0° C, they started to exhibit behavior indicative of approaching their critical thermal maximum, such as urination and salivation. Therefore, we infer that the environmental maximum temperature that makes *C. chilensis* completely inactive could be close to this temperature.

The activity pattern at environmental temperature between 22° C and 35° C coincided with the highest percentage of tortoise activity in the enclosure. Similarly, under laboratory conditions, the tortoises stayed for a longer time in sectors where temperature was between 22° C and 37° C (S1 and S2). These results suggest that the preferred environmental temperature for *C. chilensis* is within this range and provides important data to consider the optimal thermal conditions that should be provided in populations under human care in zoos or reserves. We found that the largest animals spent more time in the lowest temperature sector, whereas the smallest animals chose higher temperatures. This result indicates that, although individuals of the three body size classes reach the same body temperature, they differ in their thermoregulation strategies. Our findings are consistent with those reported for Painted Turtles (*Chrysemys picta*; Hutchinson 1966) and might be attributed to the effects of body dimensions on the cooling and heating rates of the individuals (McNab and Auffenberg 1976). On the other hand, Hailey and Coulson (1996) found a positive correlation between mean body temperature and weight in *Kinixys spekii* but under observations in the field. This difference in the results suggests the importance of measuring temperatures either in the field or in the laboratory with the purpose of understanding the relationship between thermoregulation in testudines and body mass, a potential biological indicator of the nutritional status of the animal (Paterson et al. 2014; Ardjima et al. 2020).

We observed that, under laboratory conditions, all *C. chilensis* individuals exhibited behavior indicative of critical temperature, such as rapid buccal pumping, salivating, accumulation of water around the eyes, and urination, as reported in other tortoise species (McGinnis and Voigt 1971; Cloudsley-Thompson 1974; Douglass and Layne 1978; Hailey and Coulson 1996). All the animals showed rapid body temperature recovery after 30 min. We obtained a wide range of CT_{max}, between 36.3° C and 42.0° C, and it varied inversely with body size. The smallest animals had the highest CT_{max}, indicating greater ability to perform activities under high air temperatures for those animals. The theory of heat transfer postulates that body dimensions are important in thermoregulation. This theory is also supported by Hailey and Coulson (1966), who concluded that small *K. spekii* have a larger safety margin of body temperature than larger ones. Moreover, Stevenson (1985) reported that larger ectotherms have a more restricted range of possible daily body temperatures than smaller ones. Although larger ectotherms have a restricted range of body temperatures compared to their smaller counterparts, being larger also allows them to maintain a more stable body temperature (Bulté and Blouin-Demers 2010). In addition, larger animals appear to facilitate the effectiveness of physiological thermoregulation and could be predicted to thermoregulate more accurately than small animals (Dzialowski and O'Connor 2004; Bulté and Blouin-Demers 2010).

The time to reach CT_{max} was the same for all the animals despite sex or differences in size, which supports the hypothesis that they gain or lose heat in different ways: individuals reached different body temperatures during the same period and with the same heat source. This hypothesis is important for management plans because this species should not be exposed to high temperatures without an available option to retreat. We demonstrated that heat stress for over 20 min might induce a body temperature close to stress values and bigger individuals, which are less tolerant, would require greater care.

Our findings indicate that the evaluated thermal parameters, T_{sel} and CT_{max}, did not vary between sexes. Bulté and Blouin-Demers (2010) found that large adult females of the freshwater Northern Map Turtle (*Graptemys geographica*) had a lower daily maximum body temperature and a narrower daily range than adult males and small juvenile females under laboratory conditions. For species in which the male is smaller than the female, energetically expensive behavioral and physiological processes related to male reproductive effort are triggered by an increase in plasma testosterone at the onset of sexual maturity (Bulté and Blouin-Demers 2010). The differences between the results reported for *G. geographica* and our findings may lie in the sexual differences in mass in *G. geographica* (the largest females are 8–10 times the mass of the largest males); sexual size dimorphism is not so marked in our study species.

Our study may contribute to future management plans and broaden the general knowledge of important variables in ectothermic species. We provide information about the thermal parameters of this species and support the assumptions that temperature is an important variable in ectothermic animals, because activity patterns vary with changes in environmental temperature. This information is important for *ex situ* and *in situ* conservation programs: both in zoos and protected areas, ambient temperature profiles must have a wide thermal amplitude. Our results highlight the importance of zoos as venues for conducting studies that contribute to the general knowledge of *C. chilesis*, while providing significant information about the study population, potentially leading to its improved welfare.

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Appendix Table. Morphometric variables of the population of 46 Chaco Tortoises *(Chelonoidis chilensis*) individuals in November 20 d before starting behavioral observations at the enclosure or before starting the first stage (November) in the enclosure of the Cordoba Zoo where activity patterns relative to environmental temperatures under semi-natural conditions were estimated. Abbreviations are F = female, M = male, I = indeterminate, CCL = carapace curve length, and PCL = plastron curve length.

Individual	Sex	Weight (g)	CCL (cm)	Width (cm)	PCL (cm)
1	F	1,600.0	25.0	25.5	16.7
2	F	1,550.0	26.0	24.4	17.9
3	F	1,700.0	26.0	25.0	18.0
4	F	1,430.0	25.8	24.8	17.4
5	F	1,700.0	26.5	25.0	17.0
6	M	890.0	21.4	18.7	14.9
7	M	1,100.0	22.0	19.5	15.7
8	F	2,000.0	26.7	25.6	18.9
9	M	2,300.0	31.5	24.5	19.8
10	F	1,900.0	28.3	25.7	19.1
11	F	2,300.0	28.0	26.0	21.5
12	M	2,100.0	28.0	25.5	18.5
13	F	1,320.0	25.5	22.2	16.8
14	M	1,610.0	25.2	22.0	15.8
15	M	700.0	19.1	17.2	14.0
16	F	2,100.0	27.9	27.0	20.3
17	M	1,500.0	26.2	23.2	18.1
18	M	2,210.0	32.0	28.3	22.6
19	F	1,620.0	26.2	24.6	19.5
20	F	1,600.0	25.6	24.0	18.1
21	F	1,410.0	26.9	24.0	16.1
22	F	1,200.0	22.8	21.3	15.5
23	F	850.0	21.5	20.7	15.1
24	F	510.0	16.6	17.0	12.5
25	F	1,600.0	27.6	25.2	27.8
26	F	650.0	19.5	18.5	14.2
27	M	900.0	25.0	19.5	15.5
28	F	1,700.0	27.7	26.0	19.0
29	M	1,050.0	21.5	20.5	15.0
30	F	1,510.0	27.0	25.1	17.5
31	F	2,700.0	30.0	29.5	21.5
32	F	1,310.0	24.5	21.7	17.4
33	M	1,120.0	24.0	22.0	16.5
34	M	1,000.0	23.0	19.9	15.5
35	I	270.0	16.3	16.2	11.8
36	I	530.0	16.7	17.0	11.4
37	F	1,450.0	23.5	21.0	16.5
38	M	620.0	19.3	17.5	13.4
39	M	900.0	22.0	18.5	14.3
40	M	900.0	22.5	21.0	15.5
41	M	800.0	20.5	19.0	13.8
42	M	1,000.0	22.0	20.0	15.2
43	F	560.0	19.5	18.5	13.9
44	F	1,300.0	25.0	24.5	17.2
45	F	2,000.0	25.0	24.5	18.0
46	F	1,500.0	23.3	23.9	17.8