

THERMAL MICROHABITAT AND THE OBSERVED AESTIVATION TEMPERATURES OF THE MUD TURTLE *KINOSTERNON CHIMALHUACA* (CHELONIA: KINOSTERNIDAE)

MICROHÁBITAT TÉRMICO Y LAS TEMPERATURAS DE ESTIVACIÓN OBSERVADAS DE LA TORTUGA DEL FANGO *KINOSTERNON CHIMALHUACA* (CHELONIA: KINOSTERNIDAE)

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Resumen.— El nicho térmico representa las condiciones de temperatura que afectan la historia de vida y la ecología de cualquier especie. Estudiar cómo las especies responden al nicho térmico es crucial para comprender su adaptabilidad al ambiente. Las características demográficas de la tortuga del fango *Kinosternon chimalhuaca* han sido evaluadas recientemente, pero aún se desconoce información sobre muchos aspectos ecológicos. Aquí, exploramos las temperaturas del nicho térmico de *K. chimalhuaca* durante un periodo estacional de sequía. Medimos, registramos y recopilamos información sobre las temperaturas corporales seleccionadas de microhábitat y ambientales en tortugas activas de un sitio acuático y comparamos esta información con las temperaturas de microhábitat y ambientales percibidas por tortugas estivando en un sitio terrestre. La temperatura corporal en las tortugas no estivando fue de 24 °C, las temperaturas seleccionadas en el laboratorio estuvieron entre 23-25 °C, temperaturas voluntarias mínimas de 22 °C y temperaturas voluntarias máximas de 28 °C. El rango de temperaturas en el microhábitat bajo el agua fue de 23-28 °C. Las temperaturas en el microhábitat para la estivación (dentro del bosque) fueron de 15 a 25 °C. Las condiciones térmicas fuera del bosque (temperaturas del suelo) fueron más altas que las temperaturas en el microhábitat utilizado para la estivación. Las temperaturas en el agua poco profunda fueron relativamente más bajas que las temperaturas del aire registradas alrededor del hábitat acuático. Además de la estivación facultativa de *K. chimalhuaca*, nuestros datos muestran diferentes condiciones térmicas entre los microhábitats de actividad y dormancia con el potencial de ser favorables con respecto a las temperaturas circundantes del medio ambiente.

Palabras clave.— Ambiente tropical, ecología térmica, dormancia, nicho térmico, temperatura bajo el agua, tortugas de agua dulce.

Abstract.— The thermal niche is the temperature conditions that affect the life history and ecology of any species. Studying how species respond to thermal niche is crucial to understanding their adaptability to the environment. Demographic characteristics of the mud turtle *Kinosternon chimalhuaca* have been recently evaluated, but information on many ecological aspects is still unknown. Here, we explored the thermal niche temperatures of *K. chimalhuaca* during a seasonal period of drought. We measured, recorded, and compiled information on body, selected microhabitat and environmental temperatures in active turtles of an aquatic site and compared this information with the microhabitat and environmental temperatures perceived by aestivating turtles in a terrestrial site. The body temperature in active turtles was 24 °C, selected temperatures in the lab were between 23-25 °C, minimal voluntary temperatures of 22 °C and maximal voluntary temperatures of 28 °C. The range temperatures in the underwater microhabitat were 23-28 °C. Temperatures in the microhabitat for aestivation (inside forest) were 15 to 25 °C. Thermal conditions outside the forest

(soil temperatures) were higher than the temperatures in the microhabitat used for aestivation. Temperatures in the shallow water were relatively lower than the air temperatures recorded around the aquatic habitat. In addition to facultative aestivation of *K. chimalhuaca*, our data show different thermal conditions between activity and dormancy microhabitats with the potential to be favorable regarding the surrounding temperatures of environment.

Keywords.— Dormancy, freshwater turtles, thermal niche, thermal ecology, tropical environment, underwater temperature.

INTRODUCTION

The thermal ecology of species is a topic of scientific interest due to accelerated and widespread climatic and habitat changes (Tuff et al., 2016; Buckley et al., 2022). Currently it is necessary to understand the state of the ecological requirements and adaptive responses of species to threats such as global warming (Davis et al., 2005; Dahlke et al., 2018; Sinervo et al., 2024). In animals, dormancies are defined as inactivity and adaptive responses that are generally induced by adverse environmental conditions (Withers & Cooper, 2010; Wilsterman et al., 2021). For example, aestivation is a survival strategy for dealing with arid conditions that can occur in response to high temperatures, droughts or food shortages (Storey, 2002; Storey & Storey, 2012). Environmental conditions and dormancy responses are two ecological topics requiring further investigation in many species of ectotherms (Osborne & Wright, 2018; Lownds et al., 2023).

Aestivation in turtles is a behavioural trait that has evolved several times and independently in larger lineages of pleurodires and cryptodires species (Macip et al., 2023). Laboratory studies on metabolic and physiological traits in active and aestivating turtle species are those that dominate the contribution to current knowledge (Roe et al., 2008; Haskins & Tuberville, 2022; Jiang et al., 2023). For example, Ligon and Peterson (2002) suggest that turtles under prolonged aestivation periods have a significant reduction in metabolic and body water evaporation rates. While turtles with short periods of aestivation or no aestivation have high percentages of dehydration (29-32 % hydrated body mass) and almost unaltered metabolic rates. Unlike laboratory studies, radio tracking monitoring of turtles facilitates some technical possibilities to understand more about their ecology and behavior during active or inactive periods in the field (McKnight & Ligon, 2020; Bowers et al., 2021), even to record short migrations to a new habitat (Gibbons et al., 1983). Research on the thermal ecology in turtles that alternate periods of activity and aestivation is a topic with little biological knowledge (Litzgus & Brooks, 2000; Jiang et al., 2023).

The mud turtles (family Kinosternidae) are exclusively distributed in the New World (Berriozabal-Islas et al., 2020). The

genus *Kinosternon* showed their largest diversity in Mexico (Legler & Vogt, 2013). There are at least five endemic species with limited distribution along the Pacific coast of Mexico (Macip-Ríos et al., 2015), one of these endemic species is the Jalisco Mud Turtle, *Kinosternon chimalhuaca*, which was described in the 90's (Berry et al., 1997). However, very few information is published besides their description (Casas-Andreu, 2002). A recent ecological study showed that an urban population can be highly abundant with sexual ratios biased towards females than a population in the conserved forest (Garrido et al., 2021). In addition, monitored individuals of *K. chimalhuaca* in an urban aquatic habitat showed a population trend of growth and stability in their demographic structure and reproductive condition (Raya-García et al., 2025). The aestivation of 242 days in *K. chimalhuaca* has been observed only in individuals that inhabit the dry tropical forest (Macip-Ríos et al., 2023), while urban individuals apparently have a behaviour of non-aestivation in the presence of an aquatic and perennial habitat (pers. obs.). The aim of this research is to document the basic thermal biology of *K. chimalhuaca* and compare the environmental temperatures between the aquatic-active microhabitat and the terrestrial-aestivation microhabitat during a seasonal period of drought.

MATERIALS AND METHODS

During November 2021, we look for turtles in the urban locality of Emiliano Zapata (19° 23' 11.76" N, 104° 58' 2.2794" W) and the Chamela-Cuixmala biosphere reserve (19° 29' 54.24" N, 105° 2' 39.48" W). Both sites located on the coast of Jalisco, Mexico with mean annual temperature of 24.9 °C (range 13.8-32 °C; Bullock, 1986) and highly seasonal precipitation with an average of 749 mm from June to September.

Urban turtles were captured in a ditch used by the town to move the grey waters and forest turtles were captured in an ephemeral stream with many shallow pools. We sampled turtles from both sites overnight using partially submerged hoop-nets baited with sardines in soy or olive oil (Moll & Legler, 1971). Captured turtles were individually marked using Cagle (1939)

code. Each turtle was measured using an analogue calliper (Swiss, Precision Instruments, Altstätten, Switzerland; 0.1 mm) and weighted with digital scale (American Weight Scales, Cumming, Georgia).

Prior to release, we attached VHF telemetry transmitters (TXC-125G Telenax, Playa del Carmen, Quintana Roo) and temperature micro dataloggers (iButton Thermochrons, Dallas Semiconductor, Dallas, TX; accuracy 70.5 °C) to the posterior carapace of each turtle using epoxy clay (Grayson & Dorcas, 2004). Before attachment, dataloggers were programmed to record temperatures at 90-min intervals and were then covered in plastic tool dip (Plasti-Dip International, Circle Pines, MN) to prevent water damage. A thick layer of epoxy was used as an insulating base to prevent contact between the iButton and the turtle's shell, allowing a closer record of environment (microhabitat temperatures) rather than shell temperatures. The microhabitat temperatures in free-ranging turtles were recorded during the dry months of January to April. Additionally, three thermal data loggers (Hobo® Pendant temp/light) were placed for recording environmental temperatures of December to March in the air, water, and soil external habitats. The water data logger was under the ditch water (submerged about 20 cm), air data logger was hidden and hanging under a tree (< 1 m high and close to the ditch) in Emiliano Zapata village, and one data logger was the forest soil (clear and exposed area) in the Chamela forest. The environment data loggers (water, air and soil) were programmed to record temperatures at 60 min intervals. In addition, we used a Blackview BV9900-Pro smartphone equipped with a FLIR thermal camera (Lepton 2.5 IR Sensor) during the turtle monitoring to record the microhabitat and shell temperature of aestivating turtles and avoid interrupting the *in situ* dormancy.

During March 2022 we monitored eight individuals and in August we remove the devices and recover the information from all data loggers. Later in December, we collected and recorded the body temperature of the shell and cloaca of aquatic and active individuals from Emiliano Zapata and carry out thermal gradient experiments to record selected temperatures in the lab of the Instituto de Biología, Biological Station at the Chamela-Cuixmala Biosphere Reserve. The thermal gradient design was a dry and linear environment inside an acrylic plastic container (150 x 30 x 30 cm) with decreasing temperatures. The temperature gradient ranged from 20-40 °C and the length of the tests was 17:30-23:30 h with body temperature recordings every 30 min.

The selected temperature range was obtained by averaging the first and third quartiles of all data. The minimum and maximum

voluntary temperatures were calculated by obtaining the average of lowest and highest data recorded in each individual throughout the experiment. All body (shell and cloacal) and selected temperatures of active individuals were recorded using a digital thermometer (Amprobe model TMD-50) and a K thermocouple (± 0.1 °C) immediately after of handling (< 60 sec). The nets remained in the water for approximately 30 min and then individual by individual was extracted from the nets between 9:00-11:00 hours to measure temperatures. We used a two-way ANOVA to look for differences between shell and cloacal body temperatures and for differences between sexes. All statistical tests were conducted in R version 4.1.2 (R Core Team, 2019).

RESULTS

We captured and recovered a total of four active individuals and one aestivating individual of the *K. chimalhuaca* turtle with fully functioning data loggers and transmitters. An individual from Emiliano Zapata was collected with data logger and transmitter damaged and one individual from the Chamela forest was found dead between the forest and the dry stream path with a functioning transmitter but a missing data logger. One remaining individual was never located or recaptured. The aestivating individual was sheltered under the roots of trees and plant detritus within the dry tropical forest of Chamela, approximately 5-7 m away from the path that forms the mainstream (Fig. 1). The shell temperature of the aestivating turtle was 15 °C and the average thermal around the microhabitat was 17 °C, with a minimum of 15 °C and a maximum of 20 °C (Fig. 1).

The average of the cloacal temperature in 63 active and aquatic individuals was 23.6 ± 0.5 °C and was not significantly different than the average of 23.5 ± 0.6 °C of the temperature in the shell ($F = 0.44$, $p = 0.50$) between sexes ($F = 3.63$, $p = 0.06$) or the sex/body interaction ($F = 0.04$, $p = 0.83$). The temperature for the underwater microhabitat showed two patterns of day-night oscillation, the first during January and February ranging from 25 °C to 28 °C and the next during March-April ranging from 23 °C to 27 °C (Fig. 2A). The range of selected temperatures for 14 adult individuals was 23 °C to 25 °C (Fig. 2A). The minimum voluntary temperature was 22 °C and the maximum voluntary temperature was 28 °C, covering the microhabitat, body, and selected temperatures recorded for *K. chimalhuaca* (Fig. 2A). The temperature in the microhabitat for aestivation showed a day-night oscillation ranging from 15 °C to 25 °C, mostly not meeting the average of body and selected temperatures recorded for active individuals (Fig. 2B).

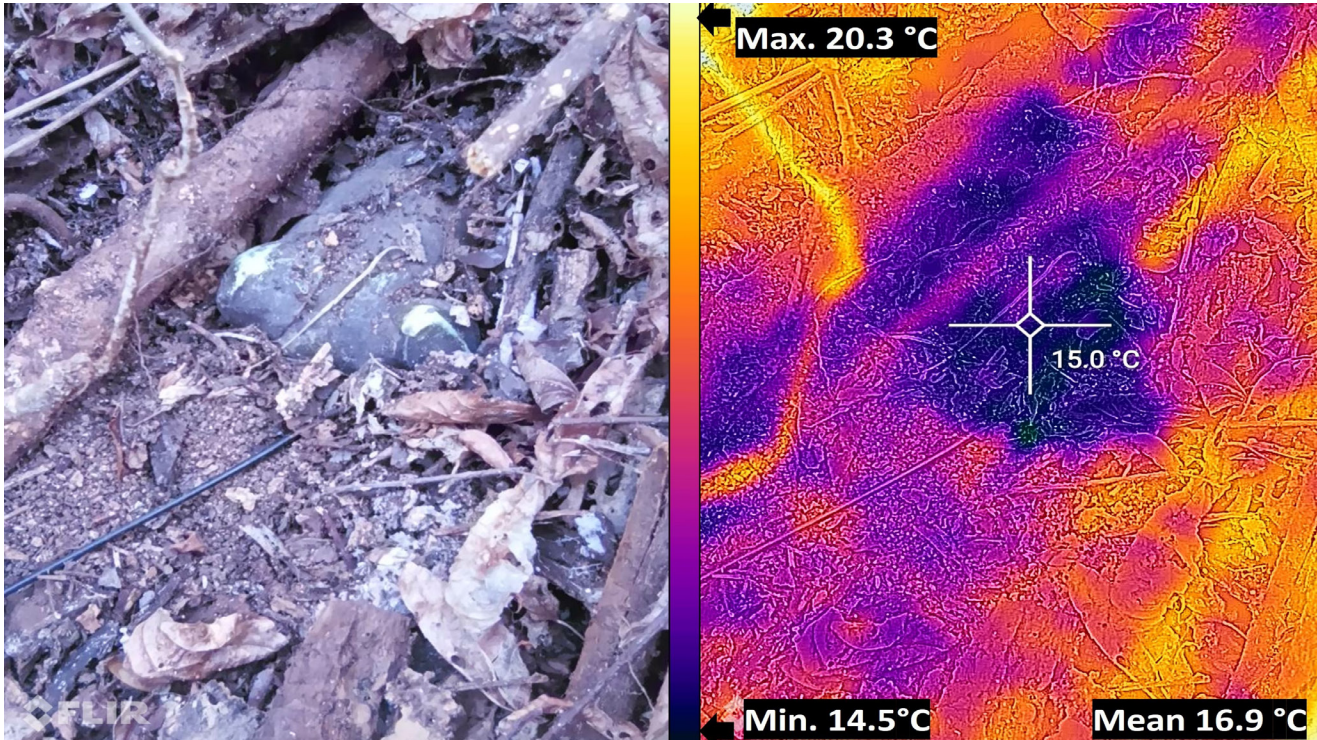


Figura 1. Estivación y temperaturas del microhábitat en la tortuga del fango *Kinosternon chimalhuaca* visualizadas por termografía en el bosque tropical de Chamela, Jalisco.

Figure 1. Aestivation and microhabitat temperatures in the mud turtle *Kinosternon chimalhuaca* visualized by thermography in the tropical forest of Chamela, Jalisco.

The environmental temperatures recorded on the dry soil of the terrestrial habitat were highly variable with nocturnal temperatures of 13 °C to 25 °C, and diurnal temperatures of 25 °C to 46 °C (Fig. 3A). Environmental temperatures in the shallow water of the aquatic habitat (Fig. 3B) showed more variation than the microhabitat temperatures in the deep underwater (Fig. 2A). Environmental temperatures in the air around the aquatic habitat (Fig. 3C) were higher than the temperatures in shallow water (Fig. 3B) but with thermal ranges smaller than the temperature ranges in the soil of the terrestrial habitat (Fig. 3A).

DISCUSSION

Although the kinosternids are a diverse group of turtles (Legler & Vogt, 2013), thermal ecology has been a scientific topic with limited research in the family Kinosternidae and other families of semi aquatic turtles (Macip-Rios et al., 2015; Berriozabal-Islas et al., 2020). A study by Berriozabal-Islas (2018) makes a significant contribution to the study of the thermal ecology of several species of mud turtles of the genus *Kinosternon* from Mexico. Some of the main conclusions of Berriozabal-Islas (2018) were that mud turtles have low to moderate thermal preferences (17–22 °C), low thermal precision, thermal limits of 37–41 °C for high temperatures and 6–8 °C for low temperatures, and generalized

thermoconformity. Although results of Berrizoabal-Islas (2018) showed a low thermal quality of the habitat for *Kinosternon chimalhuaca*, their study focuses on the terrestrial environment with limited description on the used microhabitats. Our results show a subaquatic and an aestivation microenvironment with thermal conditions that have the potential to be favorable for active and inactive turtles. Results for body and selected temperatures in *K. chimalhuaca* of Berrizoabal-Islas (2018) differ slightly with our results. The voluntary temperatures reported in our study suggests that the basic thermal requirements of active individuals are covered by temperatures provided by the subaquatic environment. Additionally, the minimum 7 °C and maximum 41 °C of critical temperatures reported by Berrizoabal-Islas (2018) for *K. chimalhuaca*, suggest that turtles of our study are out of thermal stress both inside the water and aestivation sites during a hot and dry period in the environment.

Understanding how species respond to thermal heterogeneity is a fundamental question in ecology (Angilletta, 2009; Buckley et al., 2015). Ectotherms in water experience rates of heat transfer at least two orders of magnitude greater than in air (Fitzgerald & Nelson, 2011). Therefore, the aquatic habitat could constrain the thermoregulatory capabilities. However, body temperatures in some turtles can be modulated via subaquatic behaviors such

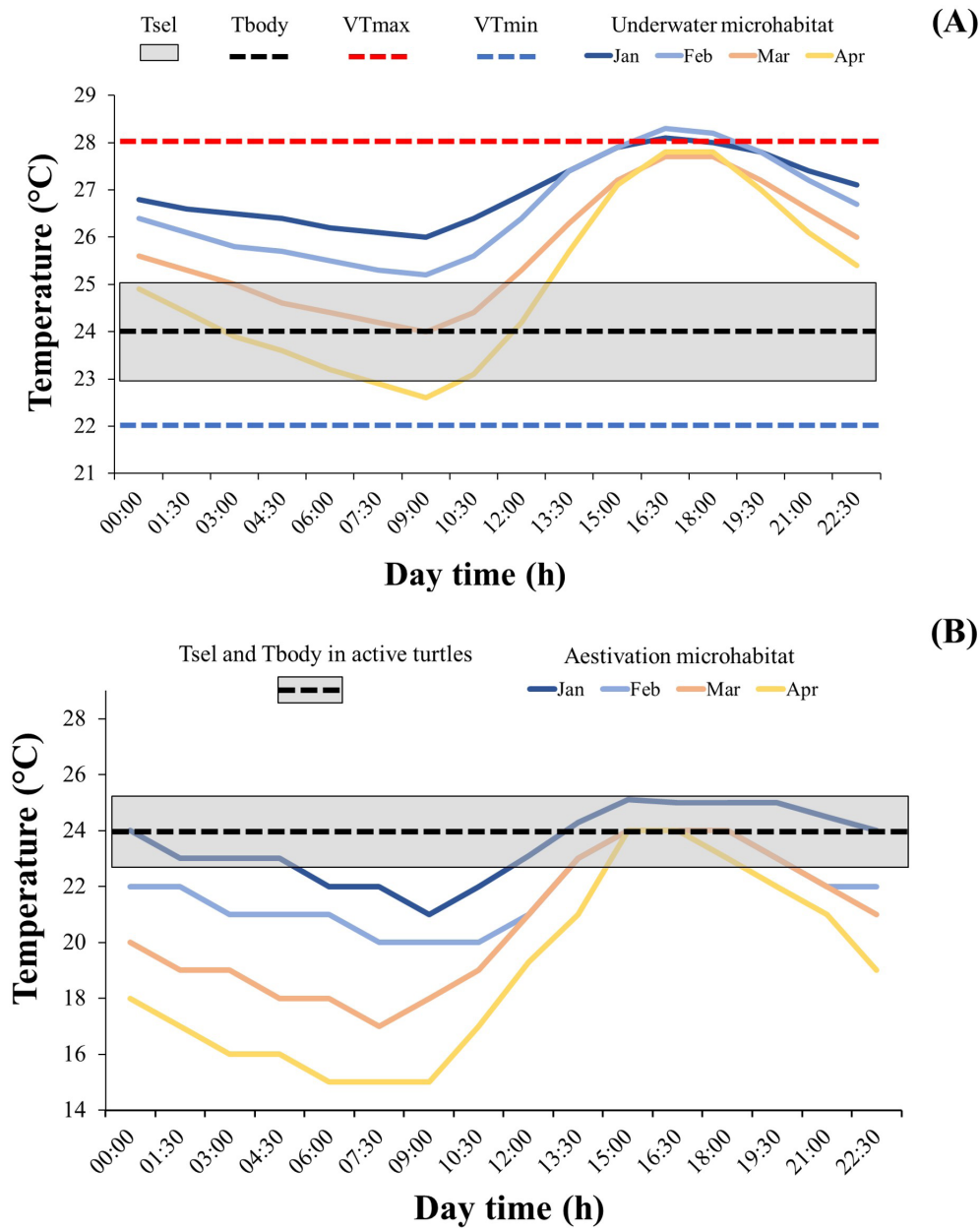


Figura 2. Temperaturas diarias en los microhábitats bajo el agua (A) y estivación (B) de *Kinosternon chimalhuaca* durante un periodo estacional seco en Jalisco, México. Temperaturas de la cloaca (*T*body), temperaturas seleccionadas (*T*sel), temperaturas voluntarias máximas (*VT*max) y temperaturas voluntarias mínimas (*VT*min).

Figure 2. Daily temperatures in the underwater (A) and aestivation microhabitat (B) of *Kinosternon chimalhuaca* during a dry seasonal period in Jalisco, Mexico. Cloacal temperatures (*T*body), selected temperatures (*T*sel), maximum (*VT*max) and minimum (*VT*min) voluntary temperatures.

as selecting thermally favorable microhabitats (Akens et al., 2014; Chandler et al., 2020). So far, our data suggests that free-ranging turtles were accessing underwater temperatures that do not exceed their voluntary thermal range. However, it is important to note that underwater temperatures during February and March

are entirely above the preferred temperatures. This climatic condition may be due to a reduction in thermal conditions in the environment since the tropical study area receives the first intense droughts during the winter and water temperatures decrease, which probably motivates the turtles to seek warmer



water columns. However, our study requires a continuation over time to determine the thermal factors under the water (e.g., temperatures in mud depth and water column) and terrestrial environments (basking temperatures and duration) that best explain the body temperature and the thermal niche in this species.

Otherwise, we have observed that unlike other species of turtles from temperate climates, *K. chimalhuaca* does not appear to have a diurnal basking (R. Macip & E. Raya, direct observation), and although having greater activity times during the night, nocturnal basking may also not be occurring. Our data indicate that temperatures outside the aquatic habitat (aerial environment) are regularly cooler at night (e.g. < 23 °C from 00:00 onwards) which does not match with the warmer temperatures recorded in the aquatic microhabitat during the night (e.g. >23 °C from 00:00 onwards). The underwater habitat appears to have a low cost for thermoregulation of this tropical mud turtle, but additional studies could evaluate the unknown role of physical and chemical properties of the water (e.g., turbidity, pH, solubility), biotic factors (e.g., vegetation, predation, competition), and their interactions on the thermoconformity observed in Kinosternids.

Aestivation is often induced by high temperatures and the absence of water, which raises the question of how aestivating animals regulate their body temperatures in response to environmental changes (Jiang et al., 2023). The body temperature (T_b) of ectotherms is determined by the ambient temperature (T_a) to which they are exposed during hypometabolic states (Jiang et al., 2023). In semi-aquatic turtles, the metabolic responses can be decreased exponentially with lower temperatures (Haskins & Tuberville, 2022). Our study denotes that temperatures in the aestivation microhabitat of *K. chimalhuaca* are lower than physiological temperatures of active individuals, which suggests that the body temperatures of aestivating turtles could be influenced by moderately cool microhabitats within the forest vegetation compared to the external habitat (soil forest temperatures) that was usually warmer. These apparently favorable thermal conditions of aestivation and subaquatic microhabitats in *K. chimalhuaca* require greater research effort. For example, with the help of biophysical models it is necessary to address the accuracy of thermal niches in different and potential aestivation sites. At this same address, it is necessary to devise practical solutions for the use of optimized biophysical models for the recording of operating temperatures at underwater conditions for active turtles. In the future, much scientific research is required to evaluate how the threats of global warming and loss-degradation of habitat affect thermal and dormancy ecology in semi-aquatic reptiles.

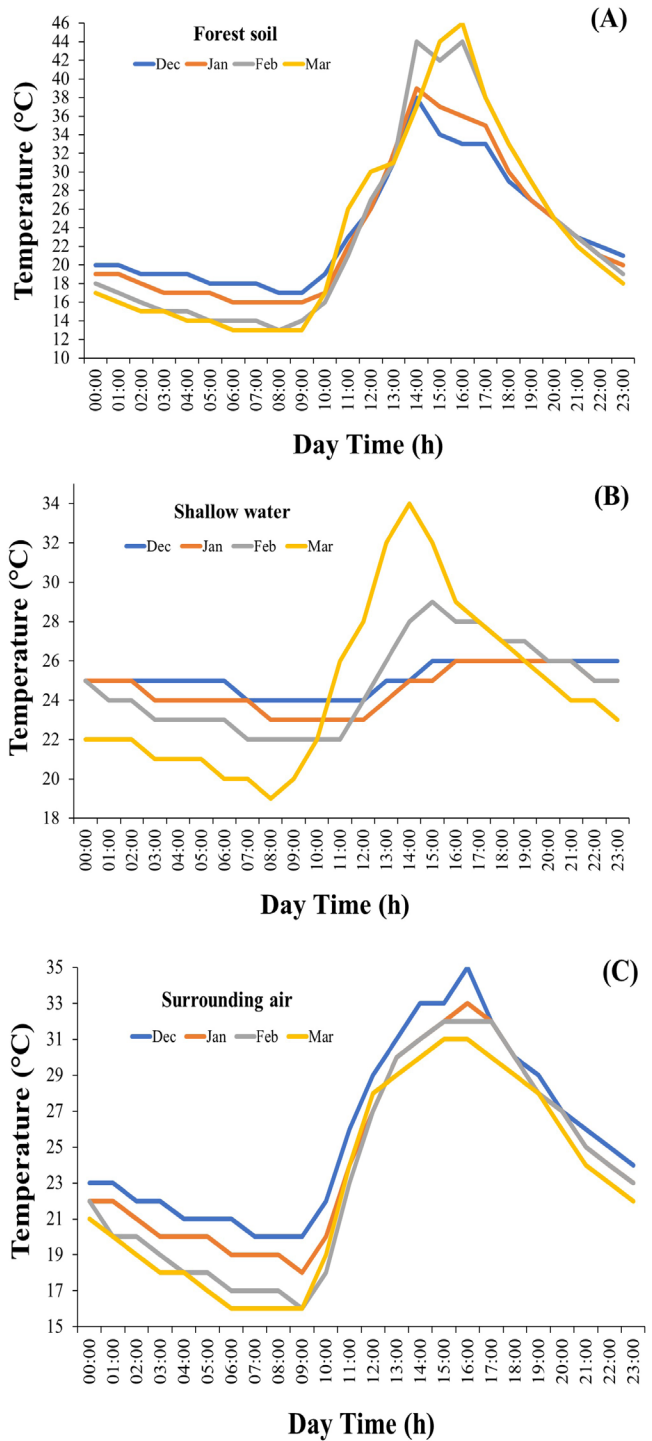


Figure 3. Temperaturas ambientales diarias en el hábitat terrestre (A) y hábitat acuático (B, C) de *Kinosternon chimalhuaca* durante un periodo estacional seco en Jalisco, México

Figure 3. Daily environmental temperatures in the terrestrial (A) and aquatic habitat (B, C) of *Kinosternon chimalhuaca* during a dry seasonal period in Jalisco, Mexico.



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