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ORIGINAL ARTICLE

Rural occupancy in a montane burrowing snake: the importance of thermal and microhabitat resources during the rainy season

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Abstract
Thermal and microhabitat resources are two fundamental requirements that affect the life history of any ectotherm. Furthering our understanding of how reptilian species meet these ecological requirements is crucial for assessing the impact of environmental and anthropogenic changes on populations. Here, we explored some fundamental aspects of the thermal and microhabitat ecology of *Conopsis biserialis*, a small, burrowing, and endemic earthsnake of central Mexico. The study was conducted during the rainy season in a montane site disturbed by rural activities. The mean field body temperature (Tb) of *C. biserialis* was 26 ± 0.6 °C. Field Tb did not differ significantly between sex and development stages. However, we found that Tb was positively correlated with substrate, air, and under-rock temperatures (Ts, Ta, and Tr) in the rural microhabitat. Regression analysis showed that substrate and under-rock temperatures (Ts and Tr) were the parameters that best explained Tb variability in the individuals. The temperature and relative humidity under shelter did not differ significantly among shelter types and/or rock sizes. In addition to these thermal traits, earthsnakes selected and utilized six common biotic and physical elements of the rural microhabitat. Most individuals used high proportions of large and medium rocks for sheltering, and these rocks were selected around crop fences and cleared grasslands where the soil can be either covered with low vegetation or bare. Our results suggest that, during the rainy season, individuals of *C. biserialis* use and select some biotic and structural resources of the rural microhabitats, and were capable of actively regulating their temperature by using shelters with high values of microclimatic homogeneity.

Keywords Disturbed habitat · Ectothermic vertebrate · Hemisinanthrope · Montane reptiles · Suburban ecology

Introduction

Thermal and microhabitat ecology are two topics that have often been studied independently in many ectothermic taxa. For example, in reptiles, thermal and microhabitat characteristics are closely related to behavioral abilities and are pivotal features for survival (Martín-Vallejo et al. 1995; Melville and Schulte II 2001; Scheffers et al. 2014; Chukwuka et al. 2021). Reptiles can respond to variations in the availability of thermal and microhabitat resources across different spatial and temporal scales, daily and seasonal activity patterns, and changes in habitat use (Bauwens et al. 1996; Maia-Carneiro and Duarte-Rocha 2013; Muri et al. 2015). However, this thermal and microhabitat dependence on the environment could be compromised given the effects of climate change (Böhm et al. 2016; Winter et al. 2016) and habitat modification (Block et al. 2013; French et al. 2018).

Environmental transformation by human activities is generally perceived as posing a serious threat to biodiversity (McKinney 2006; Hamer and McDonnell 2010). Rural and urban landscapes were both originally natural environments that have been fragmented or transformed into areas of economic development for human populations (Fahrig 2003). In rural landscapes, certain species that are resilient to anthropogenic changes are commonly dominant (Blair 2001; Zipperer and Guntenspergen 2009). One of the great challenges in the science of ecology and behavior is to understand how these resilient species can be non-sensitive to changes in their habitat and survive within these new

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anthropogenic environments (synanthropic phenomenon: Guetté et al. 2017).

Although many species of reptiles (e.g., resource specialists) can be vulnerable to extirpation caused by the transformation or destruction of their natural environment (Garden et al. 2007; Mitchell et al. 2008; French et al. 2018), there are other ecologically versatile and habitat generalist reptiles (i.e., euryecious species) that cope better with anthropogenic changes (Zappalorti and Burger 1985; Powell and Henderson 2008).

The ecology of many species of burrowing snakes that inhabit transformed sites has been poorly studied (How and Shine 1999; Castañeda-Gonzalez et al. 2011). The highly secretive and small burrowing earthsnake *Conopsis biserialis* (Taylor & Smith, 1942) is an ambush-hunter species with a mean snout-vent length (SVL) of 200.3 mm and geographic distribution in the Trans-Mexican volcanic belt (Goyenechea and Flores-Villela 2006; Castañeda-Gonzalez et al. 2011). Frequently, these earthsnakes are found sheltering under rocks or fallen trunks in pine-oak forests (conserved habitat) and in transformed environments such as mosaics of agricultural and small patches of reforested land (Castañeda-Gonzalez et al. 2011; Raya-García et al. 2019). According to the ecological characteristics and life history of their populations (Castañeda-Gonzalez et al. 2011; Arteaga-Tinoco 2018; Raya-García et al. 2016), C. *biserialis* seems to mainly be a hemisynanthropic species (species that typically occur in both synanthropic and natural environments).

Although ecological and behavioral knowledge of *C. biserialis* has been increasing (Castañeda-Gonzalez et al. 2011; Raya-García et al. 2020), the influence of transformed habitats and the resilient characteristics that allow this species to survive in modified environments remain unknown. Here, we studied the basic thermal ecology and microhabitat selection of *C. biserialis* individuals inhabiting a rural montane site. The main objective was to evaluate the use of thermal and microhabitat resources during the rainy season when the species presents its highest abundance. We hypothesized that, within this montane rural environment, the earthsnakes will select and use microhabitats that provide stable microclimatic conditions suitable for their thermoregulatory activities.

Materials and methods

Study site and snakes

We conducted fieldwork during the rainy season (July-September: summer) of 2018 in the locality of Ichaqueo, municipality of Morelia, Michoacán, Mexico (19°56’86’’N, 101°13’10’’ W; elevation 2500 m a.s.l). The rainy season is the time of peak abundance of this species and few or no individuals can be observed/captured during the dry season of the year (Castañeda-Gonzalez et al. 2011). Ichaqueo is a rural town located within the Transversal Neovolcanic Axis region of Mexico and is characterized by the presence of farming and forestry activities (Arteaga-Tinoco 2018). Data from the National Meteorological System of Mexico (San Miguel del Monte Meteorological Station: 16,114) showed that the regional environmental temperatures during the rainy seasons from 2015 to 2018 were (average: 18.6 °C, max: 29.8 °C, min: 8.5 ºC) and total annual rainfall was 2550.1 mm. The natural vegetation of Ichaqueo is dominated by pine-oak associations (Rzedowski 1978). Since the highest number of observations of *C. biserialis* comes from both abandoned and productive farming fields (Arteaga-Tinoco 2018), we defined the study area around crop and livestock grazing fields.

We manually collected all earthsnakes found under rocks or bark fragments via the method of visual encounter survey (VES). From each individual, we recorded body mass using a Pesola 20 g scale and body size (SVL in mm) using a tape measure. We also determined the sex of each individual using probing techniques for small snakes (Raya-García et al. 2017), while development stages were estimated based on the SVL value (Castañeda-Gonzalez et al. 2011). The minimum SVL of adult individuals is 190 mm and we therefore assumed that an individual with SVL $\geq$ 190 mm was an adult and SVL $<$ 190 mm was a juvenile (Castañeda-Gonzalez et al. 2011). To avoid resampling the same individuals, all captured earthsnakes were marked by ventral scale clipping and released at the point of capture.

Thermal and microhabitat data

The body temperature of snakes, microclimatic conditions, and structural traits of the used and available microhabitats were recorded in the field with a sampling time of 09:00–19:00 h. We measured the following thermal characteristics: (1) earthsnake body temperature (Tb), directly from the cloaca with a digital thermometer (Fluke model 51-II) and a K thermocouple ($\pm$ 0.1 °C) immediately after capture ($<$ 10 s); (2) microenvironmental temperatures at the observation site (substrate temperature (Ts), with the probe of the thermometer slightly buried in the soil, air temperature (Ta), at height 5 cm above the ground, and under-rock temperature (Tr), approximately at the center of the bottom face of the rock); and relative humidity of the substrate under each shelter, recorded with a weather microstation (Kestrel 4000).

For microhabitat use (presence vs. absence), we categorized the type and size of shelter into small rocks ($<$ 20 cm in diameter), medium rocks (20–40 cm in diameter), large rocks ($>$ 40 cm in diameter), and bark fragments

(> 25 × 65 cm in area). Shelter position was categorized into three available areas: close to crop fences (< 1 m), close to cattle fences (< 1 m), and in cleared grasslands. Finally, we recorded the presence or absence of the following variables around the shelter: trees, shrubs, ground vegetation, and bare soil. The previous categorization of the shelters, biotic, and structural resources corresponded to those observed during fieldwork in the study site. To determine the microhabitat used by the earthsnakes, we took a circular area of 50 cm in radius around the point at which the individual was found.

To determine whether the selection of microhabitats by the earthsnakes is non-random, data were collected from 86 random refuge sites. Microhabitat availability in the study area was estimated along a series of random transects covering the whole area. A sample was taken every 10 m, choosing the nearest rock to a given transect point as the center of the sampling area. We then followed the same procedures to measure the microhabitat variables as those used when encountering earthsnakes. We visited the field site regularly (two times per month) from July to September of 2018. We walked over the site covering all available fallen objects (rocks, logs, barks, etc.) as possible terrestrial microhabitats, subterranean microhabitats (Raya-García 2024) were not evaluated in this study. Walks were conducted on warm sunny days at between 09:00 and 19:00 h (GMT-6). We lifted all visible rocks and bark fragments searching for earthsnakes, which were fully active under these shelters (Raya-García et al. 2019). Most of these rural shelters are abandoned by the earthsnakes during the dry season (Arteaga-Tinoco pers. comms.). All animals found were processed and released at the exact point of capture.

Data analysis

We performed a multiple regression analysis to examine the associations between field body (Tb) and microenvironmental (Ts, Ta, and Tr) temperatures and used Spearman correlation analyses (Zar 1996) to determine whether there were significant relationships between these thermal variables. Assumptions of normality and homoscedasticity in the multiple regression were confirmed with Shapiro-Wilk and Breusch-Pagan tests. Collinearity and autocorrelation were evaluated with the Variance Inflation Factor (VIF) and the Durbin-Watson test, respectively. We selected the best model using the mixed stepwise strategy and validation by AIC values. To determine if the Tb temperatures differ according to the development stage and sex of the snakes, comparisons were made using the non-parametric Mann-Whitney test. An ANOVA was implemented to assess differences among substrate temperatures (Ts) and the four types of shelters used by snakes. In the case of the temperatures Tb, Ta, Tr, and the percentage of relative humidity (RH) in the shelters, we used a Kruskal-Wallis test (Zar 1996). Post hoc pair-wise comparisons were tested for significance, where the p-value was adjusted by Dunn's method with Bonferroni correction (non-parametric) or Tukey test (parametric), as appropriate. We used a chi-square test to assess whether there were significant differences between the frequency of individuals and the type of shelter used, and a Fisher's test of independence to assess whether there is an association between the use of different shelters and the sex of the snakes (Zar 1996).

Finally, we estimated Manly's Selection ratios (Manly et al. 2007) with the adehabitatHR R package (Calenge 2023) to analyze the selection of structural and biotic attributes in the microhabitat of *C. biserialis*. This index considers the proportion of all used and available microhabitat sites and computed the resource selection ratios (wi index) for design I, II, and III data types, with resources defined by several categories (Manly et al. 2007). An index value of -1 indicates that a particular microhabitat was totally avoided, while + 1 indicates maximum preference. Significant differences associated with the level of preference were evaluated using a log-likelihood chi-square test (Khi2L) for overall microhabitat selection. All analyses were performed using R software v4.0.5 (R Core Team 2013).

Results

We collected 54 individuals of *C. biserialis*, of which 42 were adults with a mean snout-vent length (SVL) of 220.7 mm (± 3.7 mm), with a range of 190–260 mm, and a mean body mass of 13.03 g (± 0.4 g), with a range of 7.3–22 g. Twelve individuals were juveniles with a mean snout-vent length (SVL) of 156.2 mm (± 4.5 mm), with a range of 115–185 mm, and a mean body mass of 4.5 g (± 0.2 g), with a range of 2.2–6.9 g. The highest capture rate per month was in August ($n = 24$). The higher peak of observations occurring between 10:00 and 16:00 h during the field search.

On the four types of temperatures recorded in the field, mean Tb was 26 ºC, Ts was 21.6 ºC, Ta was 20.1 ºC, and Tr was 26.8 (Online resource: Table S1). Body temperature (Tb) did not differ significantly between the sex (Tb: $W = 360$, $p = 0.894$) and development stage of the earthsnakes (Tb: $W = 187$, $p = 0.176$). The Tb of the earthsnakes was positive and significantly correlated with microenvironmental temperatures (Fig. 1). The best regression model found that 89.7% of the variance observed in Tb is explained by the contribution of Ts and Tr ($F = 222$, $p < 0.001$), with Tr being significant within the model ($t = 15.86$, $p < 0.001$). Correlations of Tb and Tr were also positive and significant between sex and development stages (Online resource: Figs. S1 and S2). Throughout the day, earthsnakes generally

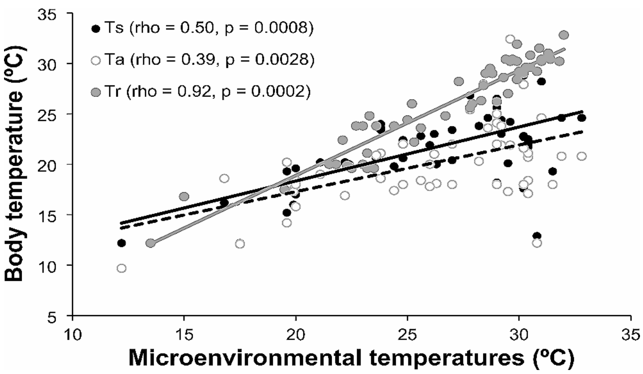

Fig. 1 Multiple regression analysis of field body temperature (Tb) against substrate temperature (Ts), air temperature (Ta) and under rock temperature (Tr) of *C. biserialis* earthsnakes

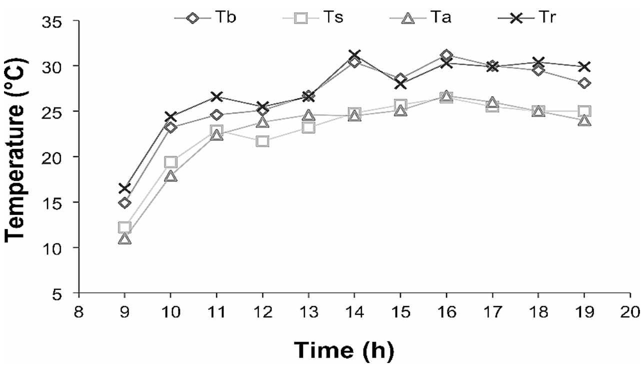

Fig. 2 Average variation of field body temperature (Tb) and microenvironmental temperatures (Ts, Ta, Tr) throughout the sampling hours by day for *C. biserialis* earthsnakes

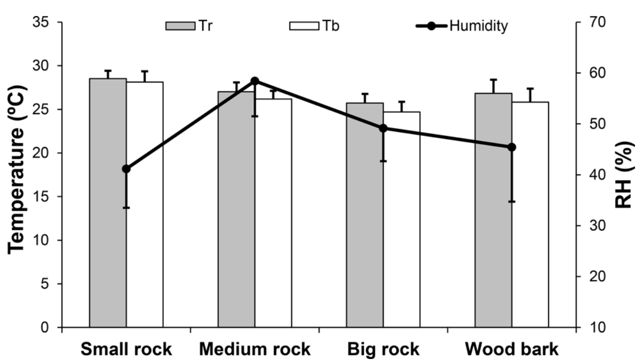

Fig. 3 Body temperatures (Tb), under rock temperatures (Tr) and relative humidity (RH) under four different shelters used by *C. biserialis* earthsnakes. Bars and points on the line show mean ± SE.

present Tb fluctuating with Tr more than with the temperatures of the substrate (Ts) or air (Ta) recorded at the time of capture (Fig. 2).

We found no significant differences in Tb ($\chi^2 = 4.15$, $p = 0.24$), Tr ($\chi^2 = 3.97$, $p = 0.26$) or RH ($\chi^2 = 3.28$, $p = 0.34$) among the different shelters used by the snakes (Fig. 3). However, the Ts ($F_{3,50}$ = 4.03, $p = 0.012$) and Ta values ($\chi^2 = 14.89$, $p = 0.001$) differed among shelter types (Online

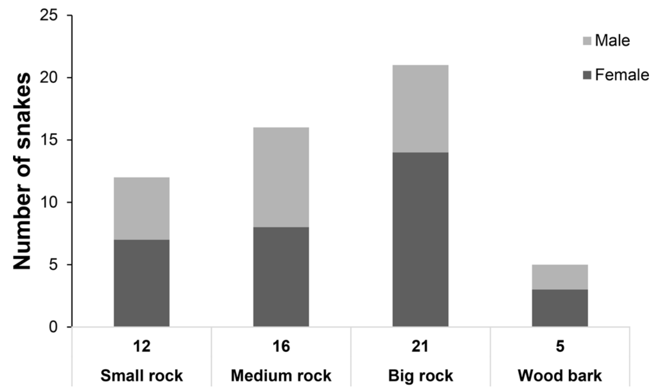

Fig. 4 Frequencies of male and female *C. biserialis* occupying four different shelters. Numbers under the bars indicate the total number of observed individuals

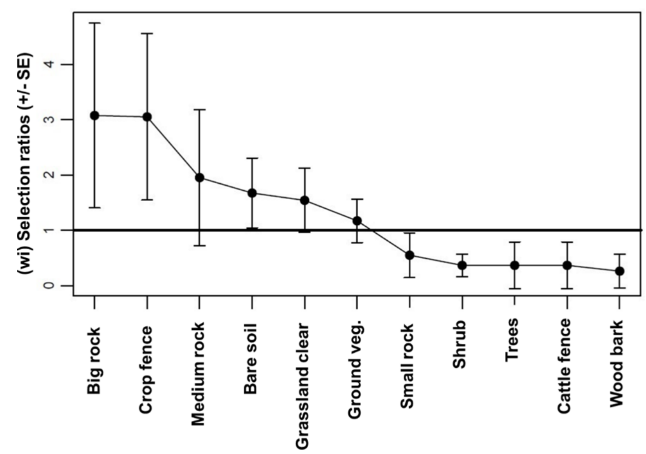

Fig. 5 Resource selection ratios (± SE) from a Manly selectivity analysis on biotic and abiotic components of rural microhabitat used by *C. biserialis* eathsnakes

resource: Figs. S3 and S4). The small and medium-sized rocks have higher Ts ($p = 0.02$, $p = 0.04$, respectively) and higher Ta ($p = 0.02$, $p = 0.001$, respectively) than the large rocks. The bark fragments and large rocks did not differ in terms of Ts ($p = 0.26$) and Ta ($p = 0.14$).

The frequencies for the use of shelters differed significantly ($\chi^2 = 10.148$, df = 3, $p = 0.01735$). Most individuals were found sheltering under rocks (90.7%, Fig. 4) with relatively few found under bark fragments (9.3%, Fig. 4). The observed sex ratio in the studied population was 1:1.5 (male: female) and the sex ratios according to each shelter type was close to 1.1 under bark fragments, small and medium rocks, but 1:2 under large rocks. There were no associated significant differences between the use of different shelters and the sex of the individuals (FET, all $p \geq 0.797$, Fig. 4).

In the rural microhabitat of this small snake, most individuals used high proportions of medium and large rocks for sheltering (Figs. 4 and 5). These rocks were located around crop fences and on cleared grassland where the soil can be either covered with low vegetation or bare (Fig. 6). While small rocks and bark fragments were used as shelter in lesser proportion, these shelters were often located near cattle fences with lower proportions of trees and shrubs (Fig. 6). The following five structural and biotic resources of the microhabitat are more widely available in the rural environment but are used to a significantly lesser extent by snakes (Fig. 6): small rocks ($p=0.037$), bark fragments ($p=0.018$), cattle fences, trees, and shrubs ($p=0.025$, for all).

There is a significant degree of selection for some of the structural and biotic resources of the rural microhabitat (Khi2L = 130.2985, df = 10, $p<0.0001$). The two structural resources of large rocks and crop fences were highly selected, followed by medium rocks and bare soil (Fig. 5). The biotic elements that were slightly preferred were cleared grassland and ground vegetation (Fig. 5). In all six of these selected resources, there were no differences between biotic or structural components, indicating that all were selected equally (> 1, Fig. 5). The non-preferred structural and biotic resources (< 1, Fig. 5) were those that of highest availability in the environment (Fig. 5).

Discussion

Our results show evidence of low thermal heterogeneity and similar humidity conditions under the shelters occupied by the burrowing earthsnake *C. biserialis* in a cool, modified rural microhabitat. Variation in Tb is explained by microenvironmental temperatures under shelters (mainly Tr) but not by shelter size and type or earthsnake sex and development stage. Findings in microhabitat occupancy indicate a combined influence of the physical features of shelters, such as size and spatial distribution, in determining microhabitat selection by these small and cryptic earthsnakes. In the rural fields, the earthsnakes chose mainly larger shelters (big and medium rocks) with low thermal heterogeneous characteristics, that were closer to crop fences and cleared grasslands and where the soil could be either covered with low vegetation or bare. All the results and patterns observed here are for the rainy and summer seasons, but it is necessary to implement inter-seasonal and habitat comparisons for a better understanding of the use of resources in transformed and conserved environments.

In reptiles, the response to habitat change is complex and diverse, both within and among all scales of ecological organization (French et al. 2018; Gainsbury et al. 2022). This has caused the effect of habitat fragmentation on reptiles to be a topic that generates constant debate among scientists (French et al. 2018). Some studies find inert or even positive effects of habitat transformation (Araujo 2003; Luck 2010; Roe et al. 2011), while others show the opposite (Todd et al. 2010; Hunt et al. 2013; Lazić et al. 2015). This variability in results is partly due to the heterogeneity of transformed landscapes and the diversity of biological responses in the species (French et al. 2018).

Thermoregulation indices were not calculated in this work due to the lack of records of selected and operative temperatures. However, we can make an approximation of thermoregulatory or thermoconformist tendencies using the criterion of Huey and Slatkin (1976). The slope values of the linear regression of Tb on environmental air temperatures were close to zero, suggesting that *C. biserialis* is a thermoregulatory species. Regarding the acquisition of heat by *C. biserialis*, we observed that the correlation between Tb vs. Tr was higher than that of Tb vs. Ta. As a result, a tendency for *C. biserialis* to be thigmothermic is assumed.

Frequently, fossorial and thigmothermic reptiles have lower body temperatures and thermal preferences than other basking and heliothermal reptiles (Brattstrom 1965; Matias and Verrastro 2018). In amphisbaenias (full subterranean reptiles), body temperatures are related to variations in the surrounding habitat substrate (López et al. 2002). We found a similar pattern in *C. biserialis*, with a wide range of body temperatures throughout the day that vary with the temperatures occurring under the shelter. This wide range of body temperatures is a eurythermic characteristic that probably allows *C. biserialis* to inhabit cold environments, as has been observed in other mountain species (Jaramillo-Alba et al. 2020). In addition, Paternina-Cruz and Calderón-Espinosa (2022) reported that snakes with similar environmental conditions such as *Atractus crassicaudatus* (Duméril, Bibron & Duméril, 1854) has different thermoregulatory strategies to deal with daily and seasonal temperature variations (Paternina-Cruz and Calderón-Espinosa 2022). Here,

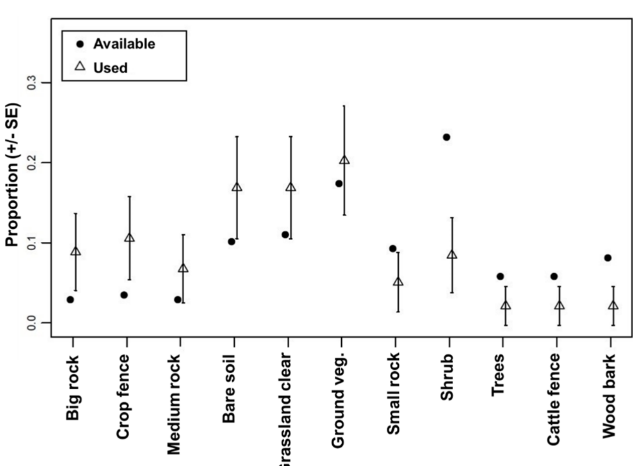

Fig. 6 Mean proportion (± SE) of biotic and abiotic components of rural microhabitat available and used by *C. biserialis* earthsnakes

we do not evaluate the behavioral and physiological adjustments of *C. biserialis* but a continued study could explore this issue.

Some studies consider that montane environments exhibit a high degree of thermal heterogeneity, thus presenting considerable additional thermoregulatory challenges for ectotherms (Tewksbury et al. 2008; Angilletta 2009; Jaramillo-Alba et al. 2020). Habitats at high elevations or latitudes generally have low thermal qualities for reptiles (Huang et al. 2014; Bouazza et al. 2016). In addition, if these thermally unfavorable montane habitats are found at sites modified by anthropogenic activities (e.g., agriculture, industry, urban development), the environmental heterogeneity is expected to be much higher, and the environmental challenges for reptiles of transformed areas are thus increased (Block et al. 2013; Stellatelli et al. 2013). Contrary to this expectation, at a small spatial scale, our results indicate that the rural microhabitat of *C. biserialis* in a cool montane site of 2500 m a.s.l was microclimatically little heterogeneous and the Tb obtained by thigmothermia was not affected by the thermal or structural variation among microshelters. Castañeda-Gonzalez et al. (2011) reported that the Tb of *C. biserialis* was higher than the mean temperature under the rocks, but the methodology for measuring temperatures was ambiguous and with limited thermal exploration in the microenvironment.

Rural or farming landscapes are the type of modified environments that most closely resemble the conserved habitats of many species. In small ectotherms that inhabit rural environments, structural and thermal characteristics of the microhabitats are crucial to satisfy several ecological, physiological, and behavioral requirements (Huey et al. 2012; Stellatelli et al. 2018, 2020). Our results show that the presence of rock shelters represents an important microhabitat resource for *C. biserialis* inhabiting montane and human-modified environments. Under laboratory conditions, rock shelter selection in *C. biserialis* is influenced by favorable thermal conditions and foraging opportunities (Raya-García et al. 2019). The availability of food resources is another possible factor affecting the abundance of earthsnakes in these rural microhabitats; however, additional field studies are required to adequately explore hypotheses regarding diet and foraging.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s11756-024-01680-y.

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Author contributions ERG and IAT performed field data collections. ERG analyzed the data and prepared illustrations. ERG and IAT prepared the manuscript. All authors approved the final version of the manuscript.

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Data availability All data are provided within the manuscript and supplementary material.

Declarations

Ethical approval This study was carried out in strict accordance with the guidelines for use of live amphibians and reptiles in field research compiled by the American Society of Ichthyologists and Herpetologists (ASIH). In the research protocol, adult snakes were visually detected and captured without any harm. All procedures with animals were carried out in accordance with the standards of bioethics and biosafety of the Universidad Michoacana de San Nicolás de Hidalgo.

Competing interests ERG and IAT declare that they have no conflicts of interest.

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