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Tracing Invisible Tracks: Spatial Ecology and Activity Patterns of the Neotropical Rattlesnake *Crotalus simus* (Serpentes: Viperidae)

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Abstract

Background: Spatial ecology provides valuable insights into animal natural history, behaviour, and conservation. Radiotelemetry is one of the few techniques available to monitor snakes over extended periods. However, most research has focused on a few species from temperate regions, leaving a significant gap in our understanding of tropical snake spatial ecology and translocation effectiveness. We studied the tropical rattlesnake *Crotalus simus*, taking advantage of the extensive spatial ecology research available for the genus. Specifically, we determined (1) spatial ecology patterns, (2) environmental influences on activity and shelter use, and (3) translocation effects.

Methods: We used radiotelemetry to track 14 Mesoamerican rattlesnakes (*C. simus*), five residents and nine translocated, for over two years in northwestern Costa Rica. We estimated home ranges using minimum convex polygons (MCP), kernel density estimators (KDE and aKDE), and dynamic Brownian bridge movement models (dBBMM), and assessed movement and activity patterns. We compared spatial-use parameters between resident and translocated individuals.

Results: The dBBMM provided the most suitable home-range estimates, averaging 10.31 ± 4.14 ha, with core areas of 1.82 ± 0.69 ha. Mean daily movement was 14.49 ± 2.15 m. Greater moon visibility and lower humidity were associated with longer displacements, whereas movement probability increased with temperature and humidity. Snakes exhibited predominantly nocturnal sit-and-wait behaviour, remaining inactive during the day and ambushing prey at night. Shelter use was also diel-dependent, with snakes more often sheltered during the day and unsheltered at night. Temperature and habitat features, including canopy cover, understory complexity, and proximity to fallen logs, were associated with

activity and shelter use. Translocated individuals were less likely to move than residents, but no differences were detected in other spatial-use parameters.

Conclusions: Our findings provide new insights into the spatial ecology of *C. simus* in tropical forests. Although translocated snakes were less likely to move, translocation had no detectable effect on home-range size or other spatial-use parameters, and recorded mortalities were similar between groups. In Costa Rica, translocation may therefore represent a viable management alternative to sacrificing snakes in human–snake conflict situations.

Key words

Snakes, Space use, Home range, Movement, Radiotelemetry, Translocation, Tropical Ecosystems, Minimum Convex Polygon, Kernel Density Estimators, dynamic Brownian Bridge Movement Models

Background

Understanding the implications of space use in animals provides valuable insights into aspects of their natural history, ecology, behavior, and conservation [1]. In snakes, the spatial ecology of a few species has been widely studied, particularly in temperate zones [e.g. 2–5]. The development of remote sensing techniques and the use of implantable radio-transmitters starting in the early 1970s enabled the long-term monitoring of snakes, overcoming their secretive habits that make field research challenging [6–7]. These techniques have facilitated our understanding that factors such as food acquisition, diet, and foraging [8–9], sex and reproduction [2, 10], body size and growth [3, 11], ectotherm

thermophysiological requirements [12–13], and the processes of ecdysis and digestion [8], are closely related to how snakes use their space.

Additionally, spatial ecology studies have also helped clarify the effectiveness of translocation programs–or the intentional release of individuals of a species into a site different from their place of origin–in snakes [5, 14–16]. Snake populations are declining worldwide mainly due to habitat loss and fragmentation [17–18]; however, a frequently overlooked driver of mortality is direct human persecution, as snake-human encounters often result in the killing of the animal [19]. Therefore, translocation has become a widely used management strategy worldwide to reduce human-caused mortality [20].

Unfortunately, most research on the spatial ecology of snakes has focused on temperate ecosystems [21]. Despite comprising more than 4,000 species, snakes remain poorly studied in this regard, particularly in tropical regions [21–22]. In temperate species, space use is largely driven by the need to find thermal refuges during winter and exploit seasonally abundant resources during the active season [23–24]. Moreover, translocated snakes in these regions tend to travel greater distances, exhibit abnormal movement patterns, have larger home ranges, and experience lower survival rates than resident individuals [5, 15, 25–26]. These outcomes have made translocation a controversial conservation tool [20, 27], although successful translocations have also been reported in temperate snakes [14, 28–29]. This research bias limits our understanding of the spatial ecology of tropical snakes and the implications of their space-use patterns for translocation as a conservation tool in tropical ecosystems. In contrast to temperate species, space use in tropical snakes may be less constrained by seasonal thermal limitations and more strongly influenced by food availability [30–32].

In order to develop studies about the spatial ecology of tropical snakes, rattlesnakes (genus *Crotalus*) have certain advantages. Primarily, spatial ecology data available for this genus are among the most extensive in snakes [e.g. 2, 4, 9]. Moeover, although this genus originated in the Nearctic region, where most of its species inhabit temperate and desert ecosystems [33–34], one lineage is distributed throughout neotropical ecosystems in Central and South America [33, 35], representing a wide diversity of habitats occupied. Therefore, using *Crotalus* as a study system allows for direct ecological comparisons among species with evolutionary affinity.

Within this tropical lineage, the Mesoamerican rattlesnake *Crotalus simus* (Fig. 1) is a key species for comparing spatial ecology with its temperate-zone relatives. Distributed from southern Mexico to northwestern Costa Rica [33, 36], this species is generally found in semi-arid, low-elevation regions with dry to very dry tropical forests and arid scrub. However, while most populations are found below 1000 m.a.s.l., higher-elevation records exist in Costa Rica [36]. Its habitat is highly variable, including coastal vegetation, open and disturbed areas, grasslands, primary and secondary forests, rocky crevices, riverbanks, and occasionally human settlements [33, 37]. In northwestern Costa Rica, *C. simus* is relatively abundant in pastureland and rural human settlements [36]. As with other snakes found in Costa Rican environments, firefighters frequently remove them from residential areas and relocate them to less populated regions or reserves. However, the effects of snake translocation in the country, despite being a common practice, have not been formally assessed, highlighting a crucial research gap in conservation.

In this study, we present the data on the spatial ecology of 14 Mesoamerican Rattlesnakes (*Crotalus simus*)—five residents and nine translocated—obtained through radiotelemetric monitoring in Nosara, Guanacaste Province, Costa Rica. Our objectives were

to (1) describe home range size and movement ecology patterns in *C. simus*, (2) determine whether environmental features influence activity patterns, and (3) determine the impact of translocation on the spatial ecology parameters of this snake species.

Methods

Study site

Field research was conducted from January 2nd, 2023 to November 29th, 2024 in the Protected Forest Area of the Nosara Civic Association (NCA) in Nosara, Nicoya Peninsula, Guanacaste, Costa Rica (09°57'48.5" N. 85°39'03.8" W) (Fig. 1). This site is located within a humid subtropical biotic unit characterized by a five-month dry season [38] and is classified under the dry forest herpetological province [37]. Nosara is located inside the Biological Corridor Río Nosara, which connects the Monte Alto Natural Reserve, the Diriá National Park, and the Ostional National Wildlife Refuge. This Corridor consists mainly of secondary forests followed by pastures [39], and a few population centers, like Nosara.

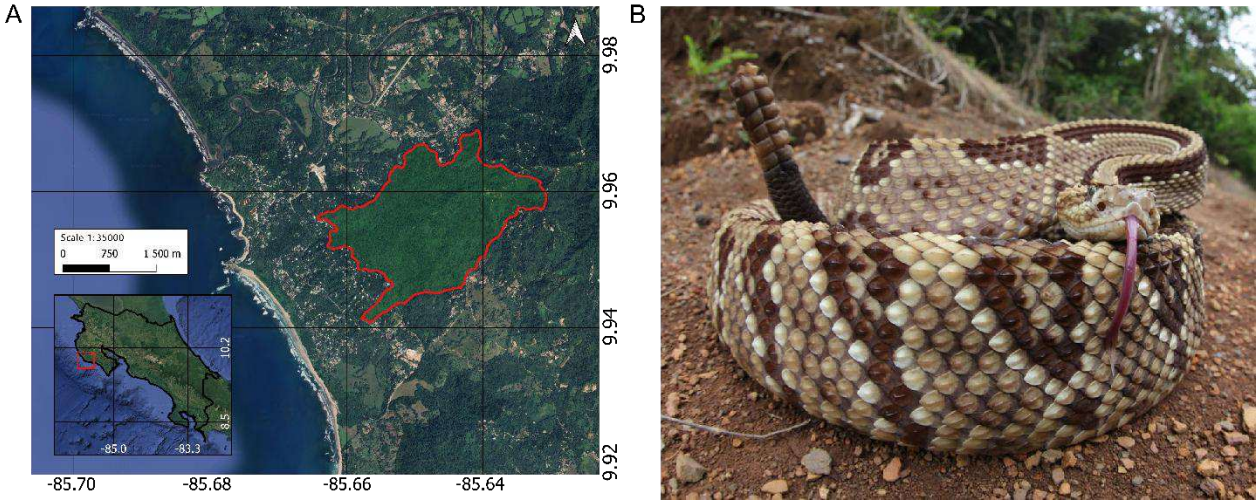


Fig. 1. (A) Nosara, Costa Rica. The outlined area corresponds to the Protected Forest Area of the Nosara Civic Association (NCA). The map shows the developed areas and

grasslands surrounding the forest patches where the rattlesnakes were monitored. (B) The Mesoamerican rattlesnake *Crotalus simus*. Photo by Andrés Vega.

Field and telemetry methods

Animal care protocols and research permits were approved under the resolution ACT-OR-DR-021-2024 of the Sistema Nacional de Áreas de Conservación (SINAC). We established that only adult individuals would be used in the study. Resident *C. simus* were located and captured by active searching in the Protected Forest Area of the NCA in Nosara. This area does not receive translocated rescued snakes by the authorities, ensuring that the individuals encountered here were indeed residents. Translocated individuals, on the other hand, were rescued and captured by the Volunteer Firefighters of Nosara when an encounter between snakes and humans occurred.

Animals used in the study were brought to the laboratory and held in captivity for a maximum of two days. During this time, they were weighted (g), measured—as snout-vent length (SVL)—(cm), sexed, anesthetized with Isoflurane administered via inhalation, and implanted with a very high frequency (VHF) radiotransmitter (Wildlife Materials Inc., 6 g, model SOPI-2190) following the methods of Hardy & Greene [40]. Radiotransmitters weight never exceeded the 5% of the snake weight.

We observed the animals for a maximum period of 96 hours after surgery prior to release. Following this period, Resident snakes were released at their original capture locations, whereas translocated individuals were released at random locations within the same forest patch. The protocols for animal translocation established under Costa Rica's Wildlife Conservation Law (Law 7317) do not specify particular habitat features or translocation distance ranges for release sites. Instead, they state that releases must occur in

areas that provide appropriate conditions for the survival of the organisms involved and that are located within the species' natural distribution range. For this reason, firefighters typically translocate snakes to forest patches away from residential areas but close enough to avoid affecting them. Therefore, our translocations aimed to closely represent the actual procedures carried out nationwide. All translocated individuals were in the Protected Forest Area of the NCA at distances ranging from 1 to 5 km from their original rescue site.

To minimize disturbance, we attempted to relocate snakes each 2-3 days, alternating between day and night—determine by sunrise and sunset. At each snake relocation we use a GPS to georeferenced the site (Garmin, model GPSMAP 64s), maintaining the error constant at 4 m, and we also noted the GPS error. If the snakes were not visible at a safe distance, we located them by triangulation to avoid disturbing them. In each relocation, we recorded their activity and shelter use. Following Wasko & Sasa [22], activity was categorized as: inactive, when the snake was lying coiled and with its head resting; moving, when individuals were actively moving; and ambushing, when if snakes were lying coiled and alert with its head raised in approximately 45°. Shelter use was categorized as: unsheltered, when the animal was completely exposed and there was no structure covering it; sheltered, when the animal's entire body was covered, either by vegetation or because it was inside or underneath any structure; and semisheltered; when part of the animal's body was covered either by vegetation or by any structure.

When a rattlesnake was relocated, we measured the environmental temperature (°C) and relative humidity (%) with a thermohygrometer next to the animal. At the subsequent relocation, when the snake had moved to a different area, we also measured the distance to the nearest large tree (m)—with a circumference at chest height (CCH) > 20 cm—, distance to the nearest small tree (m)—CCH < 20 cm—, distance to the nearest fallen log (m)—

circumference > 20cm—, distance to the nearest water body (m; distances >50 m were treated as 50), canopy coverage (%), and number of structures in the understory. Canopy coverage was recorded by tacking a picture with a north facing cellphone equipped with a 360° lens and then analyzing it with ImageJ [41]. For counting the number of structures in the understory, we place a 1.5 m rod at a 30 cm heigh from the ground, with the middle of the rod upon the point where the snake was found. The rod was placed facing north and then east. We counted all the structures (usually leaves, branches, and logs) that touched the rod in the cross. Finally, using a lunar calendar, we calculated the percentage of visible moon by averaging the percentages for each night between two consecutive relocations.

Analyses

All analyses were performed in R Studio [42]. To estimate home range, we calculated 100% and 95% isopleths of the Minimum Convex Polygon (MCP), and the 95% and 50% Kernel Density Estimators (KDE) with a reference bandwidth (h), using the package adehabitatHR [43]. We also calculated the 95% and 50% autocorrelated KDE (aKDE) with the package ctmm [44]. Finally, we estimated the 95% and 50% dynamic Brownian Bridge Movement Models (dBBMM) with the package move [45].

MCP estimates home range by constructing the smallest polygon in which no internal angle exceeds 180°; while KDE calculate bidimensional probability densities from each relocation point [46]. However, MCP and KDE do not take into account the time between relocations—assuming that the data are independent of each other—, are highly dependent on sample size, and incur in Type I and Type II errors—by not incorporating used areas or by including unused zones [47]. aKDE account for temporal autocorrelation in the data [48]; nonetheless, they are not good estimators for animals that keep moving to new locations, not

following a range resident pattern [49]. dBBMM estimate the probability of an animal being in a given area based on the distance between relocations, the time elapsed between consecutive points, and the speed of movement, allowing to recognize that different behaviors generate distinct movement patterns [1, 50]. Although dBBMMs are not well suited for estimating home range, as they do not extrapolate data into the future, they are effective in determining where an animal was located during a defined tracking period, particularly in species that do not exhibit a resident range [48, 51].

To determine what type of movement patterns *C. simus* followed, and therefore, which estimator calculates its home range sizes the most accurately, we plotted the MCP 100% and the net squared displacement (NSD) against sample effort. The NSD measures the straight-line distances between the starting location and subsequent locations to infer the movement path of an individual [52]. Additionally, we performed linear regressions to determine the influence of weight, SVL, or body condition on home range sizes (Table S1). Moreover, to ascertain differences in home range size between resident and translocated individuals, and between sexes, we performed non-parametric Mann-Whitney U tests (Table S2).

For movement, we first calculated the distances (m) and daily movements (m/d) between two consecutive points, using the package move2 [45]. Here, we reported the mean daily movement and its standard error (m/d) from all the individuals we sampled.

Second, we made (1) a subset where movement was treated as a binomial variable called moving—0 when snakes stayed in the same spot and 1 when snakes move independently of the displacement magnitude—and (2) a subset in which movements of 0 were excluded, to account only for periods when animals actually moved from one location to another. We performed two generalized linear mixed model (GLMM) using the package

glmmTMB [53–54]. In the first model, the response variable was moving (0 or 1) with a binomial distribution. In the second one, the response variable was daily movement with a Gamma distribution, excluding when movement was 0. In both models, the visible moon percentage, temperature, humidity, and translocation (0 = residents. 1 = translocated) were the predictor variables; while individual ID was included as a random effect in the models to account for the non-independence of multiple observations from the same individual. We ran a set of candidate models removing predictor variables from the full models and ranked them using the corrected Akaike Information Criterion (AICc) to select the models that best fit the data (Table S3-S4). Finally, we checked overdispersion and zero-inflation for the selected models using the DHARMa package [55].

To test for differences in activity and shelter use by day or night, we fitted two Bayesian multinomial logistic models (categorical family, logit link) using the brms package [56]. In the first model, the response variable was activity (inactive, moving, ambushing); while for the second one the response variable was shelter use (unsheltered, sheltered, semisheltered). The fixed effect for both models was the diel period (day vs night), while individual ID was included as a random intercept to account for the non-independence of the data. Inactive, unsheltered and day were the reference levels. We used weakly informative priors: Normal(0, 1) for the regression coefficients, Exponential(1) for the standard deviations of the random intercepts, and the *brms* default Student-t(3, 0, 2.5) for the intercepts. Each model was run with four chains of 4000 iterations (2000 warm-up) and adapt_delta = 0.99. Convergence was assessed with R-hat (< 1.01), effective sample sizes and the absence of divergent transitions. Values of odds ratios, with 95% credible intervals (CrI), the probability of direction (pd), the predicted probability of each category, and the night–day difference in percentage points can be seen in Table S5.

To determine whether (1) the probability of each activity (inactive, moving, ambushing) and (2) the probability of each degree of shelter use (unsheltered, semisheltered, sheltered) depended on microhabitat and environmental conditions, we fitted two Bayesian multinomial logistic models with the same structure indicated above. Inactive and unsheltered were the reference levels in their respective models. Both models included eight predictors: temperature, relative humidity, distance to the nearest large tree, to the nearest small tree, to the nearest fallen log and to the nearest water source, canopy cover, and number of understory structures. All predictors were standardized by centered them at their mean and divided by their standard deviation. Individual ID was included as a random intercept to account for repeated observations of the same animals. We use the same priors, sampler settings and convergence criteria described above. To evaluate the sensitivity of the results to the prior, both models were refitted with Normal(0, 2) and Normal(0, 5) priors for the coefficients (Tables S6-S7). Finally, convergence was assessed with R-hat (< 1.01), effective sample sizes and the absence of divergent transitions (Table S8). Only predictors with a clear effect were plotted.

Results

During the study period, we observed seven site-resident individuals and 11 that were rescued elsewhere and translocated by the Volunteer Firefighters of Nosara. Of these, we tracked five residents and nine translocated individuals, as they met the criteria for being adults (Table 1). Tracking days and number of relocations per individual snake is shown in Table 1. We were able to visibly detect snakes 439 of 539 times (81.45%), while the remaining relocations were obtained by triangulation.

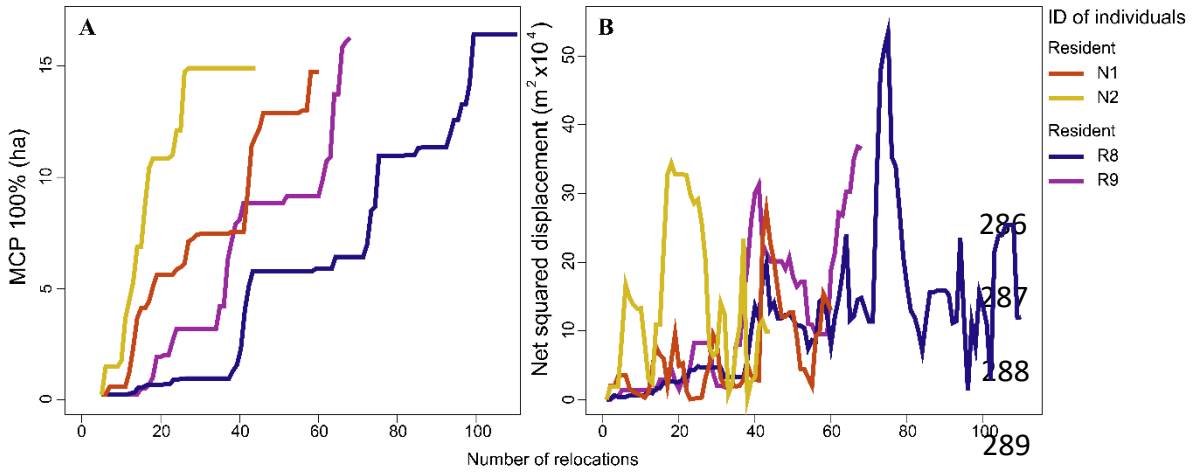
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275 **Home Range and Movement Ecology**

276 Home range estimates varied across estimators (Table 1). While MCP and dBBMM yielded
277 comparable results, KDE and aKDE produced significantly higher estimates. Home range
278 areas of *Crotalus simus* increased with sampling effort, without reaching an asymptote (Fig.
279 2). Likewise, NSD behavior in both time and direction, was irregular (Fig. 2), making their
280 movements more consistent with nomadic patterns [57], and suggesting that the species
281 might not exhibit range residency. Values obtained from dBBMM estimated home ranges of
282 10.31 ± 4.14 ha with core areas of 1.82 ± 0.69 ha (Fig. 3). We did not find any influence of
283 SVL and weight (Table S1), or of sex (Table S2) in the home range size for any estimator.

284

285 [Table 1 in this position]



290 **Fig. 2.** (A) Home range estimates based on the 100% Minimum Convex Polygon
291 (MCP) and (B) net squared displacement (NSD) for four tracked *C. simus* individuals. Only
292 four individuals are shown to facilitate visualization due to overlapping lines.

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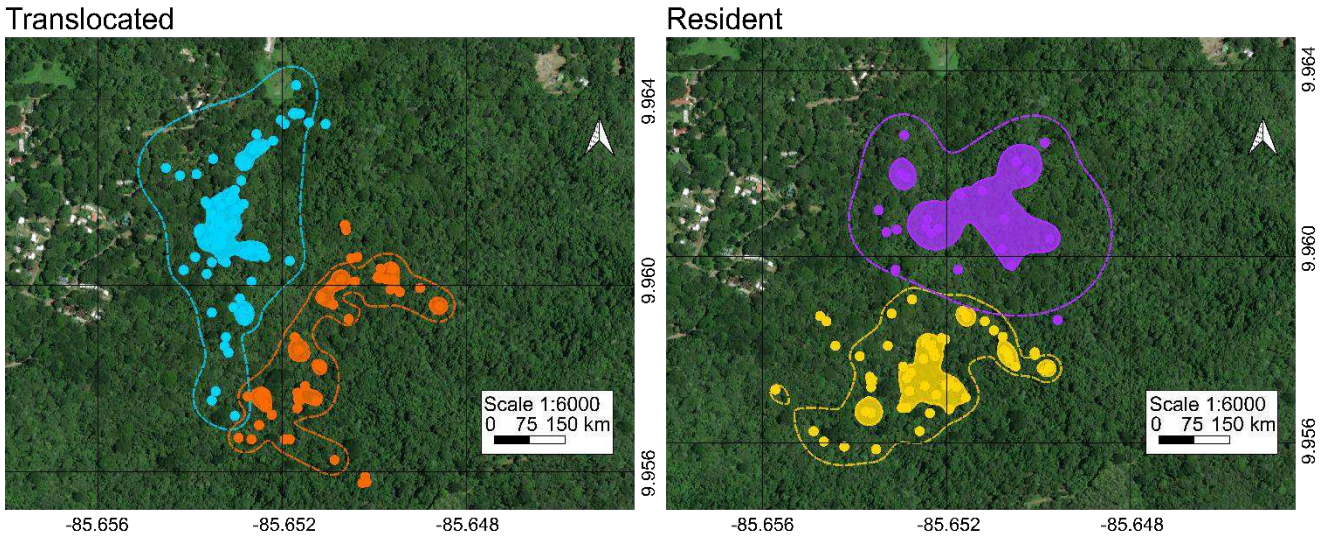


Fig 3. Home range of four *C. simus* tracked in Nosara, Costa Rica; estimated by 95% dBBMM (dotted line) and 50% dBBMM (shaded area). Home range sizes were estimated at 10.31 ± 4.14 ha, while core areas corresponded to 1.82 ± 0.69 ha. Points correspond to the relocations of each individual. Light blue = R8, orange = R9, purple = N4, yellow = N1. Only four individuals are shown to facilitate visualization due to overlapping polygons.

Mean daily movement was 14.49 ± 2.15 m/d. The movement magnitude increased as the percentage of the visible moon increased (Table 2, Fig. 4A), whilst it decreased as relative humidity increased (Table 2, Fig. 4B). The Kolmogorov–Smirnov test for this model indicated that scaled residuals followed the expected uniform distribution ($p = 0.665$), with no significant overdispersion (ratio = 1.37, $p = 0.13$). Likewise, the probability that Mesoamerican rattlesnakes would move increased as both the relative humidity and the environmental temperature increased (Table 2, Fig. 4C-D). The Kolmogorov–Smirnov test for this model also indicated that scaled residuals followed the expected uniform distribution ($p = 0.344$), with no significant overdispersion (ratio = 1.01, $p = 0.90$) or zero-inflation (ratio = 1.06, $p = 0.95$).

311 **Table 2.** Coefficient estimates of the two generalized mixed models (glmm) fitted to
312 determine movement patterns in *C. simus* from Nosara, Costa Rica. Translocation is a
313 binomial variable (Translocated vs Resident), where Resident was the reference value. Model
314 selection can be seen in Tables S3 and S4.

Movement Magnitude ~ Moon % + Humidity (1 | individual),

family = Gamma(link = "log")

	Estimate	Standard error	z value	p
Intercept	-0.24	0.20	-1.19	0.23
Moon %	0.12	0.05	2.52	< 0.05
Humidity	-0.18	0.07	-2.70	< 0.01

Probability of Movement ~ Temperature + Humidity + Translocation + (1 | individual),

family = binomial

	Estimate	Standard error	t value	p
Intercept	1.50	0.32	4.69	< 0.001
Temperature	0.04	0.14	2.90	< 0.01
Humidity	0.55	0.18	3.17	< 0.01
Translocation	-0.93	0.41	-2.25	< 0.05

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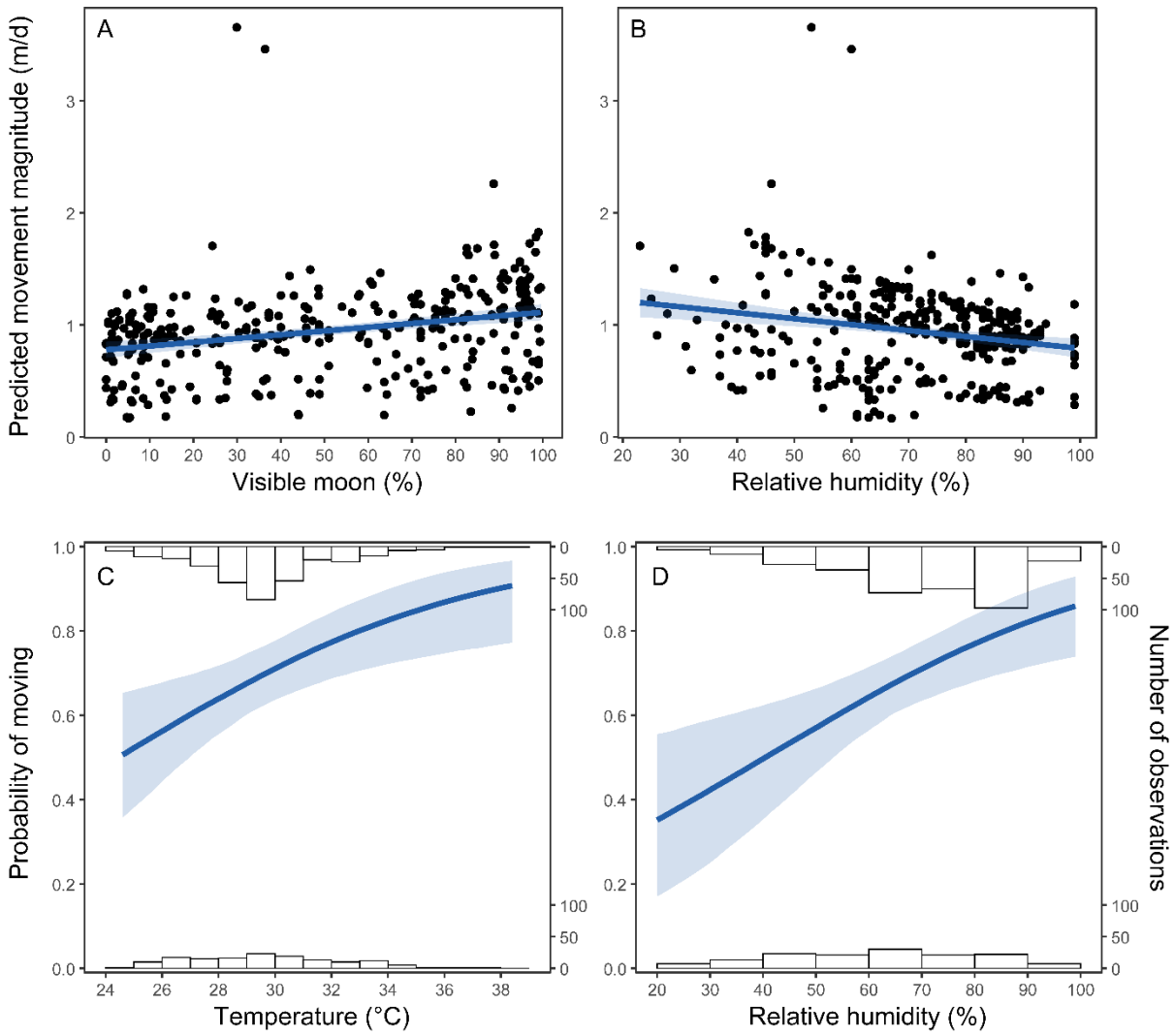


Fig 4. Movement ecology patterns in tracked *C. simus* from Nosara, Costa Rica. Movement magnitude according to the (A) percentage of visible moon, and (B) relative humidity. A and B plots show the values predicted by the model with a 95% confidence interval (CI) (shaded area). Probability of moving according to (C) temperature, and (D) relative humidity. The histogram at the top shows the number of observations in which snakes moved, and the histogram at the bottom shows the number of observations in which snakes stayed in the same spot. The lines in C and D represent the predictions of the model with a 95% CI (shaded area).

Activity Patterns

The proportion of observations of rattlesnakes performing an activity were affected by day or night (Fig. 5, Table S5). Individuals spent the day mostly inactive (84.2% predicted probability by day vs. 36.1% at night), while at night they preferred to ambush (7.4% by day vs. 57.0% at night; OR = 18.04, 95% CrI [10.38, 32.73], pd > 0.999). The probability of moving did not clearly differ between day and night. Shelter use was also affected depending on diel period (Fig. 5, Table S5). Although rattlesnakes preferred to be unsheltered at any time, it was more probable to be unsheltered during the night than during the day (48.1% vs. 67.7%), while the probability of being sheltered or semisheltered was greater during the day (sheltered: 23.7% by day vs. 16.2% at night; OR = 0.49, 95% CrI [0.29, 0.81], pd = 0.998; semisheltered: 27.3% by day vs. 15.4% at night; OR = 0.40, 95% CrI [0.23, 0.67], pd > 0.999).

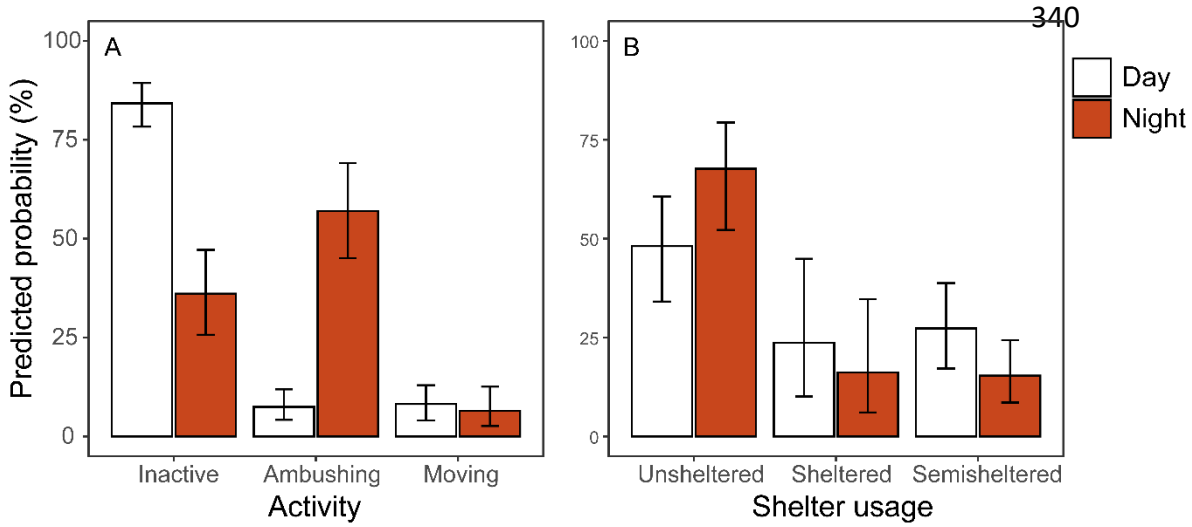


Fig 5. Day and night differences in (A) activity and (B) shelter use of *Crotalus simus* from Nosara, Costa Rica, shown as predicted probabilities (posterior median and 95% credible interval, CrI) from Bayesian multinomial models with individual ID as a random intercept.

Activity levels and shelter use were influenced by environmental and microhabitat features (Table 3-4, Fig. 6). Higher temperatures correlated with higher inactivity and a reduced the likelihood of ambushing (Table 3, Fig. 6A). Greater distances to the nearest fallen log also correlated with higher inactivity and a reduced likelihood of ambush behavior (Table 3, Fig. 6B). Likewise, as the number of structures in the understory increased, snakes were more likely to remain inactive than moving or ambushing (Table 3, Fig. 6C). Distance to the nearest large and small tree, and to the nearest water source, canopy coverage and humidity had no clear effect on activity (Table 3).

For shelter use, higher temperatures increased the probability of being sheltered or semi-sheltered and decreased the probability of finding snakes unsheltered (Table 4, Fig. 6D). Higher canopy coverage increased the probability of finding snakes unsheltered (Table 4, Fig. 6E). Moreover, as the number of structures in the understory increased, the probability of being unsheltered decreased, while sheltered and semi-sheltered probabilities rose (Table 4, Fig. 6F). Distance to the nearest large and small tree, to the nearest fallen log, to the nearest water source, and humidity had no clear effect on shelter use (Table 4).

Table 3. Bayesian multinomial model of activity (inactive, moving, ambushing) in Crotalus simus from Nosara, Costa Rica. Inactive was the reference category. Values are odds ratios (OR) per 1 SD of the predictor, given as posterior median [95% credible interval, CrI], together with the probability of direction (pd). Values for moving vs ambushing are the OR of moving vs inactive divided by the OR of ambushing vs inactive. A value of 1 means the predictor affects both categories equally, and values above 1 indicate a more positive effect (or less negative) on moving than on ambushing. Bold = 95% CrI excludes 1 (clear effect).

369 The random-effect SD for individual is estimated separately for each non-reference category
370 and is given on the logit scale (not an OR).

Activity ~ DLT + DST + DFL + DWS + CC + SU + T + H + (1 | ID) *						
	Moving vs Inactive		Ambushing vs Inactive		Moving vs Ambushing	
Predictor	OR [95% CrI]	pd	OR [95% CrI]	pd	OR [95% CrI]	pd
DLT	0.74 [0.45, 1.16]	0.905	0.85 [0.61, 1.17]	0.841	0.88 [0.49, 1.46]	0.700
DST	1.21 [0.79, 1.76]	0.819	1.00 [0.74, 1.34]	0.505	1.21 [0.77, 1.87]	0.803
DFL	0.78 [0.48, 1.12]	0.898	**0.68 [0.46, 0.93]**	**0.994**	1.15 [0.67, 1.91]	0.698
DWS	1.27 [0.82, 2.40]	0.847	1.00 [0.76, 1.33]	0.500	1.26 [0.81, 2.42]	0.831
CC	1.26 [0.75, 2.25]	0.793	1.19 [0.83, 1.74]	0.828	1.05 [0.57, 2.00]	0.569
SU	**0.51 [0.29, 0.81]**	**>0.999**	**0.65 [0.47, 0.89]**	**0.997**	0.78 [0.43, 1.32]	0.809
T	0.67 [0.39, 1.20]	0.914	**0.29 [0.19, 0.43]**	**>0.999**	**2.35 [1.21, 4.53]**	**0.995**
H	1.15 [0.63, 2.11]	0.680	0.82 [0.51, 1.36]	0.786	1.40 [0.68, 2.89]	0.825
Random effects (logit scale)						
SD intercept	0.35 [0.01, 1.24]		0.82 [0.31, 1.61			

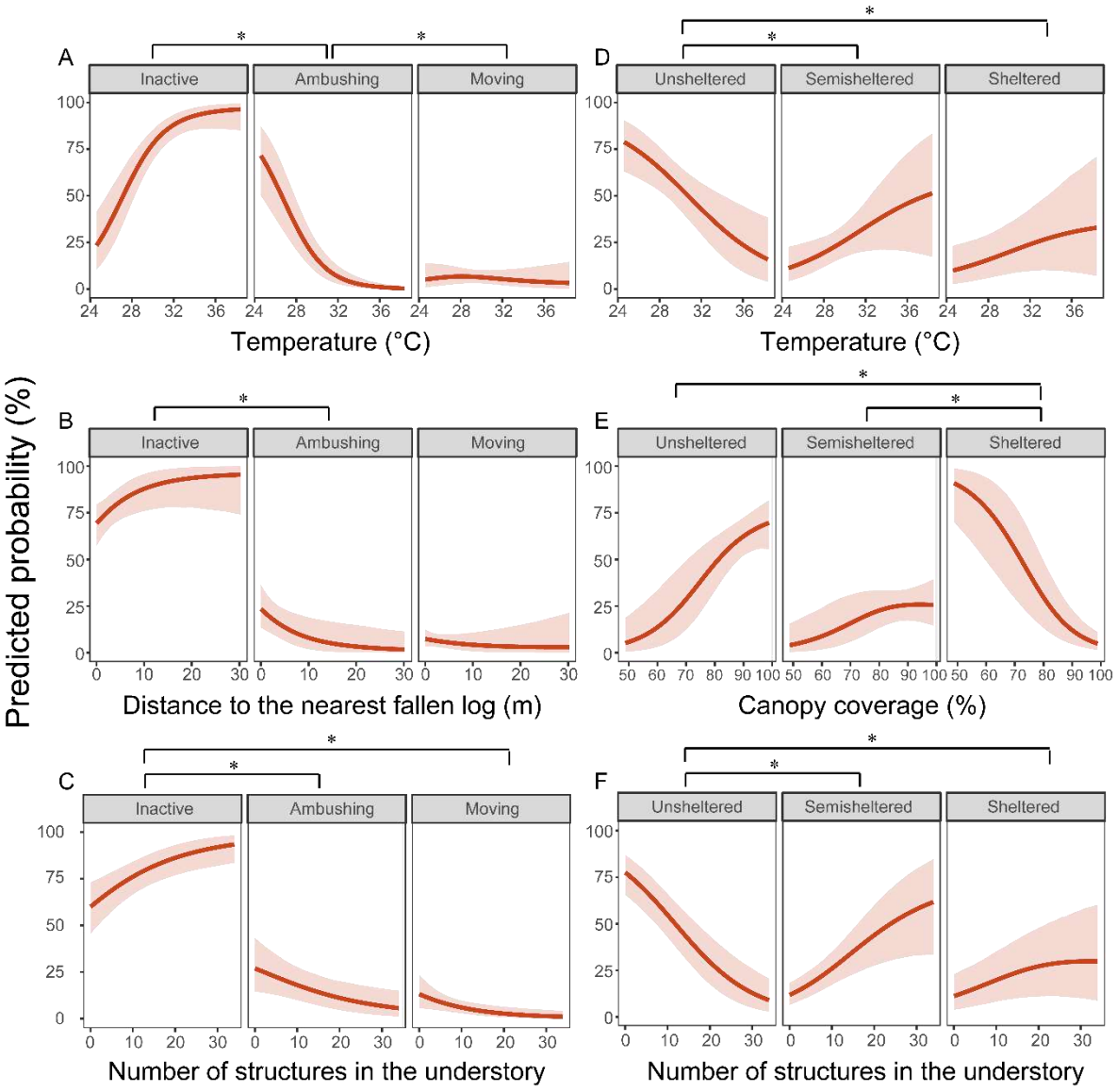
371 * DLT = distance to the nearest large tree (m), DST = distance to the nearest small tree (m),
372 DFL = distance to the nearest fallen log (m), DWS = distance to the nearest water source
373 (m), CC = canopy cover (%), SU = number of structures in the understory, T = temperature
374 (°C), H = humidity (%).

Table 4. Bayesian multinomial model of shelter use (unsheltered, semisheltered, sheltered) in Crotalus simus from Nosara, Costa Rica. Unsheltered was the reference category. Values are odds ratios (OR) per 1 SD of the predictor, given as posterior median [95% credible interval, CrI], together with the probability of direction (pd). Values for semisheltered vs sheltered are the OR of semisheltered vs unsheltered divided by the OR of sheltered vs unsheltered. A value of 1 means the predictor affects both categories equally, and values above 1 indicate a more positive (or less negative) effect on moving than on ambushing. Bold = 95% CrI excludes 1 (clear effect). The random-effect SD for individual is estimated separately for each non-reference category and is given on the logit scale (not an OR).

Shelter use ~ DLT + DST + DFL + DWS + CC + SU + T + H + (1 | ID) *						
	Semisheltered vs Unsheltered		Sheltered vs Unsheltered		Semisheltered vs Sheltered	
Predictor	OR [95% CrI]	pd	OR [95% CrI]	pd	OR [95% CrI]	pd
DLT	1.17 [0.86, 1.57]	0.840	1.12 [0.82, 1.58]	0.762	1.04 [0.72, 1.49]	0.585
DST	1.30 [0.96, 1.73]	0.958	1.16 [0.83, 1.62]	0.809	1.11 [0.78, 1.60]	0.719
DFL	0.99 [0.70, 1.32]	0.528	0.83 [0.51, 1.25]	0.802	1.19 [0.76, 1.91]	0.775
DWS	1.09 [0.80, 1.56]	0.690	0.79 [0.58, 1.07]	0.937	1.37 [0.95, 2.06]	0.956
CC	0.88 [0.58, 1.33]	0.722	**0.34 [0.22, 0.51]**	**>0.999**	**2.59 [1.69, 4.08]**	**>0.999**
SU	**2.31 [1.71, 3.19]**	**>0.999**	**1.99 [1.41, 2.86]**	**>0.999**	1.16 [0.84, 1.62]	0.814
T	**1.77**	**0.999**	**1.67**	**0.995**	1.07	0.610

	[1.19, 2.68]		**[1.12, 2.54]**		[0.68, 1.67]	
H	1.28 [0.81, 2.05]	0.857	0.99 [0.58, 1.68]	0.517	1.30 [0.70, 2.42]	0.804
Random effects (logit scale)						
SD intercept	0.40 [0.02, 1.03]		1.34 [0.73, 2.36]			

* DLT = distance to the nearest large tree (m), DST = distance to the nearest small tree (m), DFL = distance to the nearest fallen log (m), DWS = distance to the nearest water source (m), CC = canopy cover (%), SU = number of structures in the understory, T = temperature (°C), H = humidity (%).



389 **Fig 6.** Influence of environmental conditions on the probability of *C. simus*
390 performing an activity (A-C) and shelter use (D-F). Activity was categorized as inactive,
391 when the snake was lying coiled and with its head resting; moving, when individuals were
392 actively moving; and ambushing, when if snakes were lying coiled and alert with its head
393 raised in approximately 45°. Shelter use was categorized as unsheltered, when the animal
394 was completely exposed and there was no structure covering it; sheltered, when the animal's
395 entire body was covered, either by vegetation or because it was inside or underneath any
396 structure; and semisheltered; when part of the animal's body was covered either by vegetation

or by any structure. Lines represent the posterior median, while shaded area the 95% credible interval (CrI) of the predicted probability from the Bayesian multinomial models. * join the pairs of categories whose 95% CrI excluded 1 in the corresponding table.

Effects of translocation

Translocation in *C. simus* did not affect home range size under any of the estimation methods (Table S2) or the movement magnitude (Table S3). However, translocation affected the probability of movement, as translocated rattlesnakes remained in the same location in 123 of 328 observations, whereas resident individuals did so in only 27 of 179 observations (Table 2, Fig. 7).

The number of recorded mortalities was similar between resident and translocated *C. simus*: two resident and one translocated individual were found dead during the study. The cause of death could not be established for any of these individuals. One of the resident ones was found with a hole in its body, which may have been caused by a human, although its origin could not be determined. The other resident snake's transmitter signal was lost, and the transmitter was recovered several months later, approximately 750 m from the snake's last known location. No skeletal remains were found near or buried around the transmitter, raising the possibility that the snake had been preyed upon. The translocated snake showed signs of dehydration and had moved very little before it was found dead, but no apparent signs of infection were observed. In addition to these three confirmed mortalities, one resident and two translocated snakes could not be relocated again, however these were not classified as mortalities.

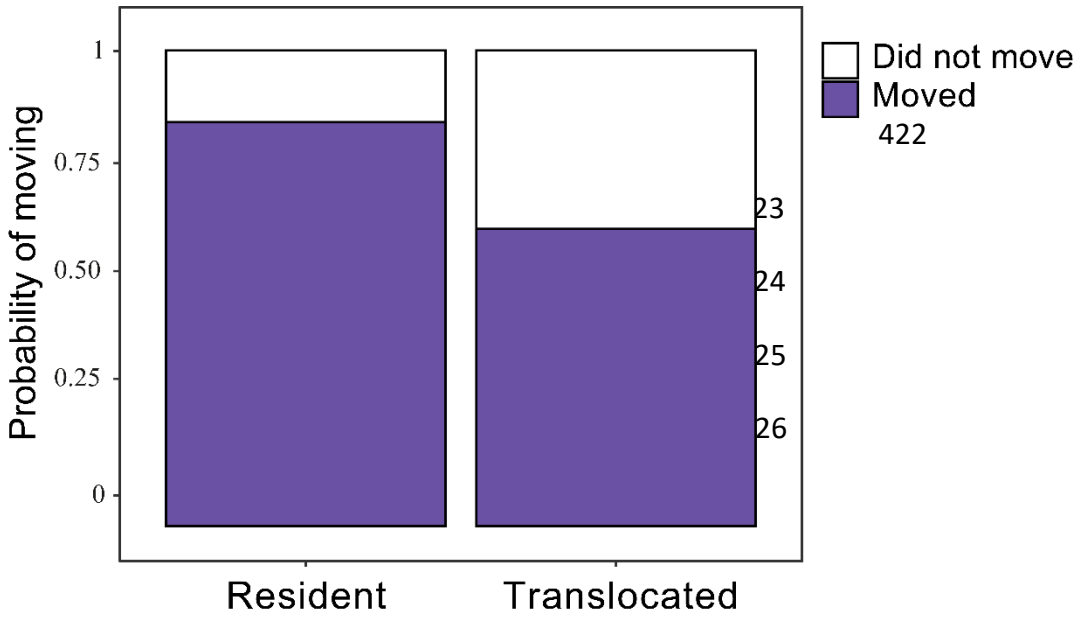


Fig 7. Probability of moving among resident and translocated individuals of *C. simus*.

Discussion

Home range and movement ecology

This study offers novel information on the spatial and movement patterns of the Mesoamerican rattlesnake, one of the few species of the genus with a strictly tropical distribution. We consider that dBBMM produces the most accurate estimates for the population under study because this model has been shown to perform particularly well in terrestrial reptiles and in species without range residence [48, 51], a pattern we observe in *C. simus*. This nomadic pattern can be attributed to either (1) the species' biology, in which individuals continuously incorporate new areas into their home ranges—thus the "nomadic" movement—, or (2) the temporal scope of the study, which may not have fully captured the emergence of range residency. Although we cannot conclude that *C. simus* strictly follows a nomadic movement strategy, we do not consider the temporal scope of our study to be the reason why range residency was not detected. Our tracking regime was comparable to those

444 used in studies of other tropical pit vipers in which range residency has been documented
445 [e.g. 22, 31]. Therefore, we consider nomadic-like movements to be a plausible explanation
446 for the movement patterns observed in C. simus.

447 While nomadism has emerged as a cornerstone of movement ecology in avian and
448 large mammalian taxa [57–60], its exploration within terrestrial reptiles remains largely
449 incipient. Historically, herpetological research has been governed by the paradigm that these
450 ectotherms maintain stable, well-defined home ranges [e.g. 22–23, 61]. However, this
451 prevailing view may be an artifact of the low temporal resolution characteristic of legacy
452 monitoring techniques in terrestrial snakes, which potentially underestimates the inherent
453 spatial plasticity and itinerant capabilities of this group.

454 We did not find a significant influence of sex, SVL, or weight on the home range size
455 of *C. simus*. This contrasts with findings for other *Crotalus* species in temperate regions,
456 where males typically show higher home range estimates [e.g., 4, 62–64]. However, some
457 studies [e.g., 24, 65] have shown that sex-based home range differences are seasonal and
458 linked to the reproductive period. Thus, male rattlesnakes expand their home ranges during
459 the reproductive season to seek females but refrain from doing so during the feeding season.

460 The observed similarity in home range size between the sexes in *C. simus* is, therefore,
461 puzzling. One reason for this phenomenon may be a lack of statistical power due to the small
462 sample sizes, typical of radiotelemetry studies on tropical snakes [22, 31, 66]. Other cases in
463 which there is no effect of sex on spatial ecology parameters have been reported in tropical
464 and subtropical snakes [22, 66]. However, it could also explain a pattern in the ecology of
465 tropical snakes. Because tropical systems exhibit less seasonality, differences in those
466 systems may be more subtle in those regions, although point estimates during reproductive
467 periods could contradict this situation.

In our case, the mating season of *C. simus*, from late November to January [67], precisely coincides with the loss of several male individuals. The steep mountainous terrain and dense vegetation in our study site caused frequent signal loss, which may have led us to miss males making long-distance movements to find females. Thus, it is difficult to determine whether the spatial ecology of males change during the breeding period. Further data are needed to be able to draw a definitive conclusion as to whether sex has an effect on the home range of *C. simus*.

Crotalus species in temperate regions, especially those that make annual migrations to overwintering hibernacula, generally exhibit larger home ranges than those observed here in a tropical species [e.g. 2, 23, 68]. Snakes that need to hibernate in northern regions tend to have dumbbell-shaped home ranges, as they spend long periods near the hibernaculum and also near the foraging/reproductive area, using the spaces in between mainly as migratory corridors [23]. In contrast, populations occurring in subtropical and tropical regions experience more stable environmental conditions throughout the year, eliminating the need for seasonal refugia. This is the case in rattlesnakes distributed at lower latitudes, like *C. lepidus*, *C. atrox*, *C. molossus*, and *C. tigris* [62, 69–70]. Likewise, home range estimates reported for other tropical pit vipers such as the Central American lancehead [22] or the South American bushmaster [31], are congruent with those we found in *C. simus*.

On the other hand, temperature and humidity ae key factors influencing the ecology, behavior, and physiology of snakes [71–72]. Our results show that the likelihood of *C. simus* moving was greater at higher temperatures and humidity, although the magnitude of these movements decreased as the humidity increased. The patterns observed in the probability of movement seem contrasting to the fact that this species selects microhabitats with higher

491 temperatures [73]. However, our data also show that temperature influences the activity the
492 snakes are engaged in, which may ultimately affect their propensity to move.

493 Previous research has demonstrated that snake body temperature is negatively
494 associated with relative humidity [74]. Thus, the tendency to move more often in humid
495 conditions may reflect an attempt to avoid cooling, by seeking areas where body temperature
496 is less likely to decline. This hypothesis might be further supported as *C. simus* select
497 locations with higher temperatures [73]. Observations in *C. durissus* from Brazil—a closely
498 related species of *C. simus*—have indicated that snakes control their body temperature by
499 moving to locations with different values of temperature and humidity [75].

500 Contrary to what we observed in *C. simus*, some studies have reported that higher
501 percentages of visible moonlight reduce the activity and movement of snakes [76–78]. Lower
502 activity during brighter nights may decrease the risk of detection by predators [76].
503 Nonetheless, in some vipers, increased activity during full-moon nights has been associated
504 with prey availability and detectability rather than a foraging–safety trade-off [79]. Although
505 relationships between moonlight and snake behavior have been reported, the overall effect
506 of this variable appears to be weak and inconsistent [80]. Whether the longer movements
507 observed in *C. simus* under greater moonlight are a consequence of increased prey
508 detectability remains unknown, and additional data are needed to better understand the
509 influence of visible moon percentage on the ecology of the Mesoamerican rattlesnake.

510

511 **Activity patterns**

512 The relationship between snake activity, shelter use, and temperature is consistent with the
513 observed diel activity patterns. During the day, when temperatures are higher, snakes are
514 more likely to remain inactive and sheltered. In contrast, at night, when temperatures are

lower, snakes are more likely to engage in ambush behaviour, which requires them to remain unsheltered, as reported in other pitvipers [22, 81].

As observed with other pit vipers [31, 81–82] *C. simus* strategically utilizes structural features to facilitate ambush predation. The proximity to fallen logs significantly increased the likelihood of ambush behavior, which can serve to orient the strike or mask the predator's chemical and visual profile [81]. Interestingly, we observed *Liomys salvini*—an often-abundant rodent in these forests—running around a tracked rattlesnake on two occasions, with both observations involving a snake ambushing prey next to a fallen log.

In addition, rattlesnake activity and shelter use varied with understory structure. Some individuals remained sheltered in dense undergrowth for extended periods of inactivity, suggesting that these habitats provide suitable refuges during vulnerable periods, such as ecdysis. The frequent occurrence of shed skins at these sites further supports this hypothesis. Other snake species are also known to use shelters extensively during ecdysis and prey digestion [8, 83]. Although we could not determine whether rattlesnakes used dense undergrowth for digestion, we did observe brief visits to these sites, suggesting that they may also serve this purpose. Moreover, these observations are consistent with the selection of denser, more tangled understory areas during the day and by translocated *C. simus*, potentially reflecting the use of these habitats as refuges [73].

Effects of translocation

Unlike findings of previous studies with snakes [e.g 5, 15, 25–26], translocated Mesoamerican rattlesnakes in our study did not exhibit larger home ranges, move greater distances, nor experience lower survivorship. Thermophysiological constraints and habitat complexity might play an important role in the effectiveness of translocation. In high latitude

539 rattlesnakes, the probability of not finding overwintering hibernacula increases mortality and
540 translocated individuals have more difficulties in finding suitable shelters in the unfamiliar
541 areas where they were released [5]. Likewise, specializing in a single type of prey reduces
542 the likelihood of locating it after translocation, as the new area's prey distribution is often
543 unknown [26]. In contrast, the complexity of tropical ecosystems could offer advantages for
544 translocated individuals [but see 16]. Even without prior knowledge of the release sites, the
545 lack of need to find seasonal shelter and the greater diversity of prey may be key factors
546 facilitating the ease with which translocated *C. simus* establish in these new areas, and
547 consequently, the lack of negative effects of this type of management on their spatial ecology.
548 The only parameter in which translocated individuals differed from residents was that
549 they remained longer in the same spot. Finding a site that meets both physiological and
550 ecological requirements reduces the need for movement, which represents an advantage,
551 particularly for animals in an unfamiliar area, where they are unaware of whether other
552 microhabitats will meet these requirements. It has been reported that translocated *C. horridus*
553 and *C. ruber* normalize their spatial ecological parameters, to varying degrees, in the second
554 year of monitoring [5, 25], suggesting a gradual recognition of the locality. Therefore, we
555 expect that the probability of moving in translocated *C. simus* will closely resemble resident
556 ones as time progresses, although longer monitoring is necessary to reach at conclusions.
557 The findings of this study suggest that translocation has little effect on the spatial
558 ecology of *C. simus*. This is consistent with the limited effects of translocation on
559 microhabitat selection we previously reported [73]. Although we acknowledge that these
560 results may be influenced by the small number of snakes tracked, we believe the information
561 generated is nonetheless valuable. Research on snake translocation has been heavily biased
562 towards temperate species and ecosystems [e.g. 5, 14–15]. In tropical forests, where the

greatest diversity of snakes is found, the dense and structurally complex vegetation can interfere with radio-tracking by causing signal reflection and attenuation, reducing detection distances compared with more open forests. High humidity and frequent rainfall can also compromise tracking equipment, further complicating fieldwork. These environmental and technical challenges make it particularly difficult to track snakes over extended periods, contributing to the scarcity of spatial ecology studies and the often small sample sizes reported for tropical species [e.g. 22, 31, 66].

Despite these limitations, our findings provide valuable evidence to inform decisions about the continued use of translocation as a conservation strategy in the region. This is especially important considering that translocation often represents one of the few alternatives to the extermination of snakes involved in human–snake conflict. In Costa Rica, these management practices are the result of a long-standing collaboration between the Instituto Clodomiro Picado (ICP)—an entity of the University of Costa Rica with expertise in snake handling—and the National Fire Department—which provides broad national coverage, and the human and financial resources necessary to conduct the rescues.

The case of Nosara offers important conservation advantages, providing a clear example of how to address the challenges faced by many snake populations worldwide. The area's remote location, far from the nearest state fire station, means support from national authorities is limited. However, community organization led to the creation of the Nosara Volunteer Firefighters, a private initiative, which performs emergency response functions not covered by official agencies.

Thanks to this community-led initiative, both local communities and new residents have fostered a shared culture of respect for local ecosystems, including snakes. This model demonstrates how collective action can benefit wildlife conservation, even when the species

involved may pose a risk to humans. Ultimately, Nosara underscores the importance of implementing effective wildlife management strategies in urbanized contexts, which are significantly different from protected areas.

Conclusions

Spatial ecology offers valuable insights into the behavior, physiology, and conservation of snake species, with radio telemetry being one of the few techniques available to generate this type of information. Therefore, there is an urgent need for consensus among herpetologists on analytical methodologies to better understand the biology of this group of animals and to enable meaningful interspecific comparisons. This is particularly important for terrestrial reptiles, as most current methodologies were developed for taxa with very different movement ecologies.

Our results provide novel insights into the spatial ecology of a tropical rattlesnake using internally implanted radio transmitters. Home range areas of *C. simus* were estimated at 10.31 ± 4.14 ha with core areas of 1.82 ± 0.69 ha, more closely resembling those of other tropical pit vipers than those reported for other *Crotalus* species [22, 31]. Likewise, mean daily movement was 14.49 ± 2.15 m/d, similar to that reported for the closely related and tropical South American rattlesnake [66]. Comparing the spatial and movement patterns reported here for this species with those of temperate conspecifics is a step toward understanding the ecological dynamics of tropical snakes.

Our findings also allow for an evaluation of wildlife translocation as a management tool in tropical species. The lack of ecological information from this region has often required reliance on data from temperate vipers, where translocation is frequently considered

610 unsuccessful, largely due to the challenges translocated individuals face in locating
611 overwintering hibernacula [e.g. 5]. However, such dynamics differ fundamentally from those
612 experienced by tropical vipers. We demonstrate that translocation appears to be a suitable
613 conservation strategy in tropical systems because it (1) does not negatively affect individuals
614 in terms of spatial ecology, and (2) represents one of the few alternatives to the extermination
615 of animals in human–snake conflict situations.

616 Information bias in snake spatial ecology may have led us to believe that we have
617 generated abundant data in this discipline. However, we should be aware that these data have
618 been concentrated on a few species from temperate regions. The difficulty of tracking snakes
619 with remote sensing techniques in tropical zones is one of the main reasons these studies
620 have been neglected. In a world where snake populations are declining in many ecosystems
621 [17–18], it is imperative that we understand the spatial ecology of tropical snakes, as the
622 tropics hold the highest snake diversity.

623

624 ## List of abbreviations

625 SINAC = Sistema Nacional de Áreas de Conservación, SVL = Snout-vent length, CCH =
626 Circumference at Chest Height, MCP = Minimum Convex Polygon, KDE = Kernel Density
627 Estimators, aKDE = autocorrelated Kernel Density Estimators, dBBMM = dynamic Bridge
628 Movement Models, glmm = generalized mixed models, CI = confidence interval, CrI =
629 credible interval, DLT = distance to the nearest large tree (m), DST = distance to the nearest
630 small tree (m), DFL = distance to the nearest fallen log (m), DWS = distance to the nearest
631 water source (m), CC = canopy cover (%), SU = number of structures in the understory, T =
632 temperature (°C), H = humidity (%).

Declarations

Ethics approval and consent to participate: Animal care protocols and research permits were approved under the resolution ACT-OR-DR-021-2024 of the Sistema Nacional de Áreas de Conservación (SINAC) of the Ministry of Environment and Energy.

Consent for publication: Not applicable.

Availability of data and materials: The datasets that support the findings of this study are openly available in the repositories Movebank https://doi.org/10.5441/001/1.746 (Triana et al., 2026) and Mendeley Data https://doi.org/10.17632/s94ccbvzyj.1 (Triana et al., 2026).

Competing interests: The authors declare that they have no competing interests.

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Authors' contributions: FT, FB, and MS conceptualized the study and secured funding. FT and RB collected the study individuals. FT and DAC collected field data. FT and CBV performed data analysis. FT wrote the original draft. All authors contributed to the review and editing of the manuscript. All authors read and approved the final manuscript.

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Additional files

1. File name: Table 1.
   File format: .docx

Title of the data: **Table 1.** Data from *C. simus* individuals tracked in Nosara, Costa Rica plus home range size estimates. Status categories are R = resident, T = translocated; sex is M = male, F = female. MCP = Minimum Convex Polygon, KDE = Kernel Density Estimators, aKDE = autocorrelated Kernel Density Estimators, and dBBMM = dynamic Brownian Bridge Movement Models. 100% and 95% isopleths correspond to the complete territory size, while 50% isopleths mean core territory sizes. All values for the home range estimates are reported in hectares (ha). NA are reported when estimators failed to estimate home range size due to small data on that individual.

Description of the data: Results describing the *Crotalus simus* individuals tracked in the study, including their individual measurements and home range estimates calculated using multiple methods. This table is provided as an additional file as it exceeds the width of a standard letter/A4 page.

2. File name: Supplemental material. Table S1-S8

   File format: .docx

   Title of the data: Table S1-S8.

   Description of the data: Models, analyses and coefficient values not shown in the main manuscript.

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- Table1.docx
- Supplementalmaterial.TableS1S8.docx