

Home-range and behaviour of four female Garden Treeboas, *Corallus hortulana* (Linnaeus, 1758), in French Guiana

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Abstract. Understanding the home range and behaviour of snakes provides valuable insights into their ecological roles, territorial behaviours, and the impacts of environmental changes on their populations but our knowledge of behaviour and preferred habitat characteristics of arboreal snakes in tropical forests remains largely unclear. *Corallus hortulana* (Linnaeus, 1758), commonly known as the Garden Treeboa, is fairly easy to observe in the field, but no long-term monitoring has been carried out on it to date, even though it could make an ideal study model. The primary goal of this study was to investigate the home range size and movement behaviour of *Corallus hortulana* within its natural habitat by using telemetry and field-based observations. Four adult females were equipped with radio-transmitters and tracked over 15 months between 30 March 2022 and 9 July 2023. Of the four females tracked, only two showed a stable and well-defined home range which were estimated at 18 ha and 4.6 ha with a core area of respectively of 3.6 ha and 0.9 ha. Our observation confirmed that this is an exclusively arboreal species but with good swimming abilities allowing them to cross wide streams. Finally, we showed a strong link between animal locations and the edge of the stream indicating a possible preference for edge habitats.

Keywords. Autocorrelated Kernel Density Estimation, Boidae, telemetry, snake

Introduction

The study of space use and movement patterns is crucial for understanding the ecological needs and behavioural strategies of animals. In this context, understanding the home range and behaviour of snakes provides valuable insights into their ecological roles, possible territorial behaviours, and the impacts of environmental changes on their populations. Home ranges of animals can be defined as the area most frequently used by an animal for essential activities such as foraging and mating (Burt, 1943). Its extent and structure are influenced by individual behaviour and habitat quality, linked with local biotic and abiotic conditions (Honnay, Hermý, and Coppin, 1999;

Bjørneraas et al., 2012; Regolin et al., 2021).

Ectotherms in forests face a number of constraints, particularly in terms of thermoregulation and basking opportunities, as these are environments where access to insolation sites is only possible in certain types of habitat: clearings, edges, forest gaps, and the top of the canopy (Fitzgerald et al., 2003; Martins et al., 2008). Our understanding of the behaviour and preferred habitat characteristics of tropical forest tree snakes remains largely unclear. Insights into natural behaviours and habitat preferences are key information for the establishment of conservation measures *in-situ* and *ex-situ* though these data are often partially or completely unknown, including in common species.

Corallus hortulana (Linnaeus, 1758), commonly known as the Garden Treeboa, is a non-venomous constrictor snake native to the Neotropical mainland and several continental and oceanic islands of South America and is the most geographically widespread member of the genus (Henderson, 2015). It is a strictly arboreal and medium-sized species quite easy to see at night at heights up to several meters in trees next to forest streams (Henderson, 1992). Many studies have been published on feeding and reproductive biology of *Corallus hortulana* (Henderson, 1992, 1993a, 1993b, 1993c, 1996, 2007, 2015; Da Costa Silva and Henderson, 2010, 2012; Barrio-Amorós, 2017; Arrivillaga et al., 2019), but there have been relatively few studies on the

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habitat use of this species and we found no studies on their home range size.

The primary aim of this study is to investigate the home range size and movement behaviour of *Corallus hortulana* within its natural habitat. By using telemetry and field-based observations, this research seeks to address key questions about how these snakes utilise their environment, their movement strategies, and the factors influencing their spatial distribution.

Materials and methods

Study site. The area of our study, selected for its accessibility, is located upstream of the “Crique rouge” (Red Creek; Fig. 1), in western French Guiana, 14 km from St Laurent du Maroni (5.5537°N, -53.9421°W). Crique Rouge is a tributary of Crique Vaches, which flows into the Maroni River. The influence of the tides is very strong on the Crique Rouge. The water is brackish, particularly during the height of the dry season, from August to November. The difference in stream depth between the lowest point at low tide and the highest point at high tide is commonly around two meters and can exceed three meters, particularly during high equinox tides. In the study area, dry land on the banks of the Crique Rouge is rare. At low tide it is possible to move without too much difficulty in the mangrove. At high tide, however, the entire area is flooded to a depth greater than two meters.

Mangroves occupy the entire study area (Fig. 2). It is dominated by the Red Mangrove (*Rhizophora racemosa*). Apart from the red mangroves, the flora present is essentially represented by moriche palms locally called « *palmiers bêche* » (*Mauritia flexuosa*), Dragonsblood Tree « *moutouchi rivière* » (*Pterocarpus officinalis*), Water Chestnut « *cacao rivière* » (*Pachira aquatica*), Assai palms « *palmiers pinot* » (*Euterpe oleracea*) and « *moucous-moucous* » (*Montrichardia arborescens*) plant formation characteristic of riverbanks. The plant community is more diverse further upstream, particularly including more epiphytic plants (e.g., *Philodendron* spp., *Tillandsia* spp.).

Animal capture and equipment. Animals were spotted at night from a boat while roaming the Crique Rouge and shining a light up into the tree canopy on shore. The eyeshine reflections of *C. hortulana* make them easy to spot. The animals were captured by hand and sexed by probing, weighed with an electronic scale, and total length was measured. Given the logistical difficulty of following too many animals simultaneously over a long period of time we were compelled to follow

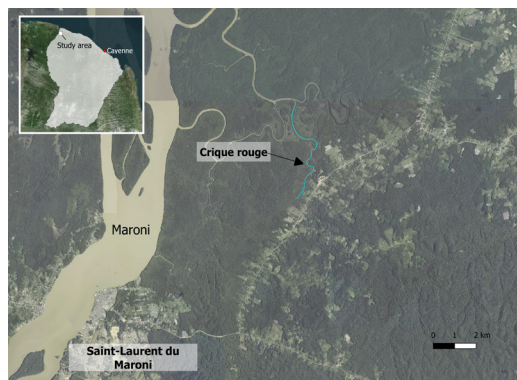


Figure 1. Location of the study site “Crique rouge” in northwestern French Guiana.

only four individuals. Consequently, it was decided to only follow females so as not to introduce a sex effect into our observations. The snakes were named Denise, Lio, Eva and Mia and their respective weights and total lengths are detailed in Table 1.

5.3g VHF radio transmitters (model SB-2T; Holohil Systems Ltd., frequency range 151.500-151.600 MHz) were used to track the animals. The VHF signal was received using a radio-receiver (Biotrack Sika, Biotrack, Dorset, UK) associated with a flexible antenna (3-element VHF Yagi Antenna, Biotrack, Dorset, UK).

To stay below 5% of the snake’s mass (Herpetological Animal Care and Use Committee (HACC) of the American Society of Ichthyologists and Herpetologists, 2004), the minimum snake mass required was 200 g, which was easily exceeded. Animals were brought to a veterinary clinic for transmitter surgical implantation by a professional. The transmitters were implanted subcutaneously and laterally, approximately 35 cm anterior to the cloaca. Due to the absence of a gas anaesthesia system in the veterinary clinic, we opted for an injection anaesthesia procedure under alfaxalone + medetomidine anaesthesia and butorphanol + meloxicam analgesia. Whip antennae 23.5 cm-long were implanted subcutaneously. This procedure was approved by the Paris Natural History Museum ethical committee (APAFIS#30735-2021022315258416v4). For recovery, animals were kept in captivity for one week and then fed one time in captivity with a freshly killed mouse before being released at the exact place of capture.

Data collection. The radio telemetry study was conducted between 30 March 2022 and 9 July 2023. The release point has not been included in the tracking

Table 1. Summary of Autocorrelated Kernel Density Estimation (AKDE) results and movement model used per individual. The table indicates animal name (ID), release date (Start) as date of the tracking end (End) and the total number of days of tracking (Days). *N* and *n* indicate respectively effective and absolute sample size. Absolute sample size (*n*) is the total number of observations in the dataset. Effective sample size (*N*) represents the estimated number of independent locations in the dataset, after accounting for temporal autocorrelation in the animals' movement. 95% AKDE correspond to the home range estimates (ha) while 50% AKDE represent the core area estimates (ha); these are calculated using the absolute sample size. 50% and 95% lower and upper AKDE's confidence intervals (CI) are also included; these are calculated using the effective sample size.

ID	Weight (g)	Total length (cm)	Start	End	Days	<i>n</i>	<i>N</i>	95% AKDE / CI	50% AKDE / CI
Denise	380	1550	30 March 2022	29 June 2022	91	16	2.0	62.0* / 26.5-113.5*	14.8* / 10.9-18.4*
Lio	1000	2200	06 December 2022	23 May 2023	168	25	4.8	18.0 / 5.8-36.8	3.6 / 2.5-4.7
Eva	500	1700	21 June 2022	05 January 2023	198	29	10.4	4.6 / 2.3-7.9	0.9 / 0.7-1.1
Mia	720	1800	07 March 2023	09 July 2023	124	18	2.5	25.8* / 6.1-59.5*	6.6* / 4.0-9.0*

* non accurate estimation due to non-stable variogram



Figure 2. Study site and typical habitat of *Corallus hortulana*. (A) One of the authors (FS) indicating the position of a *C. hortulana* in a typical mangrove habitat where animals can be found. (B) Typical habitat of Crique Rouge at high tide. In the middle is the palm tree where Mia took refuge, (see also Fig. 6A). (C) One of the authors (FJ) during one radio-tracking session on the Crique Rouge. Photos by Florence Pollier (A) and Fausto Starace (B, C).

data to allow animals to reacclimate to the wild for one week. Due to logistical constraints, each of the four snakes could only be monitored once a week on average. We collected data irregularly between 06:00

and 22:00 h, but the majority of the observations were made around 18:00–19:00 h which corresponds to sunset and the beginning of the diel activity period for this species (Henderson, 2015). The GPS position of

the animal was recorded (GPS Garmin 64sx) at each location. If the animal was visible, the height above the ground was noted with a laser meter (Titan ® TTI98 21 0COM, precision ± 3mm) as well as the habitat in which it was located (e.g. plant species, potential hiding places).

Data analysis and home range estimation. Maps were drawn using Qgis (version 3.34.2-Prizren). We applied Autocorrelated Kernel Density Estimation (AKDE) (Fleming et al., 2015) to estimate the home ranges of *C. hortulana* from our geolocated observations. This continuous-time, model-based method is advantageous as it accounts for autocorrelation in spatial data and accommodates both irregular sampling intervals (Fleming et al., 2018) and small sample sizes (Fleming et al., 2019). To ensure the most precise home range estimates, individuals must exhibit site fidelity and restricted movements over a defined time period (Horne et al., 2020). We assessed site fidelity for each individual by examining semivariograms, which depict the semivariance of positions as a function of the time lag between observations (Fleming et al., 2014). Two estimators were employed to fit the AKDEs: the perturbative Hybrid Residual Maximum

Likelihood estimation (pHREML), which mitigates biases associated with small sample sizes (Fleming et al., 2019), and the weighted AKDE (wAKDEc), which adjusts for irregularities in the sampling design (Fleming et al., 2018). For individuals with an effective sample size below 5, AKDE estimates were obtained through bootstrapping. This resampling technique repeatedly draws samples from the observed data with replacement, allowing for robust estimation of home range sizes despite a limited number of independent data points. Bootstrapping compensates for the increased uncertainty inherent in small datasets by generating a distribution of potential outcomes, thus providing more reliable confidence intervals for the estimated home ranges (Fleming et al., 2018). The best individual movement model was selected based on the Akaike Information Criterion (AIC) to estimate the 95% and 50% (core area) home range sizes.

To visually inspect the autocorrelation structure of the location data, estimated semi-variances as a function of time lag were plotted for each snake. Variograms of individuals exhibiting home-range behaviour (i.e., meeting the range residency assumption for AKDE use), and thus presenting a so-called stable home range,

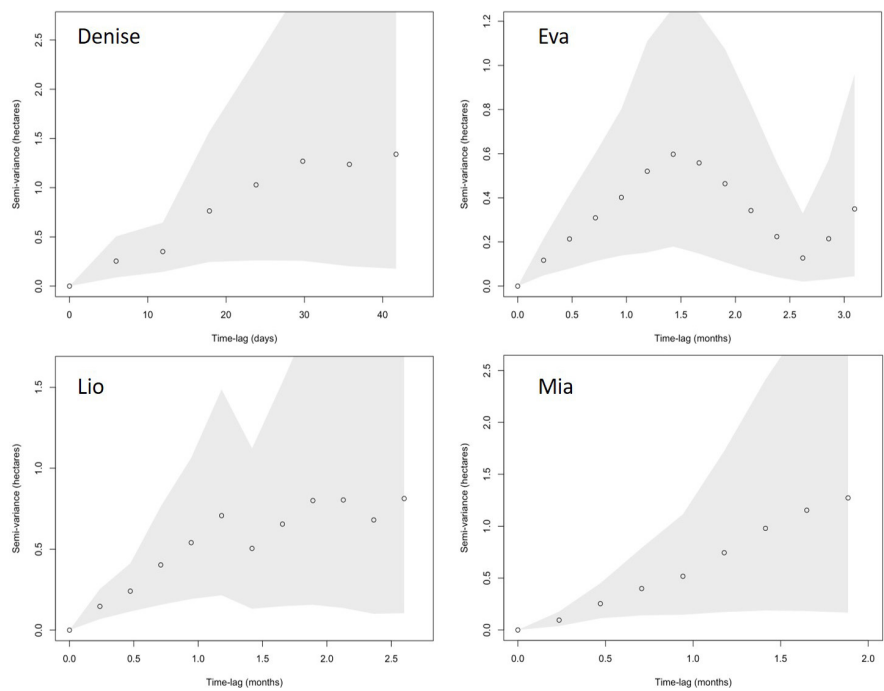


Figure 3. Variograms of 4 *Corallus hortulana* females tracked displaying semi-variance of home range area estimates with x axis starting at the beginning of each individual’s tracking period. Shaded areas display 95% confidence interval envelope.

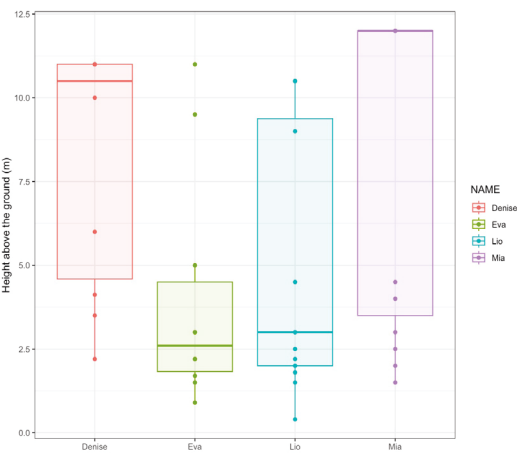


Figure 4. Boxplots of heights of the snake above the ground or the surface of the water during the tracking period. Sample size for each animal: Denise ($n = 10$), Eva ($n = 11$), Lio ($n = 20$), Mia ($n = 15$).

show an asymptote on the timescale corresponding to the home-range crossing time (Fig. 3). On the other hand, non-range resident individual variograms do not approach any asymptote and are therefore described as displaying an unstable home range. Consequently, individuals with an unstable home range would be excluded from the home range estimation analyses (i.e.,

the range residency assumption necessary for home range estimation was not met).

All analyses were performed using the `ctmm` package (Calabrese, Fleming, and Gurarie, 2016) in R software (R Core Team, 2021).

Results

Animals tracked, tracking duration and technical issues. The characteristics of animal tracking are described in Table 1. The differences in tracking time are explained by several technical issues. Concerning Denise, after 91 days her transmitter was detected without any movements and any visual contacts. Finally, her transmitter was found damaged on the ground indicating a potential predation event. The signals of Lio and Mia were lost after, respectively, 168 and 124 days, possibly due to some technical problems or a predation event. Finally, only Eva was recaptured for a health check and transmitter extraction after 198 days. Transmitter extraction followed the same surgical procedure as implantation. The scar linked to the implantation of the transmitter was perfectly healed and the extraction of the transmitter was carried out very simply without tissue adhering to the transmitter. Eva weighed 500 g at the time of capture and 700 g at the end of the tracking (198 days) indicating that the transmitter was tolerated by the boa.

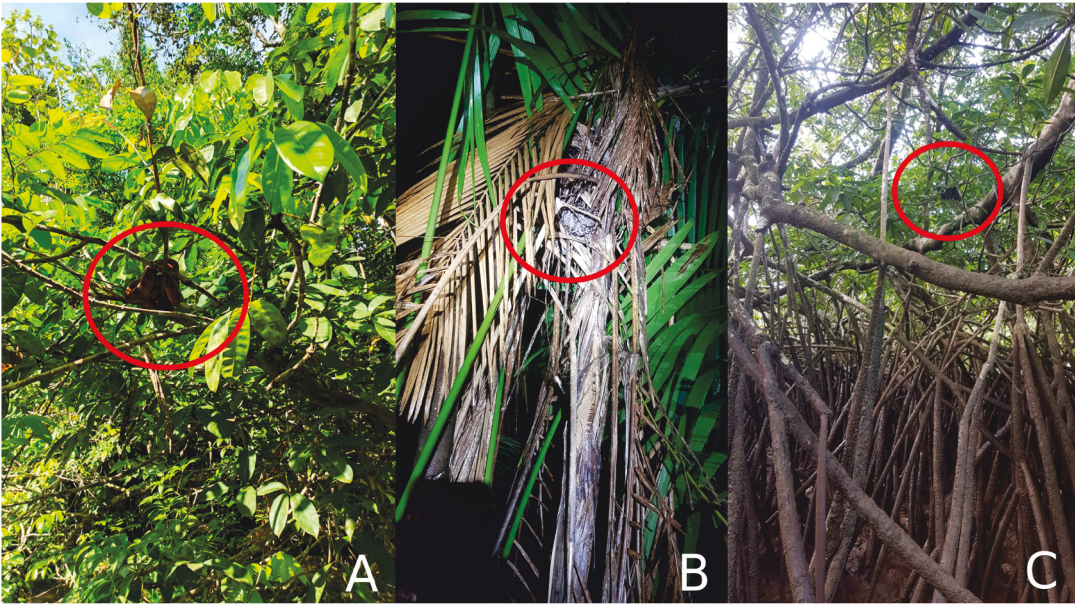


Figure 5. Arboreal resting positions observed in *Corallus hortulana*. Photos by Fausto Starace.



Figure 6. Cavity retreat sites of *Corallus hortulana*. At the axis of palm leaves (A) and in a cavity inside a branch (B). Photos by Fausto Starace.

Behaviour and habitat use. During the whole survey period, all boas stayed in the vegetation on the edge of the stream (Fig. 7). They crossed the stream on 12 occasions at a narrow part of the stream approximately 10 m in width. Three animals stayed inactive at the top of a tree (always *Mauritia flexuosa*) at heights of more than 10 m for several weeks at a time. For example, Lio stayed in the same tree at approximately 11 m height during at least 28 successive days (from 28 February to 28 March 2023) and Mia during at least 18 days (from 30 May to 17 June 2023). If we exclude this behaviour, the most common behaviour observed was moving or in an ambush posture in the trees at a mean (\pm S.D.) height of 6.3 m (\pm 4.3 m) (Figs. 4, 5), but they were also found during the day in cavities in branches or at the bases of palm leaves (Fig. 6). Animals seem to always stay close to the stream. The longest distance measured between a boa and the river border was approximately 115 m (Lio), bearing in mind that the part of the forest

where the animal was located was flooded during the study period. Other individuals of *Corallus hortulana* were observed in the study area only twice during the tracking period. Eva was seen within 10 m of two males at 18:30 h on 29 June 2022 and Mia was seen next to two males at 17:30 h on 23 May 2023.

Home range estimation. Figure 7 provides an overview of the movement trajectories of the four individuals. Three of the four animals tracked displayed a low effective sample size (< 5 ; Table 1) on which the bootstrapped pHREML wAKDEc method was used (see Materials and Methods). The model selection results are detailed in Table 2. The semivariogram did not reveal any site fidelity for Denise and Mia (Fig. 3) so their home range could not be calculated robustly. Figure 8 gives an overview of the home ranges of the four individuals relative to one another. Estimated home range sizes for Lio and Eva were 18 ha and 4.6 ha with a respective core area of 3.6 ha (CI 2.5–4.7) and 0.9 ha

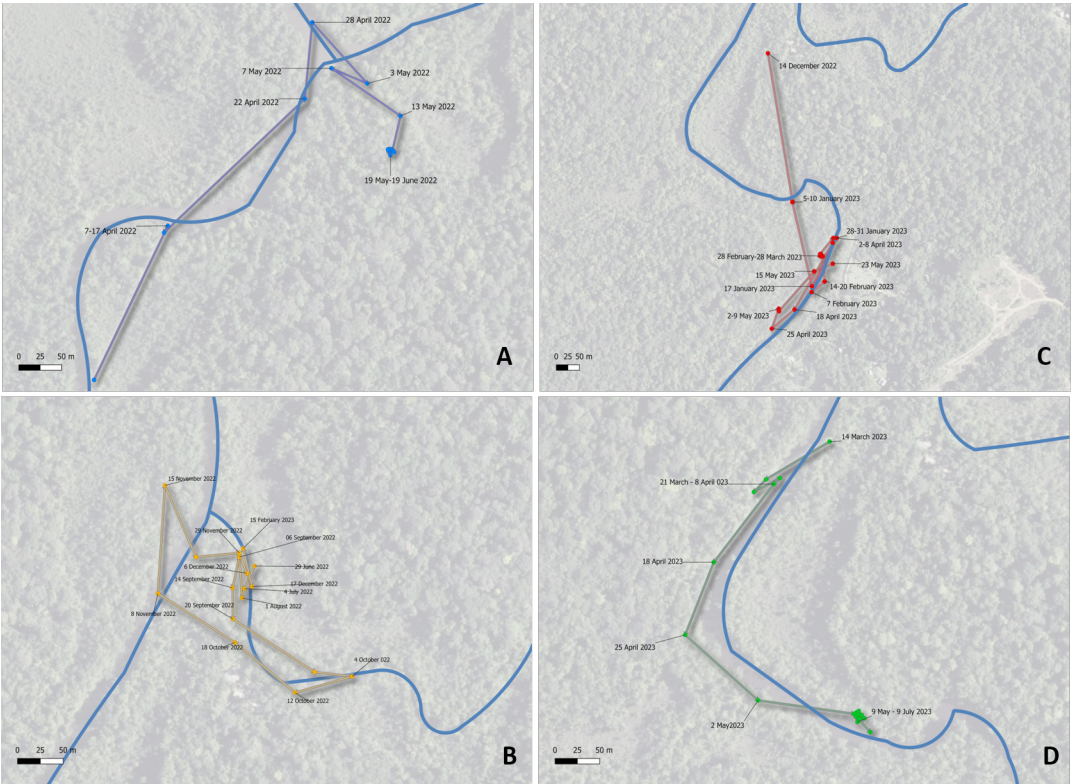


Figure 7. Maps of the different positions of the four females monitored during this study. River is indicated in blue. Denise (A), Eva (B), Lio (C) and Mia (D).

(CI 0.7–1.1). The estimated home ranges show some overlap among females but the core areas (AKDE 50%) show very little overlap (Fig. 8).

Discussion

This study provides insights into the home range dynamics of *Corallus hortulana*, contributing to a better understanding of its spatial ecology. The most robust results are mean core home range areas of 3.6 ha and 0.9 ha for our two females with an accurate home range estimation.



Figure 8. Overview of the home-range calculated for each of the 4 female *Corallus hortulana* tracked during this study. Each point indicates one GPS position. The thicker line surrounds the estimated home range (95% AKDE estimation). The thinner dotted lines indicate the limits of the confidence interval.

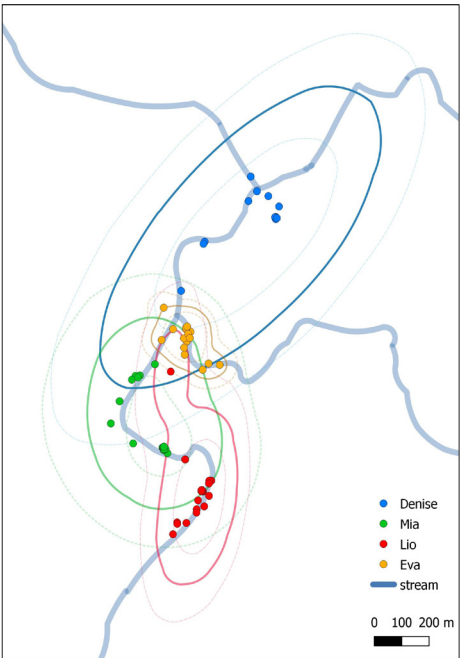


Table 2. Comparison of movement models fitted to the trajectories of the 4 individual *Corallus hortulana*. For each individual, models were ranked based on the corrected Akaike Information Criterion (ΔAIC_c), with the lowest value indicating the best-supported model. $\Delta RMSPE$ represents the difference in root mean square prediction error (in meters), and $DOF[area]$ corresponds to the estimated effective degrees of freedom associated with the utilisation distribution area. Models tested include Ornstein–Uhlenbeck (OU), Ornstein–Uhlenbeck–F (OUF), and independent identically distributed (IID) processes, each in isotropic and anisotropic forms. The best-fitting model for each individual is shown with $\Delta AIC_c = 0$.

Individual	Models	ΔAIC_c	$\Delta RMSPE$ (m)	$DOF[area]$
DENISE	OU anisotropic	0	94.238873	1.952689
	OU	0.484463	139.631373	1.689388
	OUF	3.450699	68.825626	3.792926
	OUF anisotropic	4.572736	43.463214	4.367878
	OUf anisotropic	6.450742	8.622342	6.560957
	IID anisotropic	14.398401	0	14
EVA	OUf	0	2.1229509	10.404676
	OUf anisotropic	2.751915	0.7026158	8.978279
	OUF	3.363512	0	11.539395
	OUF anisotropic	6.892944	0.7026483	4.457786
	OU	9.099115	0.4030403	8.369741
	OU anisotropic	11.016756	0.250343	8.712244
	IID anisotropic	24.769525	1.9739661	17
	IID	32.58052	1.9739661	17
LIO	OUF anisotropic	0	59.88274	4.837764
	OU anisotropic	2.680239	203.21752	1.504508
	OUF anisotropic	2.748439	139.93808	2.212402
	OUf	10.747832	57.32488	6.008027
	OUF	11.094005	163.67952	1.98893
	IID anisotropic	31.231417	0	21
MIA	OUf	0	64.53803	2.528580404
	OUF	3.07619	64.538	0.01573957
	OUF anisotropic	4.014721	129.42287	1.974829722
	OUF anisotropic	8.154751	129.35903	0.008457687
	OU	16.384129	114.21276	1.448614219
	OU anisotropic	22.803394	140.12007	1.338328303
	IID	76.877503	0	17

As it is known that home-range size is highly influenced by sex in snakes (Slip and Shine, 1988; Todd and Nowakowski, 2021; Natusch et al. 2022), these values should not be extrapolated to males. It is difficult to compare our home ranges estimations to other similar species as we were not able to find comparable data for females of closely-related arboreal boids. Nevertheless, data collected by Wilson et al. (2006) on Green Tree Pythons (*Morelia viridis*) in Australia indicate a mean

home range size of 6.12 ha for females which is in the same order of magnitude as our estimates. Likewise, home range sizes between 0.01 and 9.89 ha (mean 3.8 ha) were measured for females of the arboreal Australian elapid *Hoplocephalus bungaroides* (Croak et al., 2013). Reynolds et al. (2024) established that for female *Chilabothrus c. chrysogaster*, the average size of the home range is 1.83 ha with an average core area of 0.39 ha which is again in the same order of magnitude as our data.

Despite the proximity of the core activity areas of the four individuals and the overlap among the confidence intervals of their home ranges, the map of observation points shows almost no overlap in the areas actually occupied by the animals (Fig. 8). Based on our sample size, it is impossible to know whether this is due to chance or to an active avoidance strategy. Home range overlap has been studied in several other reptile species and seems to be highly dependent on species, sex and season (Webb and Shine, 1997; Bauder et al., 2016; Eckert and Jesper, 2024; Reynolds et al., 2024). Other individuals of *Corallus hortulana*, four in total, were only observed twice at the study site during the monitoring period. It is interesting to note that all of these individuals were males seen within a few meters of one of our females during the April-May period. This could be consistent with the hypothesis that males are less sedentary than females and that the home range of males may, at least seasonally, encompass the home range of females, as has been observed in other snake species (Slip and Shine, 1988; Todd and Nowakowski, 2021; Natusch et al., 2022).

Home-range is commonly expressed in two dimensions but it is clear that, even for terrestrial species, including a vertical dimension gives a more accurate volumetric estimate of the real space occupied by the animal (Greenberg and McClintock, 2008; Monterroso et al., 2013; Boback et al., 2022). Although we did not attempt this, including vertical habitat use for arboreal species is an important area of future research needed to understand the real behaviour of the animals. We found that we often could not estimate the height of the boas because we could not see them, which resulted in a large amount of missing data in the vertical dimension.

We observed three of our four tracked animals staying in exactly the same place at the tops of trees for periods of several weeks at a time. Because these observations took place at different times of the year, it seems to indicate that the cause is likely something about individual condition, such as the shedding process or digestion of

a large prey item (Siers et al., 2018), rather than general seasonal behaviour. That said, when Lio was at the top of a tree for 28 days, direct observation confirmed that she was not shedding nor digesting a large prey item during this period. We have no observations that would allow us to explain what factor triggers snakes to move or remain sedentary for long periods.

The movement patterns of the boas show that all four tracked individuals strictly followed the course of the stream. We can therefore assume that this species spends much of its time along forested watercourses and other ecotones, although limitations that forced us to track mostly in the evening mean that our understanding of diel variation in habitat use is incomplete. A variety of factors can influence habitat selection and may occur at multiple spatial scales from habitat to microhabitat. In a previous study, Shelton et al. (2020) showed that the preference of *Hoplocephalus bitorquatus* for riparian ecosystems can be explained by specific microclimatic conditions given by live hollow-bearing trees predominant in this type of habitat.

It is generally acknowledged that predator avoidance, food resource availability, and/or minimisation of thermal cost are strong ecological constraints that can influence habitat selection in snakes (Luiselli, 2006; Row and Blouin-Demers, 2006; Lin et al., 2007; Wasko and Sasa, 2010, 2012; Tan et al., 2024). The fact that the boas in our study never foraged far from watercourses may indicate two things: 1) that stream courses provide this snake species with all of the biotic and abiotic conditions it needs, or 2) that edge environments along watercourses are the main ecotones in dense forests. They might function similarly to other types of edge habitats, such as inselbergs, savannahs, or forest gaps. This second hypothesis has been verified for other species showing intra- and interspecific variation in their preference for edge environments (Carfagno and Weatherhead, 2006; Bonardi et al., 2008) and has already been observed in other *Corallus* species (Henderson, 2015). Preference of snakes for edge habitats remains to be clarified but prey abundance does not seem to be the primary factor. Instead, thermoregulation might be more important (see Henderson, 2015 for more details).

It is also interesting to note that the monitored individuals showed good swimming abilities, enabling them to cross watercourses more than 10 m wide on multiple occasions. We never directly observed snakes swimming. This behaviour was indirectly deduced when a snake was tracked to the opposite riverbank, to which they would have been unable to cross by land

or via aerial tree bridges. This behaviour indicates that water barriers do not necessarily constitute absolute biogeographical barriers for this species.

Out of the four animals tracked, three of them displayed a similar movement pattern after release: a unidirectional 300 to 500 m displacement over several weeks before settling down at a specific point. One hypothesis could be that the capture and the surgery temporarily modified the natural behaviour of the animals and artificially increased their movements. As a negative correlation has been shown in snakes between habitat quality and home range size (Kapfer et al., 2010), another explanation would be that animals moved until they found a suitable place with acceptable local biotic and/or abiotic conditions. This hypothesis is in line with the transient behaviour described in *Corallus grenadensis* by Henderson et al. (2021).

These findings not only deepen our knowledge of the ecological habits of *Corallus hortulana* but also have implications for conservation strategies aimed at preserving critical habitats such as forest/river ecotones. Future research should aim to include males and juveniles, track at a variety of times of day, focus on long-term monitoring and accurate microhabitat description and microclimatic data collection to further elucidate the factors shaping the spatial ecology of *C. hortulana*. Such efforts are essential to ensuring the long-term survival of this ecologically significant yet understudied species.

Acknowledgments. This study was financed by Paris Zoo research support funds and approved by the Direction Régionale Environnement Aménagement Logement (DREAL) of French Guiana. We would like to express our thanks to Cyprien Bonifay for his essential logistic support. We are very grateful to Henri Rogier for his technical help in repairing our electronic equipment. We would also like to thank Olivier Lourdais for his scientific advice and Robert Henderson and Ivan Ineich for their valuable comments, which helped improve the manuscript.

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