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## NATURAL HISTORY OF THE LARGE PIT VIPER *BOTHROPS JARARACUSSU*: HABITAT USE, MOVEMENT PATTERNS, AND HOME RANGE

EDELICIO MUSCAT<sup>1</sup>, RAFAEL MITSUO<sup>1,3</sup>, RAFAEL MENEGUCCI<sup>1</sup>, MATHEUS DE TOLEDO MOROTI<sup>1</sup>,  
MARIANA PEDROZO<sup>1</sup>, ELSIE ROTENBERG<sup>1</sup>, AND IVAN SAZIMA<sup>1,2</sup>

<sup>1</sup>Projeto Dacnis, São Francisco Xavier and Ubatuba, São Paulo, Brazil. Estrada do Rio Escuro 4754,  
Sertão das Cotias, 11680-000, Ubatuba, São Paulo, Brazil

<sup>2</sup>Museu de Zoologia, Universidade Estadual de Campinas, Rua Charles Darwin, Barão Geraldo, 13083-863,  
Campinas, São Paulo, Brazil

<sup>3</sup>Corresponding author; e-mail: dacnis.research@gmail.com

**Abstract.**—Understanding how organisms use their environment is essential for management and conservation, but little remains known about many species. We studied the natural history, including habitat use, home range, movement patterns, and reproduction, of a population of the large pit viper *Bothrops jararacussu* for 8 y in a private reserve in coastal Atlantic Forest. This viper species uses dense forest more often than forest edges and open areas. Adults remain on the ground most of the time, whereas juveniles sometimes use bromeliads and other vegetation types. Individual home ranges are relatively small and females move less frequently than males, often remaining in the same location for long periods. When females do move, however, they travel long distances. Temperature was negatively related to movement distance, but we found no relationship between humidity and movement patterns of the snake. Pregnant females shared a maternity area throughout the monitoring period and gave birth in late March. Our study provides relevant information to the understanding of the natural history of a large and difficult to study pit viper, filling knowledge gaps.

**Key Words.**—Atlantic Forest; functional traits; life history; radio telemetry; spatial ecology; thread bobbins; Viperidae

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### INTRODUCTION

Understanding how organisms use habitat is crucial to management and conservation efforts (Van Moorter et al. 2016). Home range and movement studies are needed for a better understanding of the ecological role of a given animal species (Gregory et al. 1987). Natural history-oriented studies can provide essential data on home ranges and movement, but such information is often lacking, hindering the advancement of our knowledge about biodiversity (Greene 1993; Van der Niet 2020). Movement pattern studies have recently increased because of advances in tracking technology and analysis methods (Kays et al. 2015; Shonfield et al. 2019; Smaniotto et al. 2020). Still, movement pattern and habitat-use studies of Neotropical snakes are scarce (e.g., Greene and Santana 1983; Oliveira and Martins 2001; Tozetti and Martins 2008; Rocha et al. 2014).

The large pit viper *Bothrops jararacussu*, popularly known in English as Jararacussu, is an Atlantic Forest species, found in dense ombrophilous, submontane, and deciduous forests from southern Bahia to northwestern Rio Grande do Sul in Brazil, adjacent Paraguay, southeastern Bolivia, and Argentina (Olson et al. 2001; Campbell and Lamar 2004; Nogueira et al. 2019).

*Bothrops jararacussu* is the largest species in the genus, reaching a length of up to 2.2 m (Milani et al. 1997), and its defensive strike can introduce a large amount of venom (Do Amaral 1924). Its cryptic coloration with sexual dichromatism and ontogenetic variation (Marques and Sazima 2004) hinders detection in the diverse habitats where it dwells, such as stream banks, forest interior and edges, and open areas (Hartmann et al. 2003; Hartmann et al. 2009). It is a prolific viviparous species, with litter size between 13 and 73 neonates (Marques and Sazima 2004). In captivity, births occur between February and April, with a peak in March (Marques and Sazima 2004). *Bothrops jararacussu* displays an ontogenetic diet shift, as juveniles prey mostly on frogs, often with the use of caudal luring to attract prey, whereas adults prey on small mammals, frogs, lizards, and, occasionally, other snakes (Martins et al. 2002; Marques and Sazima 2004; Sazima 2006).

*Bothrops jararacussu* is ranked as Least Concern in the Brazilian Red List (Instituto Chico Mendes de Conservação da Biodiversidade 2018) and the International Union for Conservation of Nature and Natural Resources (IUCN) Red List of Threatened species (Scott et al. 2019), but information about population size, distribution, and biological traits are

lacking (Scott et al. 2019), making natural history studies key to promote effective conservation (Michaels et al. 2014). Most studies about *B. jararacussu* do not focus on natural history, which results in a knowledge gap about this species (Greene 1993; Sasa et al. 2009). This scarcity may be partly explained by the difficulty in obtaining *in situ* data, as the snake occurs in low densities in habitats not readily accessed by researchers, has a cryptic color pattern making it difficult to detect, and is mostly nocturnal (Sasa et al. 2009). Herein we present natural history data on *B. jararacussu* recorded over 8 y in a private reserve in coastal Atlantic Forest. This long-term study allowed us to investigate several features of the natural history of this viper, such as habitat use, home range, differences in movement patterns between males and females, movement patterns in relation to abiotic factors (humidity and temperature), and reproductive activity of three gravid females.

#### MATERIALS AND METHODS

**Study area.**—We carried out the study in the Projeto Dacnis private reserve in Ubatuba municipality, São Paulo state, southeast Brazil (23.462947°S, 45.132943°W; 15–500 m elevation). The reserve is located in the Atlantic Forest biome and has diverse microenvironments in its 1.36 km<sup>2</sup> area. It contains mainly secondary submontane forest and has continuous tree canopy cover with little ground-level sunlight incidence and a dense understory rich in lianas and bushes. The reserve also has several areas of rocky streams, surrounded by well-developed moss and primary forest. In some places, vegetation succession allows more sunlight incidence. These latter places have dense, low vegetation (1.5 m) that contains marshy areas composed of toucan beak (*Heliconia* spp.; Heliconiaceae) and White Ginger Lily (*Hedychium coronarium*; Zingiberaceae). There are also areas of abandoned banana (*Musa × paradisiaca*; Musaceae) plantations with abundant sunlight.

The climate in Ubatuba is classified as tropical without a dry season (Af), with an average yearly temperature of 22.5° C and 2,552 mm of rainfall (Alvares et al. 2013). In terms of hydric availability, however, the climate of Ubatuba more closely resembles a humid subtropical climate (Cfa) without marked seasonality (Rolim et al. 2007). We obtained daily meteorological data from the station of the *Clarimundo de Jesus* base at Instituto Oceanográfico da Universidade de São Paulo (IO-USP), located 4.25 km from the Projeto Dacnis private reserve.

**Data collection.**—We monitored the area for 8 y with five 3-h field trips per week (three mornings and two nights), each by the same researchers all years. Our sampling effort was 216 person-hours per year for a total sampling effort of 2,080 person-hours. We recorded all

fortuitous encounters with *B. jararacussu* individuals from 2012 to 2020. In 2017, we began monitoring 17 individuals (nine males and eight females: ID #01–17), which were identified with implanted microchips (1.4 × 8.0 mm; model GLOBAL-IDENT XS 1.4; Anilhas Capri, São Paulo, São Paulo, Brazil) using a microchip reader (model RFID PT160; Anilhas Capri, São Paulo, São Paulo, Brazil). After marking, we determined the sex of each individual and measured its body mass with a digital scale (LEFA; model MH-500, precision of 0.1 g; China) and tail (TaL) and total length (TL) using a measuring tape. We visited daily the area of each monitored individual. To obtain the total encounters recorded during monitoring, we counted all chance encounters plus the first record of each monitored individual to avoid any counting bias.

Whenever we observed a *B. jararacussu* individual, we recorded the habitat (forest interior, forest edge, open area) and microhabitat. We classified microhabitats as ground when the snakes were found on leaf litter, between roots, or on tree bases; shrub when they were on fern clumps, shrubs, or bushy vegetation; water for records in puddles or streams; and rocks for snakes on or in between rocks. When the snakes were hidden in burrows, holes, leaf litter, or under fallen tree trunks, we classified the microhabitat as hidden. We present these results using percentages to quantify habitat use both by monitored individuals and those we found by chance.

We monitored the movements of snakes with thread bobbins (n = 17), in addition to radio telemetry (Tozetti and Martins 2007) on individuals ID #13–16 (n = 4), for a short period of time (two weeks to three months). We put bobbins only on adult individuals large enough that the bobbin would not hinder their movements (> 250 g). The bobbins had approximately 170 m of thread and weighed about 6 g. They were wrapped in polyvinyl chloride food wrap (Wyda embalagens, Sorocaba, São Paulo, Brazil) and stuck to the bodies of snakes with adhesive tape (Fig. 1). The bobbin, wrap, and adhesive tape kit weighed 12–15 g. We used a transparent plastic tube to hold the snakes and wrapped the tape around the posterior third of their bodies. The snakes were then released at the site where they were found. The bobbin unrolled from the inside out, leaving a path of thread as the snake moved (Fig. 1), and was replaced *in situ* when needed.

We attached UHF transmitters (3.5 × 1.5 cm; AXA-BIXO, São Paulo, São Paulo, Brazil) to the snakes with adhesive tape (Tozetti and Martins 2007; Fig. 1). We located individuals with the help of a directional antenna connected to a radio telemetry receiver (433.92 MHz; AXA-BIXO, São Paulo, São Paulo, Brazil). Because of the dense vegetation, numerous rocks, and subterranean galleries in the study area that interfered with and weakened the radio signal (Újvari and Korsós 2000),



**FIGURE 1.** *Jararacussu* (*Bothrops jararacussu*) individuals monitored at the Projeto Dacnis private reserve in Ubatuba municipality, São Paulo state, Brazil. (A) male ID12 with attached thread bobbin; (B) the same male with attached radio telemetry device; (C) female ID16 with attached thread bobbin basks in dappled sunlight during the first hours of the morning; (D) the same female gave birth to 46 offspring at the end of March. (Photographs A–C by Rafael Menegucci and photograph D by Rafael Mitsuo).

radio telemetry did not work well. We therefore used the bobbin method to supplement radio telemetry.

Between January and March 2020, we monitored three gravid females in an area we called maternity, a clearing in the native vegetation covered with the banana plant. Their mass was measured on the first encounter, but we did not weigh them again during pregnancy to avoid stress to the snakes. After birth, we took all neonates and post partum females to the Projeto Dacnis headquarters for morphometric processing. To standardize measurements, we photographed each neonate (model 80D; Canon U.S.A., Melville, New York, USA) at an angle of 90° with a precision scale (0.1 mm) beside it in the field of view of the image. We used ImageJ software (Abramoff et al. 2004) with the precision rule as reference to measure total length (TL). We weighed every neonate with the same digital scale that we used for adults. After processing, we released all individuals at the point of capture.

**Movements and home range.**—We estimated *B. jararacussu* movements by measuring the bobbin thread, as we presumed that this was the distance traveled by individuals fitted with bobbins. We recorded geographical coordinates (model eTrex 22; Garmin International, Inc., Olathe, Kansas, USA) at each encounter site. These methods allowed us to use the encounter coordinates to estimate the home range

of each individual using the Minimum Convex Polygon method (100% MCP). We calculated these metrics in R version 3.5.3 (R Core Team 2020), using the *adehabitatHR* package (Calenge 2006). We chose MCP because it is a common method to estimate home ranges with a low number of points per individual and because it represents the total area potentially used by the animal (Averill-Murray et al. 2020). We did not estimate home ranges for individuals observed fewer than five times (individuals 11, 13, and 14). We calculated the average distance traveled by dividing the total distance traveled by the number of recapture locations of each individual. We present the mean and standard deviation of the total displacement separately for males and females.

**Statistical analyses.**—We explored and analyzed data with R (R Core Team 2020) using the packages *lme4* (Hothorn et al. 2015), *pscl* (Wenger and Freeman 2008), and *ggplot2* (Wickham 2016). To test the relationship between the abiotic variables (temperature and humidity) and the movement distance of the monitored snakes, we used a Zero-inflated Generalized Linear Mixed Model, which includes a random effect for the individual snake. We rounded the data to the nearest meter. This model includes true zeros (Zuur et al. 2009), meaning that when the individuals did not move, it was a true value (Raffel et al. 2010, 2013). We created two models of inflated zeros to test the fit

adjustment: Zero-Inflated Poisson Regression (ZIP) and Zero-Inflated Negative Binomial Regression (ZINB). When we analyzed variance, we found that our count data displayed overdispersion, and ZINB was a better fit to the data (Zuur et al. 2009). Furthermore, we submitted the models to a Likelihood-ratio Test that confirmed ZINB as the model that provided a better fit to our data (Akaike Information Criterion [AIC] 1974.5 vs. AIC 8512.4). Because our data were not normally distributed, we described displacement for both sexes as median and interquartile interval. To test whether a difference between the movement patterns of males and females existed, we used a non-parametric Wilcoxon Test ( $\alpha = 0.05$ ).

### RESULTS

During our 8-y *B. jararacussu* study, we documented 66 encounters with 30 males, 23 females, and 13 juveniles of undetermined sex. Adults and juveniles differ in coloration, especially females through ontogeny (Fig. 2). The thread bobbin method allowed precise indication of the traveled route, use of the substrate, and did not interfere with the activities of the snake: we observed snakes with stomach bulges several times, indicating that feeding was unhindered by the thread bobbin.

We recorded the most monitored snakes in dense woods (90.4%), followed by forest edges (7.3%) and open areas (2.3%). *Bothrops jararacussu* used mainly ground microhabitat (67.1%), then shrub (23.5%). We found it less often on rocks (6.2%) and in water (3.2%). Most individuals were found exposed (67.7%), rather than hidden (32.3%). Adults relied mostly on the ground for movement and rest. We recorded two juveniles coiled on vegetation about 1 m above ground. Encounters with females were more frequent than with males in all types of habitats and microhabitats (Table 1). *Bothrops jararacussu* found during the day were mostly motionless, coiled close to fallen trunks or hidden in burrows or amid rock formations. In a few instances, we found individuals active during the day, moving on the substrate a few meters from where they were located the previous day.

We obtained similar results from incidental observations of snakes without thread bobbins or radio transmitters. In 49 encounters, 79.6% were in dense woods, followed by 16.3% along forest edges, and 4.1% in open areas. Most snakes were seen using the ground (81.6%), followed by shrubs (8.2%) and water (6.1%), all of them occupying strata from 0 to 112 cm above ground. Twice we recorded juveniles using bromeliads.

In our observations of both monitored individuals and chance encounters, there was usually a stream nearby ( $\leq$



**FIGURE 2.** Adult and juvenile *Jararacussu* (*Bothrops jararacussu*) may display different colors, especially females throughout ontogeny. (A) adult female ID17 144 cm total length (TL) moves among leaf litter on the forest floor; (B) adult male 114 cm TL alert on forest floor; (C) juvenile female about 30 cm TL in ambushing posture among leaf litter at a stream bank; (D) juvenile male about 50 cm TL basks at a stream bank. Individuals B–D were not monitored. Individuals C–D were recorded in the general area of our observations (Ubatuba municipality) but are not part of the present study. (Photograph A by Rafael Menegucci and photographs B–D by Ivan Sazima).

**TABLE 1.** Type of habitat and microhabitat used by *Jararacussu* (*Bothrops jararacussu*) monitored with thread bobbins and/or radio telemetry at the Projeto Dacnis private reserve, Ubatuba municipality, São Paulo state, Brazil (April 2017–March 2020). Values are the number of locations per individual. An asterisk (\*) indicates gravid females for which locations were in a clearing of banana plants (*Musa* × *paradisica* hybrid) inside the forest.

ID	Habitat			Microhabitat				
	Dense woods	Forest edge	Open area	Ground	Water	Bush	Rocks	Hidden
1	34	0	0	22	0	12	0	9
2	18	0	0	3	0	7	8	8
3	2	3	0	5	0	0	0	2
4	9	0	0	4	5	0	0	4
5	5	0	0	4	1	0	0	4
6	43	0	0	40	3	0	0	30
7	14	1	0	11	0	4	0	3
8	24	0	1	20	0	5	0	8
9	14	0	0	14	0	0	0	11
10	1	28	9	18	5	15	0	0
11	3	0	0	1	0	2	0	0
12	35	0	0	26	0	5	4	13
13	4	0	0	4	0	0	0	4
14	3	0	0	0	0	0	3	3
15	63*	0	0	57	0	6	0	15
16	69*	0	0	25	0	32	12	27
17	56*	0	0	41	0	15	0	1
Used (%)	90.4	7.3	2.3	67.1	3.2	23.5	6.2	32.3
Male	37.3	12.5	10	38.6	28.6	22.3	44.4	50.7
Female	62.7	87.5	90	61.4	71.4	77.7	55.6	49.3

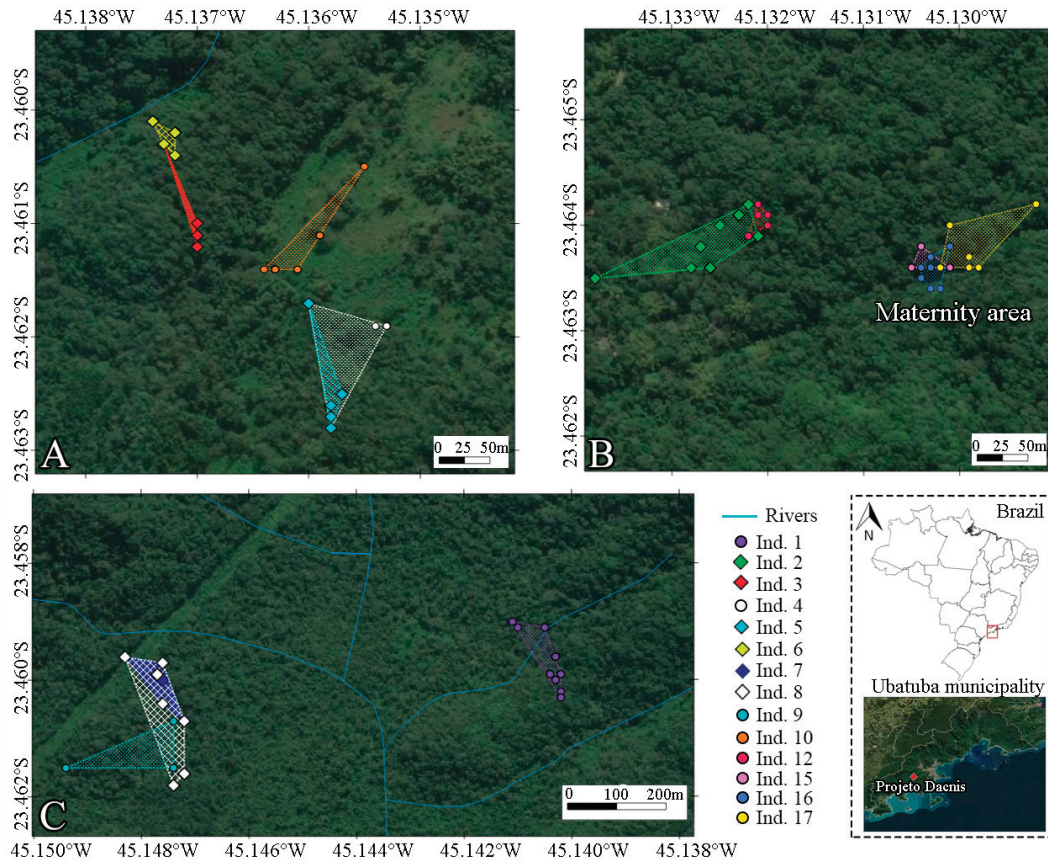
10 m). One snake remained at a stream margin with the caudal portion of its body submerged (ID #4) for three consecutive days. On another occasion, we observed an individual (ID #6) diurnally active beside a creek for two consecutive days. During our study, only one monitored individual used an open area, and it did so for seven consecutive days. The area was composed of dense *Heliconia* spp. stands, which considerably reduced solar incidence on the ground. We also observed monitored individuals moving along streams. On the first occasion, we saw the thread passing under a trunk that had fallen into the water (ID #1). The stream was about 50 cm deep and 180 cm wide. In the second observation, at the same stream, the line was in water for 20 m and then turned towards the forest (ID #10).

In September 2017, we recorded three interactions between males and females. In two of these, we observed the bobbin threads of males and females along the same route for three consecutive days. One interaction had direct contact: a female (ID #4) was coiled practically on top of a male (ID #5).

Estimated 100% MCP home range areas for *B. jararacussu* varied from 0.10 to 0.46 ha (Fig. 3). Mean

home range area of females was  $0.24 \pm 0.221$  (standard deviation) ha and they travelled a total mean distance of  $410.7 \pm 73.92$  m. The mean home range area of males was  $0.22 \pm 0.241$  ha and they travelled shorter distances ( $234.4 \pm 168.23$  m) than females (Appendix 1). Males had significantly greater displacements (median = 7 m; interquartile interval = 0–10.5 m) than females (median = 0 m; interquartile interval = 0–3.0 m;  $W = 17,330$ ,  $n = 430$ ,  $P = 0.001$ ). Temperature was negatively related to the movement of monitored snakes ( $Z = -2.897$ ,  $df = 7$ ,  $P = 0.003$ ); however, humidity was not related to *B. jararacussu* activity patterns ( $Z = -1.414$ ,  $df = 7$ ,  $P = 0.157$ ; Fig. 4).

In January 2020, we found three gravid females (ID #15–17) in the same area using forest edges and a clearing in an abandoned banana plantation. They remained in the same area during their gestation and were found resting, curled up, in the same place for up to five consecutive days. The females were frequently seen basking during the first hours of the morning (Fig. 1). Monitoring of gravid females varied from 56 to 70 d. The females gave birth at the end of March to 43–55 offspring (Fig. 1). The neonates had a mean mass of



**FIGURE 3.** Home range area of 14 *Jararacussu* (*Bothrops jararacussu*) individuals monitored at the Projeto Dacnis private reserve in Ubatuba municipality, São Paulo state, Brazil, 2017–2020.

$9.9 \pm 1.67$  g;  $SVL = 219.4 \pm 12.05$  mm;  $TaL = 36.9 \pm 4.03$  mm; and  $TL = 256.1 \pm 13.81$  mm (Table 2). The largest female had the fewest, but largest and heaviest, offspring (Table 2). Females 15 and 17 gave birth to undeveloped neonates ( $n = 2$  and  $3$ , respectively). After parturition, females lost approximately 48.9% of their body mass compared to their initial mass.

### DISCUSSION

We observed *B. jararacussu* mostly in densely forested habitats with high canopy cover and low to

moderate incidence of sunlight, which agrees with Rocha et al. (2014). These habitats have a great variety of microhabitats and structures that favor prey availability (Vanzolini 1948; Valdujo et al. 2002). *Bothrops jararacussu* uses ambush as its main foraging strategy (Hartmann et al. 2003), and viperids that use this strategy commonly select ambush sites within fallen tree trunks, which were plentiful in forested habitats at our study site (Reinert et al. 1984; Theodoratus and Chiszar 2000; Brito 2003). *Bothrops jararacussu* individuals, however, were also found at forest edges and even in open areas (Hartmann et al. 2009; this

**TABLE 2.** Gravid *Jararacussu* (*Bothrops jararacussu*) females (ID = identification number) and their mass (g), litter size, neonate mass (g), and neonate snout-vent length (SVL), tail length (TL), and total length (TTL). These females were monitored with thread bobbins at the Projeto Dacnis private reserve, in Ubatuba municipality, São Paulo state, Brazil, 2017–2020. Values correspond to mean  $\pm$  standard deviation (range). Undeveloped neonates were not included in the litter size.

ID	Mass before parturition (g)	Mass after parturition (g)	Litter size	Mass (g)	SVL (mm)	TL (mm)	TTL (mm)
15	1800	940	55	$9.5 \pm 0.49$ (8.4–10.6)	$212.8 \pm 5.56$ (199–225)	$34.9 \pm 3.31$ (29–42)	$247.6 \pm 5.49$ (238–259)
16	1500	780	46	$8.5 \pm 0.76$ (6.4–10)	$213.7 \pm 9.44$ (192–229)	$36.4 \pm 3.32$ (30–43)	$249.8 \pm 9.05$ (224–266)
17	2000	980	43	$12.0 \pm 0.61$ (10.7–13.1)	$233.7 \pm 7.51$ (216–250)	$39.9 \pm 3.81$ (32–46)	$273.7 \pm 7.95$ (249–289)

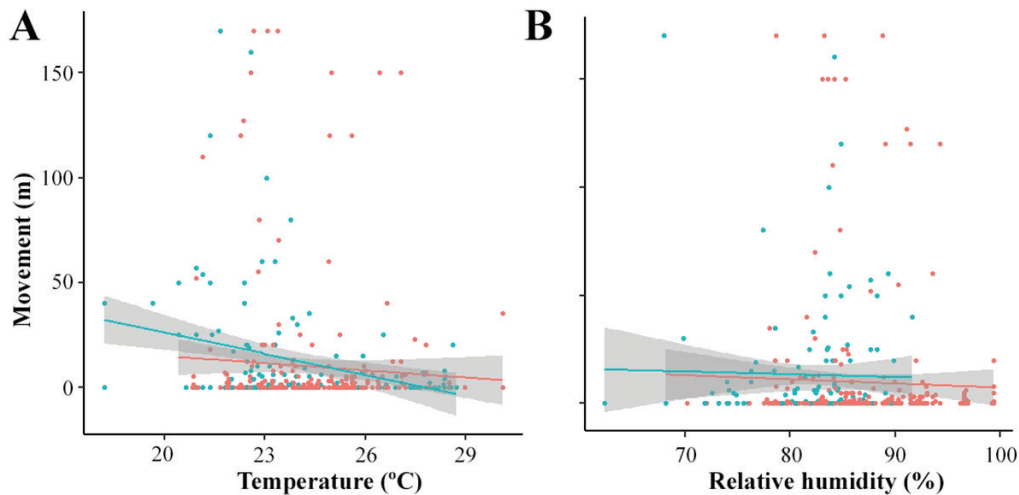


FIGURE 4. Zero-inflated Generalized Linear Model of the movement patterns of *Jararacussu* (*Bothrops jararacussu*) females (pink points) and males (blue points) monitored at the Projeto Dacnis private reserve, Ubatuba municipality, São Paulo state, Brazil, 2017–2020.

study). The advantages and disadvantages in the use of these habitats are not yet completely understood (Rocha et al. 2014).

Our results indicate that *B. jararacussu* females move less frequently than males and may remain in the same place for long periods, similar to the habits of the pit viper Jararaca (*Bothrops jararaca*) from southeast Brazil (Sazima 1988, 1992). Still, when they do move, *B. jararacussu* females travel longer distances compared to males. Several Neotropical viperids have small home ranges (< 0.05 ha) and may remain in the same area for months (e.g., Nogueira et al. 2003; Tozetti et al. 2009). This pattern is commonly associated with high food availability (Fujisaki et al. 2014; Walters et al. 2016; Smaniotto et al. 2020). Individual home range areas vary, however, during the reproductive season, when males roam more in search of females (Viitanen 1967; Moser et al. 1984; Brito 2003).

There was a negative relationship between temperature and movement of *B. jararacussu*, where they move less as the temperature increases. Humidity does not seem to affect their movement. In a forest environment, temperature varies between shaded and sunny areas (Barros et al. 2020), and reptiles adopt behavioral strategies to optimize thermoregulation (Cowles and Bogert 1944; Huey 1974; Barros et al. 2020). *Bothrops jararacussu* may adopt behavioral strategies for thermoregulation on colder days, which would explain the movement pattern we found. Still, reptile movements cannot be attributed to one specific abiotic condition alone (Price-Rees et al. 2014): snake movements are strongly influenced by various abiotic and biotic factors such as food availability, shelter, reproductive behaviors, temperature, and rainfall (Madsen and Shine 1996; Duvall and Schuett 1997; Bernarde and Abe 2006).

The small home range of the three monitored gravid females, in comparison to males and non-gravid females, may be explained by the reduction of their motor performance (Bauwens and Thoen 1981; Garland and Else 1987). Gravid females may share the same area, here called the maternity area, when it has advantageous environmental features for the development of offspring (higher solar incidence and shelter availability), as recorded for other vipers (Greene et al. 2002). The advantage for gravid females using such habitats is probably related to their need to thermoregulate for the developing brood (Sazima 1988, 1992; Rivas 2015; De La Quintana et al. 2017). Silva et al. (2020) suggested that larger *B. jararacussu* females tend to have larger broods than smaller females, but we did not find this. The largest of our monitored females had the smallest brood ( $n = 43$ ), but the average mass of the neonates was highest.

In summary, we found that *B. jararacussu* use dense forests more frequently than forest edges and open areas. Adults and juveniles remain on the ground most of the time, although some juveniles may also use vegetation. Individual home ranges are relatively small for such a large snake (e.g., Secor 1994; Sasa et al. 2009; Smaniotto et al. 2020). Females move less frequently than males and may remain in the same place for long periods, but travel long distances when they move. Air temperature plays an important role in movements of this snake. Gravid females in our study shared a maternity area during the entire observation period and gave birth at the end of March. Our research adds valuable information to the understanding of the natural history of a large and difficult to study pit viper, filling knowledge gaps and providing useful information for the management and conservation of this stately snake.

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#### LITERATURE CITED

- Abramoff, M.D., P.J. Magalhaes, S.J. Ram. 2004. Image Processing with ImageJ. *Biophotonics International* 11:36–42.
- Alvares, C.A., J.L. Stape, P.C. Sentelhas, J.L.M. Gonçalves, and G. Sparovek. 2013. Köppen's climate classification map for Brazil. *Meteorologische Zeitschrift* 22:711–728.
- Averill-Murray, R.C., C.H. Fleming, and J.D. Riedle. 2020. Reptile home ranges revisited: a case study of space use of Sonoran Desert Tortoises (*Gopherus morafkai*). *Herpetological Conservation and Biology* 15:253–271.
- Barros, F.C. 2020. Fisiologia térmica em répteis não-avianos. Pp. 177–201 *In: Fisiologia Térmica de Vertebrados*. Bicego, L.H., and K.C. Gargaglioni (Eds.). Cultura Acadêmica, São Paulo, São Paulo, Brazil.
- Bauwens, D., and C. Thoen. 1981. Escape tactics and vulnerability to predation associated with reproduction in the lizard *Lacerta vivipara*. *Journal of Animal Ecology* 50:733–743.
- Bernarde, P.S., and A.S. Abe. 2006. A snake community at Espigão do Oeste, Rondônia, southwestern Amazon, Brazil. *South American Journal of Herpetology* 1:102–113.
- Brito, J.C. 2003. Seasonal variation in movements, home range, and habitat use by male *Vipera latastei* in northern Portugal. *Journal of Herpetology* 37:155–160.
- Calenge, C. 2006. The package “adehabitat” for the R software: a tool for the analysis of space and habitat use by animals. *Ecological Modelling* 197:516–519.
- Campbell, J.A., and W.W. Lamar. 2004. *The Venomous Reptiles of the Western Hemisphere*. Comstock Publishing Associates, Ithaca, New York, USA.
- Cowles, R.B., and C.M. Bogert. 1944. A preliminary study of the thermal requirements of desert reptiles. *Bulletin of the American Museum of Natural History* 83:261–296.
- De La Quintana, P., J.A. Rivas, F. Valdivia, and L.F. Pacheco. 2017. *Eunectes murinus* (Green anaconda): dry season home range. *Herpetological Review* 49:546–547.
- Do Amaral, A. 1924. On the biological differentiation of the neotropical species of snakes, *Bothrops atrox* (Linné, 1758), *B. jararaca* (Wied, 1824) and *B. jararacussu* Lacerda, 1884. *American Journal of Tropical Medicine and Hygiene* 1:447–452.
- Duvall, D., and G.W. Schuett. 1997. Straight-line movement and competitive mate searching in Prairie Rattlesnakes, *Crotalus viridis viridis*. *Animal Behaviour* 54:329–334.
- Fujisaki, I., K.M. Hart, F.J. Mazzotti, M.S. Cherkiss, A.R. Sartain, B.M. Jeffery, and M. Denton. 2014. Home range and movements of American Alligators (*Alligator mississippiensis*) in an estuary habitat. *Animal Biotelemetry* 2:1–10.
- Garland, T., and P.L. Else. 1987. Seasonal, sexual, and individual variation in endurance and activity metabolism in lizards. *American Journal of Physiology - Regulatory, Integrative and Comparative Physiology* 252:439–449.
- Greene, H.W. 1993. What's good about good natural history? *Herpetological Natural History* 1:3.
- Greene, H.W., and M.A. Santana. 1983. Field studies of hunting behaviour by bushmasters. *American Zoologist* 23:897.
- Greene, H.W., P.G. May, D.L. Hardy Sr, J.M. Scituro, and T.M. Farrell. 2002. Parental behavior by vipers. Pp. 179–205 *In Biology of the Vipers*. Schuett, G.W., M. Höggren, M.E. Douglas, and H.W. Greene (Eds.). Eagle Mountain Publishing, Eagle Mountain, Utah, USA.
- Gregory, P.T., J.M. Macartney, and K.W. Larsen. 1987. Spatial patterns and movements. Pp. 366–395 *In Snakes: Ecology and Evolutionary Biology*. Seigel, R.A., J.T. Collins, and S.S. Novak (Eds.). Blackburn Press, Caldwell, New Jersey, USA.
- Hartmann, P.A., M.T. Hartmann, and L.O.M. Giasson. 2003. Habitat use and feeding in juveniles of *Bothrops jararaca* (Serpentes, Viperidae) in the Atlantic Forest of southeastern Brazil. *Phyllomedusa* 2:35–41.
- Hartmann, P.A., M.T. Hartmann, and M. Martins. 2009. Ecologia e história natural de uma taxocenose de serpentes no Núcleo Santa Virgínia do Parque Estadual da Serra do Mar, no sudeste do Brasil. *Biota Neotropica* 9:173–184.
- Hothorn, T., A. Zeileis, R.W. Farebrother, C. Cummins, G. Millo, D. Mitchell, and M.A. Zeileis. 2015. Package ‘lmtest.’ Testing linear regression models. R package version 0.9-38. <https://cran.r-project.org/web/packages/lmtest/lmtest>.
- Huey, R.B. 1974. Behavioral thermoregulation in lizards: importance of associated costs. *Science* 184:1001–1003.
- Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio). 2018. *Livro Vermelho da Fauna Brasileira Ameaçada de Extinção, Volume 1, 1st Edition*. ICMBio, Brasília, Distrito Federal, Brazil.
- Kays, R., M.C. Crofoot, W. Jetz, and M. Wikelski. 2015. Terrestrial animal tracking as an eye on life and



- planet. *Science* 348:6240.
- Madsen, T., and R. Shine. 1996. Seasonal migration of predators and prey: a study of pythons and rats in tropical Australia. *Ecology* 77:149–156.
- Marques, O.A.V., and I. Sazima. 2004. História natural dos répteis da Estação Ecológica Juréia-Itatins. Pp. 257–277 *In* Estação Ecológica Juréia-Itatins: Ambiente Físico, Flora e Fauna. Marques, O.A.V., and W. Duleba (Eds.). Holos, Ribeirão Preto, São Paulo, Brazil.
- Martins, M., O. Marques, and I. Sazima. 2002. Ecological and phylogenetic correlates of feeding habits in Neotropical pitvipers of the genus *Bothrops*. Pp. 307–328 *In* *Biology of the Vipers*. Gordon, W., M. Hoggren, M.E. Douglas, and H. Greene (Eds.). Eagle Mountain Publishing, Eagle Mountain, Utah, USA.
- Michaels, C.J., B.F. Gini, and R.F. Preziosi. 2014. The importance of natural history and species-specific approaches in amphibian ex-situ conservation. *Herpetological Journal* 24:135–145.
- Milani, R., Jr., M.T. Jorge, F.P. de Campos, F.P. Martins, A. Bouso, J.L. Cardoso, L.A. Ribeiro, H.W. Fan, F.O. França, and I.S. Sano-Martins, et al. 1997. Snake bites by the Jararacuçu (*Bothrops jararacussu*): clinicopathological studies of 29 proven cases in São Paulo State, Brazil. *Quarterly Journal of Medicine* 90:323–334.
- Moser, A., C. Graber, and T.A. Freyvogel. 1984. Observations sur l'ethologie et l'evolution d'une population de *Vipera aspis* (L.) au nord du Jura Suisse. *Amphibia-Reptilia* 5:373–393.
- Nogueira, C., R.J. Sawaya, and M. Martins. 2003. Ecology of the pitviper, *Bothrops moojeni*, in the Brazilian Cerrado. *Journal of Herpetology* 37:653–659.
- Nogueira, C.C., A.J.S. Argôlo, V. Arzamendia, J.A. Azevedo, F.E. Barbo, R.S. Bérnils, B.E. Bolochio, M. Martins, M.B. Godinho., H. Braz, et al. 2019. Atlas of Brazilian snakes: verified point-locality maps to mitigate the Wallacean Shortfall in a megadiverse snake fauna. *South American Journal of Herpetology* 14:1–274.
- Oliveira, M.E., and M. Martins. 2001. When and where to find a pitviper: activity patterns and habitat use of the Lancehead, *Bothrops atrox*, in central Amazonia, Brazil. *Herpetological Natural History* 8:101–110.
- Olson, D.M., E. Dinerstein, E.D. Wikramanayake, N.D. Burgess, G.V.N. Powell, E.C. Underwood, and K.R. Kassem. 2001. Terrestrial ecoregions of the world: a new map of life on Earth. A new global map of terrestrial ecoregions provides an innovative tool for conserving biodiversity. *BioScience* 51:933–938.
- Price-Rees, S.J., T. Lindström, G.P. Brown, and R. Shine. 2014. The effects of weather conditions on dispersal behaviour of free-ranging lizards (Tiliqua, Scincidae) in tropical Australia. *Functional Ecology* 28:440–449.
- R Core Team. 2020. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org>.
- Raffel, T.R., P.J. Michel, E.W. Sites, and J.R. Rohr. 2010. What drives chytrid infections in newt populations? Associations with substrate, temperature, and shade. *EcoHealth* 7:526–536.
- Raffel, T.R., J.M. Romansic, N.T. Halstead, T.A. McMahon, M.D. Venesky, and J.R. Rohr. 2013. Disease and thermal acclimation in a more variable and unpredictable climate. *Nature Climate Change* 3:146–151.
- Reinert, H.K., D. Cundall, and L.M. Bushar. 1984. Foraging behavior of the Timber Rattlesnake, *Crotalus horridus*. *Copeia* 1984:976–981.
- Rivas, J.A. 2015. Natural History of the Green Anaconda: With Emphasis on Its Reproductive Biology. Create Space Independent Publishing Platform, North Charleston, South Carolina, USA.
- Rocha, M.C., P.A. Hartmann, G.R. Winck, and S.Z. Cechin. 2014. Seasonal, daily activity, and habitat use by three sympatric pit vipers (Serpentes, Viperidae) from southern Brazil. *Anais da Academia Brasileira de Ciência* 86:695–706.
- Rolim, G.D.S., M.B.P.D. Camargo, D.G. Lania, and J.F.L.D. Moraes. 2007. Classificação climática de Köppen e de Thornthwaite e sua aplicabilidade na determinação de zonas agroclimáticas para o estado de São Paulo. *Bragantia* 66:711–720.
- Sasa, M., D.K. Wasko, and W.W. Lamar. 2009. Natural history of the Terciopelo *Bothrops asper* (Serpentes: Viperidae) in Costa Rica. *Toxicon* 54:904–922.
- Sazima, I. 1988. Um estudo de biologia comportamental da jararaca, *Bothrops jararaca*, com uso de marcas naturais. *Memórias do Instituto Butantan* 50:83–99.
- Sazima, I. 1992. Natural history of the Jararaca Pitviper *Bothrops jararaca* in southeastern Brazil. Pp. 199–216 *In* *Biology of the Pitvipers*. Campbell, J.A., and E.D. Brodie (Eds.). Selva, Tyler, Texas, USA.
- Sazima, I. 2006. Theatrical frogs and crafty snakes: predation of visually-signalling frogs by tail-luring and ambushing pitvipers. *Aqua Journal of Ichthyology and Aquatic Biology* 11:117–124.
- Scott, N., N. Pelegrin, R. Montero, F. Kacolis, S. Carreira, P. Cacciali, and A. Giraud. 2019. *Bothrops jararacussu*. The IUCN Red List of Threatened Species 2019. International Union for Conservation of Nature. <http://www.iucn.org>.
- Secor, S.M. 1994. Ecological significance of movements and activity range for the sidewinder, *Crotalus cerastes*. *Copeia* 1994:631–645.

- Shonfield, J., W. King, and W.R. Koski. 2019. Habitat use and movement patterns of Butler's Gartersnake (*Thamnophis butleri*) in southwestern Ontario, Canada. *Herpetological Conservation and Biology* 14:680–690.
- Silva, K.M., H.B. Braz, K.N. Kasperoviczus, O.A. Marques, and S. M. Almeida-Santos. 2020. Reproduction in the pitviper *Bothrops jararacussu*: large females increase their reproductive output while small males increase their potential to mate. *Zoology* 142:1–56.
- Smaniotta, N.P., L.F. Moreira, J.A. Rivas, and C. Strüssmann. 2020. Home range size, movement, and habitat use of Yellow Anacondas (*Eunectes notaeus*). *Salamandra* 56:159–167.
- Theodoratus, D., and D. Chiszar. 2000. Habitat selection and prey odor in the foraging behavior of Western Rattlesnakes (*Crotalus viridis*). *Behaviour* 137:119–135.
- Tozetti, A.M., and M. Martins. 2007. A technique for external radio-transmitter attachment and the use of thread-bobbins for studying snake movements. *South American Journal of Herpetology* 2:184–190.
- Tozetti, A.M., and M. Martins. 2008. Habitat use by the South American Rattlesnake (*Crotalus durissus*) in southeastern Brazil. *Journal of Natural History* 42:1435–1444.
- Tozetti, A.M., V. Vettorazzo, and M. Martins. 2009. Short-term movements of the South American Rattlesnake (*Crotalus durissus*) in southeastern Brazil. *Brazilian Journal of Herpetology* 19:201–206.
- Újvari, B., and Z. Korsós. 2000. Use of radiotelemetry on snakes: a review. *Acta Zoologica Academiae Scientiarum Hungaricae* 46:115–146.
- Valdujo, P.H., C. Nogueira, and M. Martins. 2002. Ecology of *Bothrops neuwiedi pauloensis* (Serpentes: Viperidae: Crotalinae) in the Brazilian Cerrado. *Journal of Herpetology* 36:169–176.
- Van der Niet, T. 2020. Paucity of natural history data impedes phylogenetic analyses of pollinator-driven evolution. *New Phytologist* 229:1201–1205.
- Van Moorter, B., C.M. Rolandsen, M. Basille, and J.M. Gaillard. 2016. Movement is the glue connecting home ranges and habitat selection. *Journal of Animal Ecology* 85:21–31.
- Vanzolini, P.E. 1948. Notas sobre os ofídios e lagartos da Cachoeira de Emas, no município de Pirassununga, Estado de São Paulo. *Revista Brasileira de Biologia* 8:377–400.
- Viitanen, P. 1967. Hibernation and seasonal movements of the viper, *Vipera berus berus* (L.), in southern Finland. *Annales Zoologici Fennici* 4:472–546.
- Walters, T.M., F.J. Mazzotti, and H.C. Fitz. 2016. Habitat selection by the invasive species Burmese Python in southern Florida. *Journal of Herpetology* 50:50–56.
- Wenger, S.J., and M.C. Freeman. 2008. Estimating species occurrence, abundance, and detection probability using zero-inflated distributions. *Ecology* 89:2953–2959.
- Wickham, H. 2016. *ggplot2: Elegant Graphics for Data Analysis*. 2nd Edition. Springer, New York, New York, USA.
- Zuur, A.F., E.N. Ieno, N.J. Walker, A.A. Saveliev, and G.M. Smith. 2009. Zero-truncated and zero-inflated models for count data. Pp. 261–293 *In* *Mixed Effects Models and Extensions in Ecology with R*. Springer, New York, New York, USA.



**EDELICIO MUSCAT** is a Biologist, Researcher, and the Coordinator of the non-governmental organization Projeto Dacnis in Ubatuba and São Francisco Xavier, São Paulo, Brazil. He taught at university for 13 y, was a fauna/herpetology consultant for the United Nations, participated in the management plan for the Wildlife Refuge in the Archipelago of Alcatrazes (ICMbio), and for the past 10 y has been working with natural history and conservation of the Atlantic Forest. (Photographed by Elsie Rotenberg).



**RAFAEL COSTABILE MENEGUCCI** is a Biologist who graduated from the Universidade Federal de Alfenas, Minas Gerais, Brazil, and also is a nature photographer. He has been conducting research on the natural history of reptiles and amphibians in the Atlantic Forest biome since 2014. (Photographed by Rafael M. Tanaka).

## Herpetological Conservation and Biology



**RAFAEL MITSUO TANAKA** is a Biologist who graduated from the Universidade Federal de Alfenas, Minas Gerais, Brazil. He currently works as a nature photographer. (Photographed by Rafael C. Menegucci).



**ELSIE ROTENBERG** holds Bachelor's degrees in Veterinary Medicine and Journalism from Universidade de São Paulo (USP), São Paulo, Brazil. She is the president of Projeto Dacnis Reserve, a keen birder and naturalist, and a translator. (Photographed by Xavier Muñoz).



**MATHEUS DE TOLEDO MOROTI** is a Biologist and Researcher at the Projeto Dacnis non-governmental organization. He has a Master's degree in Animal Biology and is a Ph.D. student in Ecology and Conservation at the Universidade Federal de Mato Grosso do Sul, Mato Grosso do Sul, Brazil. He carries out research on natural history, community ecology, and biogeography. (Photographed by Mariana Pedrozo).



**MARIANA PEDROZO** is a Biologist and a Researcher at the Projeto Dacnis non-governmental organization, where she also works with environmental education. She earned her Master's degree in Animal Biology at Universidade Federal de Mato Grosso do Sul, Mato Grosso do Sul, Brazil. Her passions are working with the taxonomy and phylogeography of amphibians and in environmental education. (Photographed by Matheus de Toledo Moroti).



**IVAN SAZIMA** is a Research Associate at the Zoology Museum, Universidade Estadual de Campinas (UNICAMP), São Paulo, Brazil. He has a B.Sc., M.Sc., and D.Sc. from the University of São Paulo, Brazil. His research interest is vertebrate natural history (mostly associations between organisms, feeding behaviors, and urban environment). Before his retirement, he taught Vertebrate Zoology and Animal Behavior at undergraduate and graduate levels and advised graduate students at UNICAMP. Ivan has published his research in Brazilian and foreign journals as well as books and book chapters. (Photographed by Giulia D'Angelo).

**APPENDIX 1.** Data for each Jararacussu (*Bothrops jararacussu*) individual monitored: identification (ID) number, month, year, and method (RT = Radio telemetry, TB = Thread bobbin) at the Projeto Dacnis, municipality of Ubatuba, state of São Paulo, Brazil, 2017–2020. We did not estimate home range and movement for individuals we found fewer than five times. Results for each sex (M = Male, F = Female) with mean  $\pm$  standard deviation. An asterisk (\*) indicates a gravid female.

ID	Month	Year	Method	Total Length (mm)	Body mass (g)	Sex	Number of locations	Average distance traveled (m)	Total distance traveled (m)	Home range (ha)
1	April–May	2017	TB	1,040	1,210	F	34	11.9	406	0.14
2	May	2017	TB	870	170	M	18	8.72	157	0.21
3	September	2017	TB	-	-	M	5	38.6	193	0.5
4	September	2017	TB	1,380	1,620	F	9	40.0	360	0.09
5	September	2017	TB	1,050	395	M	5	63.4	317	0.01
6	September–October	2017	TB	910	210	M	43	3.95	170	0.19
7	August–September	2018	TB	1,050	325	M	15	18.5	278	0.01
8	August–September	2018	TB	950	310	M	25	23.5	588	0.6
9	September	2018	TB	1,370	1,275	F	14	20.9	293	0.6
10	October–November	2018	TB	1,460	1,795	F	38	13.2	500	0.05
11	October	2018	TB	900	400	M	3	-	-	-
12	March–May	2019	TB	940	470	M	35	4.31	151	0.03
13	November	2019	RT/TB	750	660	M	4	5.25	21	-
14	December	2019	RT/TB	820	310	F	3	-	-	-
15*	January–March	2020	RT/TB	1,360	1,800	F	63	6.46	407	0.04
16*	January–March	2020	RT/TB	1,100	1,500	F	69	7.27	502	0.46
17*	January–March	2020	TB	1,440	2,000	F	56	7.26	407	0.32
Male	-	-	-	927.5 $\pm$ 97.50	367.5 $\pm$ 154.37	9	17	20.8 $\pm$ 21.00	234.4 $\pm$ 168.23	0.22 $\pm$ 0.241
Female	-	-	-	1,246.3 $\pm$ 231.45	1,438.8 $\pm$ 529.45	8	35.8	15.3 $\pm$ 12.00	410.7 $\pm$ 73.92	0.24 $\pm$ 0.221