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ANNUAL AND DAILY ACTIVITY PATTERNS OF THE SNAIL-EATING SNAKE *DIPSAS BUCEPHALA* (SERPENTES, DIPSADIDAE) IN SOUTHEASTERN BRAZIL

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Abstract. Annual and daily activity patterns of *Dipsas bucephala* from southeastern Brazil were characterized respectively from the Instituto Butantan (São Paulo, Brazil) collection data over a 21-year period and from individuals video-monitored in laboratory continuously. *D. bucephala* was more frequently collected in summer (second half of the rainy and warm season) with a peak in March, which indicates a seasonal and unimodal activity pattern. Temperature and precipitation seems to explain only a part of this variation. Prey availability throughout the year and reproductive events are other factors likely to shape this pattern. Higher activity in the summer would be synchronic to a higher mollusk abundance. Gravid females were found only during spring. Thus, the peak of activity in late summer may be related to an increase in male activity due to mate search. Daily activity occurred during the nocturnal period (between 17:30 and 06:00 h). Peaks were unimodal, registered between 19:00 and 02:00 h, and were longer than those observed in other snakes. This extensive activity period may be related to an intensive foraging activity in malacophagous snakes. Moreover, peaks of daily activity were higher when food was available. The lack of chemical stimulus (mucus trail) may explain the lower peak of activity in experiments without food.

Key-Words. Dipsadinae; activity patterns; climate; food availability; reproductive activity.

Introduction

Activity patterns are important ecological aspects of an organism since they have profound implications for its survival and reproduction. Animals move spatially and temporally for several different purposes such as feeding, mating, thermoregulation, and predator avoidance (Gibbons and Semlitsch, 1987; Giné *et al.,* 2012). Nevertheless, several factors may constrain organismal activity patterns. In snakes, abiotic and biotic factors can play a significant role in determining activity patterns (Gibbons and Semlitsch, 1987; Sun *et al.,* 2001). Among the abiotic factors, temperature is judged as the major factor influencing activity since it directly affects snake metabolism (Lillywhite, 1987). In fact, some species from temperate areas can even hibernate during periods of extreme low temperatures (Gregory, 1982). Biotic factors like food availability, predation, and reproduction may correlate with climatic variables resulting in variation in snake activity (Gibbons and Semlitsch, 1987; Mushinsky, 1987; Maciel *et al.,* 2003).

In snakes from temperate areas, annual activity patterns are classified as unimodal, in which a single peak occurs between the late spring and late summer, or bimodal, in which two peaks of activity occur, one in spring and another in summer (Gibbons and Semlitsch, 1987). Among tropical snakes, despite the increasing interest in this issue (*e.g.,* Marques *et al.,* 2001, 2006; Parpinelli and Marques, 2008), outlining any clear activity pattern still remains a difficult task.

Diel cycles are aspects poorly understood in tropical snakes. Neotropical snakes are generally difficult to find in suitable amounts, which makes their daily activity frequently determined by time of encounter with individuals in nature (*e.g.,* Martins and Oliveira, 1998; Hartmann *et al.,* 2009). An alternative approach is to characterize daily activity by using video-monitored specimens in laboratory (*e.g.,* Parpinelli and Marques, 2008; Stuginski *et al.,* 2012). This type of study allows us to recognize the extent of daily activity and identify peaks of activity.

The genus *Dipsas* is widely distributed in the Neotropical region where it is highly diversified (Peters, 1960; Harvey, 2008; Harvey and Embert, 2008). Despite this fact, natural history information is available for only a few species (*e.g.,* Zug *et al.,* 1979; Hartmann *et al.,* 2002; Alves *et al.,* 2005). Available data suggest that species of *Dipsas* show nocturnal and semiarboreal habits and diet specialized in snails and slugs (Sazima, 1989; Martins and Oliveira, 1998; Marques *et al.,* 2004; Bernarde and Abe, 2010). In the present study, we characterized annual and daily activity of the snail-eating snake, *Dipsas bucephala,* from southeastern Brazil and explored the possible influences of climatic variables, reproduction, and prey availability on its activity pattern.

Material and Methods

Annual activity

We inferred annual activity pattern from the number of individuals collected and brought monthly to Laboratório de Herpetologia of Instituto Butantan (IBSP), São Paulo, State of São Paulo, Brazil, mostly by laymen (see Marques *et al.,* 2001, 2006). We used snakes brought between January 1990 and December 2010, totaling a 21 year-period. In the receiving of IBSP, the individual were classified as adult or juvenile. In our study, we included only adult individuals once the juvenile category includes both newborn and young individuals, what could result in bias due to recruitment. For the adults, sex was not determined due to lack of data in register books and the impossibility to examine the animals in the herpetological collection of Instituto Butantan that was almost completely lost during a recent fire (see Franco, 2012). Detailed information and discussion about the method used can be found elsewhere (Marques *et al.,* 2001). Data for newly-hatched individuals were obtained from the literature (Braz and Almeida-Santos, 2008) and from hatchings of eggs laid on 17 October 2009 by a gravid-captured female.

Daily activity

Daily activity was inferred by continuously filming three individuals of *D. bucephala* (two females and one male). Snakes were kept individually in terraria (50 × 25 × 35 cm; length × width × height) with water *ad libitum.* Soil covered with leaves and several branches were used as substrate. Terraria were housed in a room with natural photoperiod and kept moist by spraying water daily. Average room temperature was 23.7 ± 1.1°C. Snakes were monitored 24 hours per day during 20 days, being 10 days with and 10 days without food available. Food was offered daily and consisted of snails (*Bradybaena similaris*) in amounts of 2 to 6 according to its availability. Filming were performed using a closed-circuit television system composed by the program Geo Vision, one microcamera and an infrared LED device for nocturnal filming (Parpinelli and Marques, 2008). Monitoring occurred between February and early April 2010 (mostly during summer).

Climatic data

Values of climatic variables used were calculated after combining average values for each collection locality (n = 50) of all *Dipsas bucephala* individuals used to determine annual activity pattern. First, all 50 collection localities (latitudes and longitudes) were plotted on a map using the software DIVA-GIS version 7.1.7.2 (Hijmans *et al.,* 2001). Then, climatic variables values (averages of monthly minimum temperature, maximum temperature, and precipitation) were extracted for each collection locality and the average values for each climatic variable were calculated. Thus, we used climatic data only for the localities in which individuals were collected instead of using a general climatogram for a specific location within the species occurrence area (*e.g.,* Marques *et al.,* 2006). Climate data set were from Worldclim (version 1.3) and a spatial resolution of 2.5 minutes (*ca.* 5 km) was adopted.

Data analysis

Annual activity was analyzed by comparing the number of snakes collected per season using a chi-square test. Seasons were determined as summer (January to March), autumn (April to June), winter (July to September) and spring (October to December). The influence of minimum and maximum temperatures and precipitation in annual activity was examined using a multiple regression analysis (using monthly data).

Daily activity pattern was described and evaluated graphically (Parpinelli and Marques, 2008). We defined activity as the occurrence of the individuals' movement within the terraria. Days were divided into 48 half-hour intervals. To facilitate the observation sessions films were partitioned into smaller videos with 5-min intervals (resulting in six videos per half-hour). Each 5-min video was then examined and we recorded whether individuals were inactive (ranked as 0) or active (ranked as 1). We assigned individuals as active for each half-hour interval when active individuals were registered in at least four out of six 5-min videos examined. For each individual, we calculated the percent of activity and inactivity occurrence for all 48 half-hour intervals throughout the ten days of observations. Then, we calculated the average values for activity and inactivity. Activity peaks were defined as the number of observations of active snakes equal to or exceeding 80%.

Values are presented throughout the text as mean ± one standard deviation and the significance level of all statistical tests was $\alpha = 0.05$.

Results

Annual activity

During the period analyzed (21 years), 114 adult specimens of *Dipsas bucephala* from Southeastern Brazil were brought to Instituto Butantan. Adult individuals were registered in all months of the year (Fig. 1). However, *Dipsas bucephala* was more frequently collected in summer ($\chi^2 = 40.17$; df = 3; $P < 0.001$; n = 57), with a unimodal peak in March (Fig. 1). In early autumn (April), a decrease in the number of individuals captured was observed, whereas a slightly increase occurred gradually along the spring (Fig. 1). However, the number of individuals collected in spring ($n = 24$), autumn ($n = 20$), and winter ($n = 13$) was similar ($\chi^2 = 3.26$; df = 2; $P = 0.20$). Multiple linear regression revealed that all climatic variables (average monthly minimum temperature, maximum temperature, and precipitation) together explained 63% of the variation ($r^2 = 0.63$; $F = 4.49$; $P = 0.04$) in the number of adult individuals collected throughout the year. None of the variables contributed significantly more than the others for the observed variation in the number of captures ($P > 0.25$ for all variables). Newly-hatched individuals were observed from hatching of two clutches, one in February and one in April.

Daily activity

All individuals monitored showed activity in all filming days. Activity was recorded in late afternoon (after 17:30 h) and during the night (18:00 to 06:00 h). During the diurnal period only one record was taken with an individual feeding on a snail between 12:00 and 12:30 h. Activity in monitored individuals, in general, started at 18:33 ± 00:37 h (range = 17:30-20:30 h; $n = 60$) and finished at 03:20 ± 01:40 h (range = 00:00-06:00 h; $n = 59$). Individuals of *D. bucephala* showed a unimodal daily activity pattern with peaks between 18:30 and 02:30 h with food available (Fig. 2A) and 19:00 and 00:00 h without food available (Fig. 2B). We found no differences in the extent of daily activity according to food availability (Figs. 2A and B). Activity duration averaged 09:34 ± 00:22 h with food available and 08:01 ± 01:05 h without food. However, the extent of activity peak was longer (3 hours) with food (08:00 h) than without food (05:00 h).

Discussion

Temperature is a major factor influencing activity because it directly affects snake metabolism (Lillywhite, 1987). Annual activity of *Dipsas bucephala* was higher during warmer and wetter periods of the year (peak observed in late summer), being therefore defined as seasonal and unimodal. This pattern was also observed in the congeneric *D. albifrons* from southern Atlantic forest, though peak has occurred in the spring (Hartmann *et al.,* 2002). Nevertheless, in *D. neivai* and *D. catesbyi* from southeastern Bahia, Brazil, activity was relatively uniform throughout the year (Alves *et al.,* 2005). Unlike in southern and southeastern Atlantic forest, in southeastern Bahia there is not a clear defined dry/cold season and temperatures are higher and less variable, which could explain these differences. The annual activity pattern observed in *D. bucephala* (peak in rainy/hot season) has also been observed in several snake species from southeastern Brazil (Marques *et al.,* 2001; Parpinelli and Marques, 2008; Barbo *et al.,* 2011).

Despite its importance, climatic variables explained together only a part (~ 63%) of the variation in number of individuals collected throughout the year. Thus, other factors should be considered in order to explain the seasonal activity pattern of *D. bucephala.* Biotic factors as predation pressure, prey availability, and reproduction are among the most frequently invoked ones to explain this variation (Henderson *et al.,* 1978; Gibbons and Semlitsch, 1987; Marques *et al.,* 2001). All these factors may also vary seasonally. Predation pressure is difficult to evaluate in the present study because it would involve the survey of all potential predators of snakes (mammals, birds and reptiles) and their seasonal variation in population density in the study area.

Prey availability frequently shows seasonal fluctuations and it is likely to be correlated to climatic variables (Gibbons and Semlitsch, 1987). *Dipsas bucephala* is specialized in terrestrial gastropods (Sazima, 1989). The activity of these mollusks is directly dependent on humidity (Junqueira *et al.,* 2004) and presumably periods of higher abundance of mollusks are likely to occur in rainy season. Therefore, higher activity in rainy season (summer) of *D. bucephala* would be synchronized to the period of higher abundance of terrestrial gastropods (Junqueira *et al.,* 2004). However, two other malacophagous snakes from southeastern Brazil show patterns of seasonal

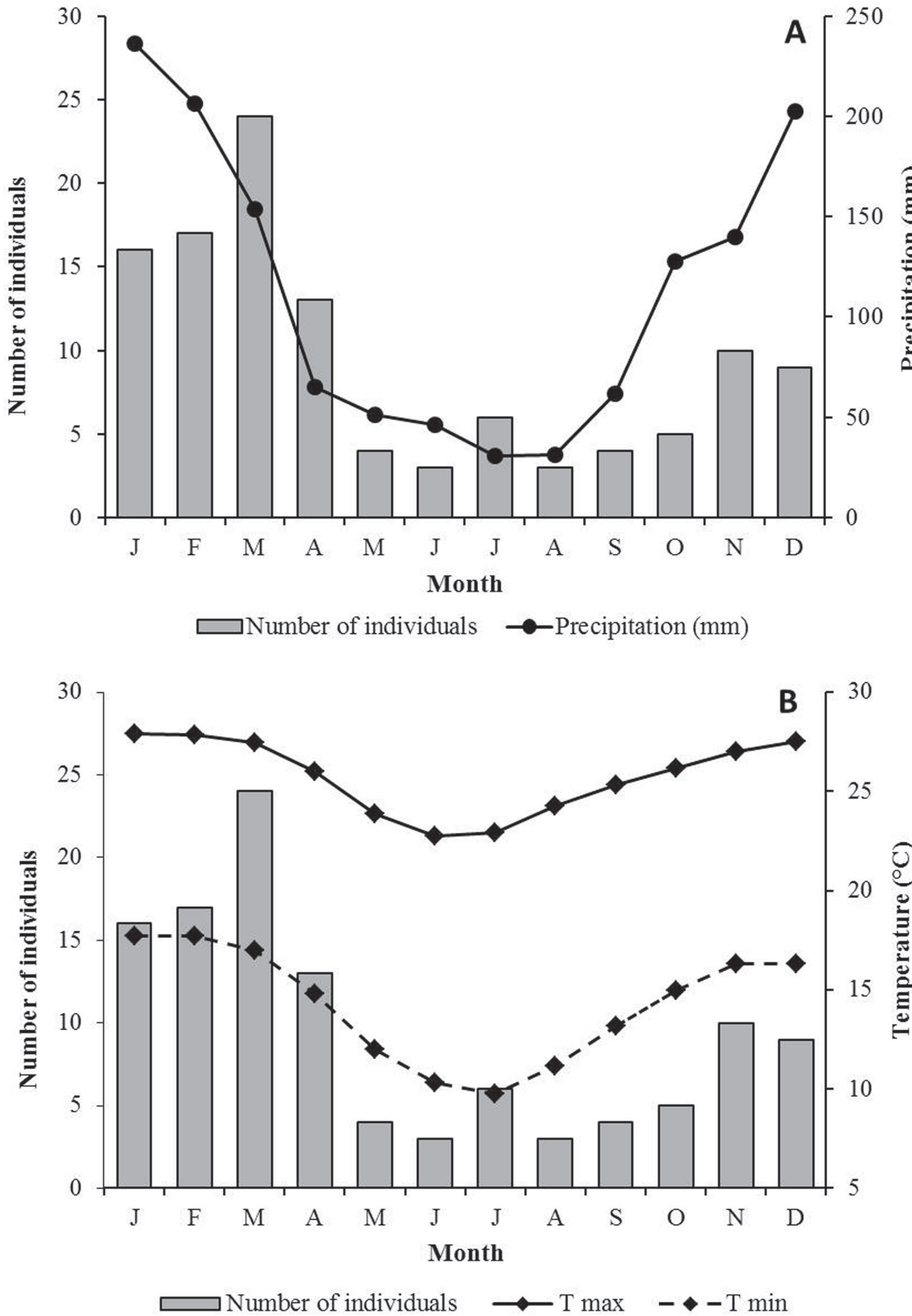

Figure 1. Seasonal variation in the number of *Dipsas bucephala* adults collected throughout the year and climatic data (A: precipitation and B: temperature; mean monthly values are shown) for localities where the specimens were collected. Number of individuals corresponds to specimens brought to Instituto Butantan by lay people between 1990 and 2010.

activity different from *D. bucephala,* weakening this argument. The dipsadine *Sibynomorphus neuwiedi* is more frequently collected during the dry season while the xenodontine *Tomodon dorsatus* is equally abundant in both seasons (Marques *et al.,* 2001). Studies quantifying slug and snail abundance throughout the year (by sampling both active and inactive individuals) would be of great value to test for correlation between prey abundance and malacophagous snake abundance.

Reproductive cycles directly influence the activity of snakes (Marques *et al.,* 2006). However, the ways in which reproductive cycles may affect activity patterns of snakes differ between sexes. Females are suggested to be more exposed and easily collected during vitellogenesis and gravidity/pregnancy periods due to their thermoregulatory necessity for embryo development (Shine, 1979; Gibbons and Semlitsch, 1987). Males may be more active during the mating season and thus may not be synchronized with the period of higher activity in females (Salomão and Almeida-Santos, 2002). Unfortunately, in our study we were unable to evaluate the intersexual differences in annual activity patterns. First, we could not access and determine sex of individuals. Second, detailed male and female reproductive cycles are unavailable for *D. bucephala.* Reproduction in the genus *Dipsas* is suggested to be seasonal in higher latitudes (Hartmann *et al.,* 2002; Marques and Sazima, 2004). The encounter of two gravid females of *D. bucephala* in October and in November seems to corroborate this idea, and suggests that gravidity and egg-laying occur in spring, during the first half of the rainy season (Braz and Almeida-Santos, 2008; present study).

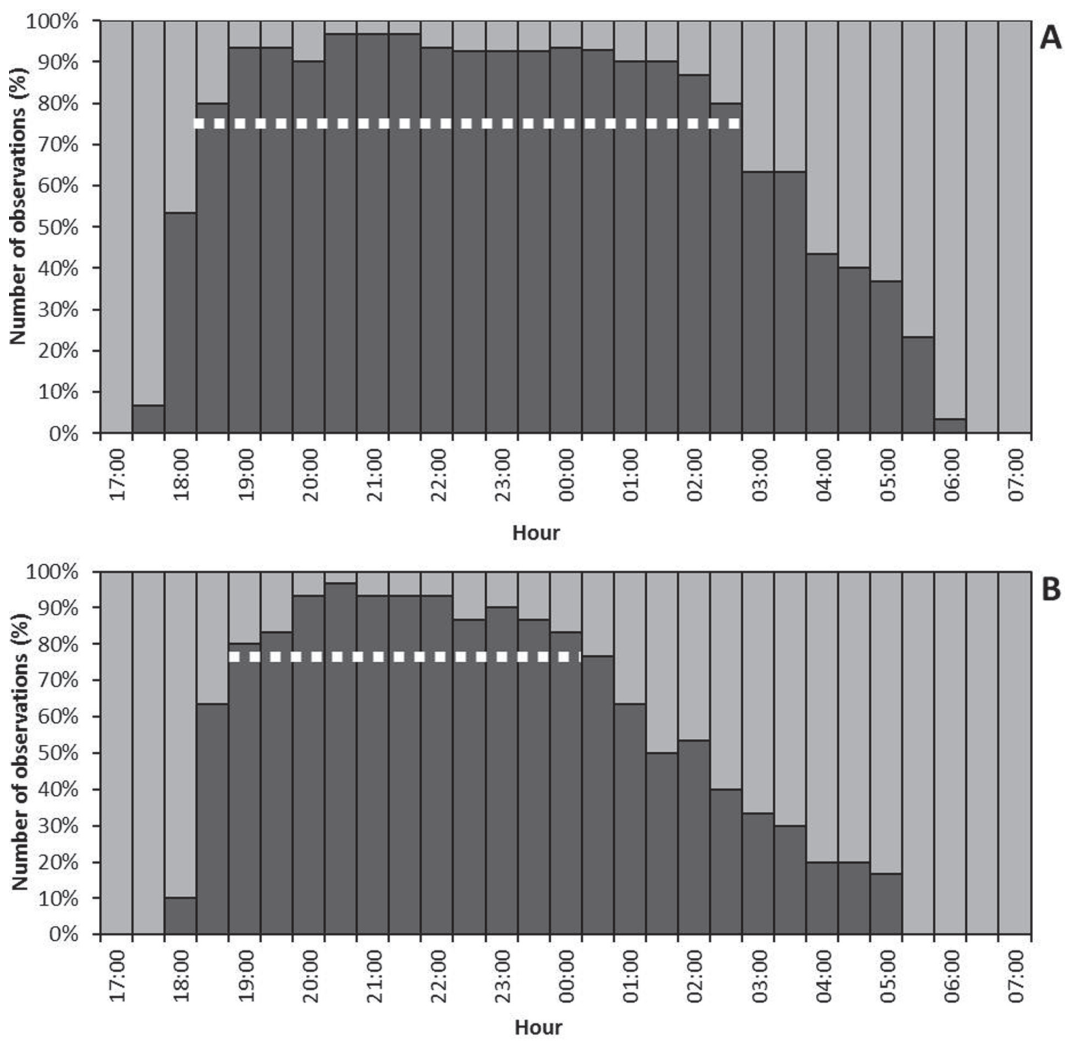

Figure 2. Daily activity of *Dipsas bucephala* based on video-monitored individuals in laboratory. (A): Snakes with food available. (B): Snakes without food available. Dashed line indicates the extent of activity peaks.

Despite this, the number of individuals collected in spring is similar to those collected in autumn and winter. Therefore, the activity peak of *D. bucephala* in the late summer (March) appears to be unrelated to female reproductive period (vitellogenesis and gravidity) but to an increase of activity of males in this period due to mate search. This is true for several other snakes from southeastern Brazil in which mating occurs in autumn (Almeida-Santos *et al.,* 2004, 2006). Studies on the reproductive cycles of male and female *D. bucephala* will allow testing this hypothesis (*e.g.,* Almeida-Santos *et al.,* 2006).

Nocturnal activity is also suggested for other congeneric species (Martins and Oliveira, 1998; Marques *et al.,* 2004) and therefore appears to be a conservative trait in the genus. Nevertheless, our data suggest that *D. bucephala* has an extensive range in daily activity when compared to other snake species studied (*e.g., Liotyphlops beui:* Parpinelli and Marques, 2008). Moreover, duration of activity peaks in *D. bucephala* appears to be longer than those of other nocturnal snakes such as *Liotyphlops beui* (Parpinelli and Marques, 2008) and *Bothrops moojeni* (Stuginski *et al.,* 2012).

This extensive activity and peak could reflect the food habits of the species. Mollusks are low caloric items as compared to vertebrate prey (Arnold, 1993). Thus, individuals of species of *Dipsas* may have to ingest a large number of food items to achieve its energetic demands. For instance, one *Dipsas indica* was found containing 11 slugs in its stomach (Bernarde and Abe, 2010). Consequently, ingestion of larger amounts of food items by malacophagous snakes may require an intensive and long foraging activity (Marques and Sazima, 2004). Malacophagous snakes forage actively and need to trail mucus tracks left by the mollusks to find them (Arnold, 1981; Sazima, 1989). This foraging behavior could explain the differences in the extent of the activity period and peak with and without food available. The shorter peaks of activity without food may reflect the lack of chemical stimulus of mucus trail left by the snails. These results also indicate that foraging activity may vary according to the prey density (Gibbons and Semlitsch, 1987).

Resumo

Os padrões de atividade anual e diária de *Dipsas bucephala* do sudeste do Brasil foram caracterizados respectivamente através de dados de exemplares trazidos ao Instituto Butantan (São Paulo, Brasil) em um período de 21 anos e de indivíduos continuamente monitorados em laboratório. *D. bucephala* foi mais abundante no verão (segunda metade da estação quente e chuvosa) com pico em março, indicando um padrão de atividade sazonal e unimodal. A temperatura e a precipitação parecem explicar somente uma parte dessa variação. A disponibilidade de presas durante o ano e os eventos reprodutivos são fatores que também podem influenciar esse padrão. A maior atividade no verão poderia estar sincronizada a uma maior abundância de moluscos nesse período. Fêmeas grávidas foram encontradas somente durante a primavera. Assim, o pico no final do verão pode estar relacionado a um aumento na atividade dos machos devido à procura por fêmeas para acasalar. A atividade diária ocorreu durante o período noturno (17:30 às 06:00 h). O pico foi unimodal (entre 19:00 e 02:00 h) e mais extenso do que o observado em outras serpentes. Isso pode estar relacionado à intensa atividade de forrageio nas serpentes malacófagas. Além disso, os picos de atividade diária foram maiores quando o alimento estava disponível. A ausência dos estímulos químicos (trilhas de muco dos moluscos) pode explicar a menor extensão do pico de atividade nos experimentos sem alimento.

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