

ACTIVITY PATTERNS IN CORALSNAKES, GENUS *MICRURUS* (ELAPIDAE), IN SOUTH AND SOUTHEASTERN BRAZIL

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ABSTRACT: Seasonal abundance of four species of *Micrurus* in Southern and Southeastern Brazil was inferred from collection data gathered during eight years at the Instituto Butantan, São Paulo, Brazil. For most species surface activity was significantly lower during drier and colder periods. Low temperature may considerably reduce snake metabolic rates and consequently constrain their activity. Year-round availability of prey may explain this activity pattern as well. Reproductive condition (extension of vitellogenesis and mating) may also influence activity patterns and explain some differences among species. One species (*M. corallinus*) shows vitellogenesis and mating restricted to the first half of the rainy season (spring), when activity peaked. Field data and activity patterns indicate that mating occurs from the end of the rainy season to the first half of the dry season (in autumn) in the other three species (*M. altirostris*, *M. frontalis*, *M. lemniscatus*), which belong to a single phylogenetic lineage, and this sets them apart of *M. corallinus*. The data obtained here indicate that differential reproductive strategies occur in two distinct phylogenetic lineages of *Micrurus*.

KEY WORDS: *Micrurus*, seasonal activity, climate, food availability, reproductive biology, phylogenetic lineages.

INTRODUCTION

Two distinct activity patterns can be recognized among temperate snakes: (1) – unimodal, with a single peak between the end of spring and the end of summer and (2) – bimodal, with one peak in spring and another in autumn (Gibbons and Semlitsch, 1987). However, it is still difficult to establish any general pattern among tropical snakes. Part of this difficulty lies in the scarcity of information for many species, but also in the large diversity of lineages and environments in tropical regions. In fact, several activity patterns can be recognized, even in a restricted region of South America (Marques *et al.*, 2000).

Several different factors can affect snake activity (*cf.* Gibbons and Semlitsch, 1987; Reinert, 1987). In general, the activity of species from temperate regions is directly affected by climatic variables, which can even lead some species to hibernate (Gregory, 1982). Temperature can be considered the main factor among the different climatic variables as it directly affects snake metabolic rates (Lillywhite, 1987).

In tropical regions, temperature is more homogeneous throughout the year; therefore, there is less direct influence of this variable on snake activity. However, rainfall is usually concentrated in certain periods of the year and other factors associated to climate (*e.g.*,

food availability, predation, and reproduction) must modulate the activity of tropical snakes (Henderson *et al.*, 1978; Marques *et al.*, 2000). Life stage may also determine the activity of a species (Shine, 1979), being responsible for activity peaks during different periods of the year.

The characterization of seasonal activity patterns in tropical snakes is generally difficult to access, mainly because many snakes are seldom found in nature (but see Oliveira and Martins, 2001). Actual activity patterns in such snakes could be studied by radio tracking, but this method is usually expensive and demand intensive fieldwork. On the other hand, data easily obtained from museum specimens can allow inferences on seasonal activity (*e.g.*, Marques, 1996; Marques and Puerto, 1998; Almeida-Santos and Salomão 2002). Several institutions, especially Instituto Butantan (IB), receive a great number of snakes throughout the year and this data allow inferences regarding seasonal activity (*e.g.*, data from the snake reception at IB allowed the description of the activity of several snakes from the Atlantic forest, *cf.* Marques *et al.*, 2000). The coral snake *Micrurus corallinus* from the Atlantic forest is relatively well known with regard to its seasonal activity, being very abundant and responsible for severe snakebites in Southeastern Brazil (Marques, 1996; Marques *et al.*, 2000). Three species of *Micrurus* from

Southeastern and Southern Brazil (*M. altirostris*, *M. frontalis* and *M. lemniscatus*) have been well sampled throughout many years, but their activity patterns remain completely unknown. These species occur in regions of the Atlantic forest with distinct climates. Moreover, these species have different reproductive strategies from that observed in *M. corallinus* (a subject of another article; O.A.V. Marques, S.M. Almeida-Santos e L. Pizzato, unpublished data). In the present study we explore the possible influences of climate and reproduction on the activity pattern of these coralsnakes from Southeastern and Southern Brazil.

MATERIAL AND METHODS

We studied three species of coralsnakes (*Micrurus corallinus*, *M. frontalis* and *M. lemniscatus*) that occur in Southeastern Brazil, as well as *M. altirostris*, from Southern Brazil. Among them, *M. corallinus* is the only one with black rings arranged in monads (Figure 1); the other three species have black rings arranged

in triads (Figure 1) and are more closely related (Slowinsky, 1995; Campbell and Lamar, 2004).

The climate of the region where each species occurs is described below. In general, tropical regions do not show marked seasons like temperate areas. There usually are two distinct seasons: a dry and generally colder season, and a rainy and generally warmer season. However, to facilitate comparisons of our results with those on snakes from temperate areas, we here deal with the four seasons that characterize temperate areas.

Micrurus corallinus occurs mainly in the Serra do Mar region, which is characterized by abundant rainfall throughout the year (Nimer, 1989). There is a distinct rainy season (spring and summer) in this region, with a higher incidence of rainfall and higher temperatures from September to April, and a “dry” season (autumn and winter), with less rainfall and lower temperatures from May to August (Figure 2). *Micrurus frontalis* and *M. lemniscatus* occur in seasonal forests and “cerrado” formations Southeastern Brazil (Silva and Sites, 1999; Campbell and Lamar, 2004), with a marked

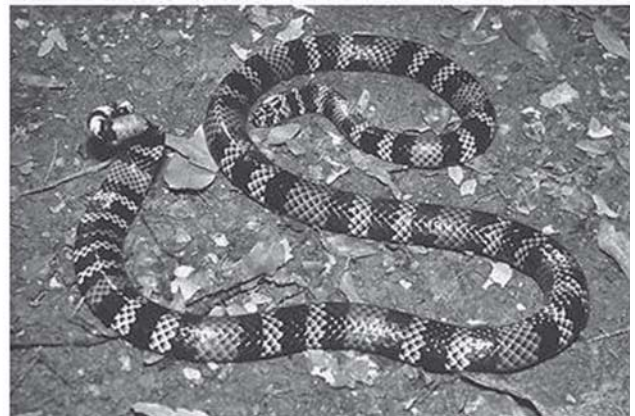
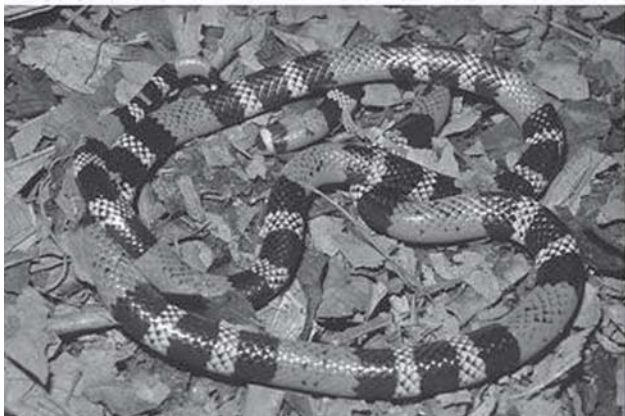
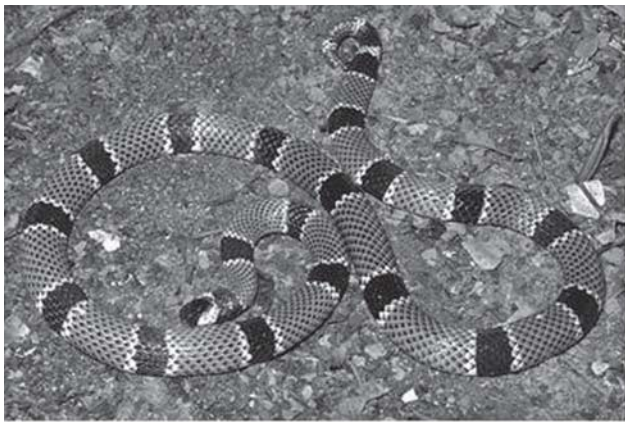


Figure 1: The coral snakes: *Micrurus corallinus* (upper left); *M. frontalis* (upper right); *M. lemniscatus* (lower left); and *M. altirostris* (lower right).

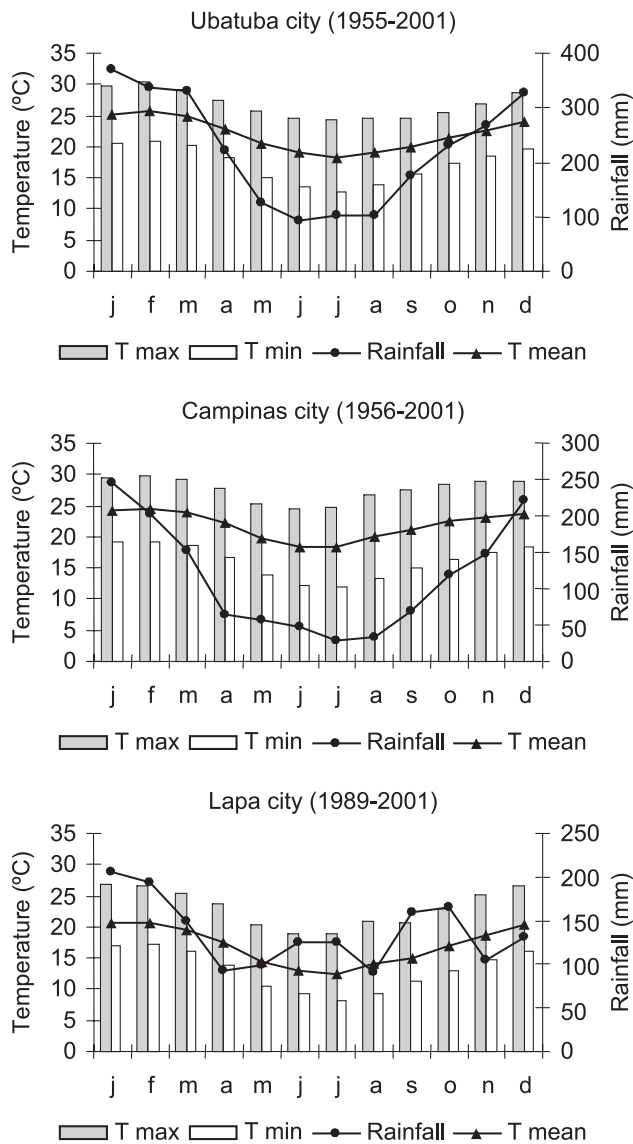


Figure 2: Climatic variation in three representative localities from the regions where the four species of *Micrurus* occur. Ubatuba (SP) – Serra do Mar; Campinas (SP) – seasonal forests and “cer-rado” in southeastern Brazil; and Lapa (PR) – seasonal forests in southern Brazil. Bold letter represents rainy season.

rainy season from October to April (spring to early autumn), and a dry season from May to September (late autumn to winter; see Nimer, 1989 and Figure 2). *Micrurus altirostris* inhabits seasonal forests in Southern Brazil (Silva and Sites, 1999; Campbell and Lamar, 2004), where temperature varies markedly, with lower values occurring from May to September (late autumn to winter), during a slightly drier season (Figure 2). However, rainfall is less variable throughout the year (Nimer, 1989, Figure 2).

The seasonal activity pattern of each species was inferred from the number of adult snakes brought each

month to the Laboratório de Herpetologia of Instituto Butantan, São Paulo, Brazil, mostly by lay people (see Oliveira and Martins, 2001). Information and queries about the method used (*e.g.*, influence of the collection effort throughout the year) can be found in Marques *et al.* (2000).

The records of snakes received from 1982 to 1990 were used since this period showed a huge sample effort by lay people that brought snakes to Instituto Butantan. However, data from 1986 were not used, since a campaign for the collection of coralsnakes took place in October, causing a pronounced difference in the sampling effort throughout the year (a preliminary analysis of the data showed an unusually high peak for these species in October, 1986). In order to compare the monthly collection frequency of each species, chi-square tests were used.

RESULTS

During the period analyzed, 1508 adult specimens of the four species from Southern and Southeastern Brazil were brought to Instituto Butantan. *Micrurus corallinus* was the most abundant species ($n = 1020$, 67.6% of the total number of coralsnakes), followed by *M. frontalis* ($n = 219$, 14.5%), *M. altirostris* ($n = 169$, 11.3%) and *M. lemniscatus* ($n = 100$, 6.6%).

There was a significant increase in the number of individuals of *M. corallinus* captured in the rainy season ($X^2 = 266.71$, $df = 1$, $P < 0.01$), with a peak in the first half of this season (spring and early summer; Figure 3), confirming previous findings (Marques, 1996). Likewise individuals of *M. frontalis* were significantly more captured in the rainy season ($X^2 = 8.65$, $df = 1$, $P < 0.05$), with apparent peaks in January (early summer), March and April (late summer/early autumn), and in June (late autumn) (Figure 3). However, there was no significant seasonal difference in the number of individuals of *M. lemniscatus* captured ($X^2 = 0.72$, $df = 1$, $P = 0.39$), despite a peak during the first half of the dry season (autumn) (Figure 3). The seasonal peak of captures recorded for *M. frontalis* and *M. lemniscatus* is highly significant for both species ($X^2 = 35.11$, $df = 3$, $P < 0.01$ and $X^2 = 56.48$, $df = 3$, $P < 0.01$, respectively). *Micrurus altirostris* was more captured in the rainy season (spring and summer) ($X^2 = 23.72$, $df = 1$, $P < 0.01$), and showed apparent peaks in abundance in January (early summer), April (the onset of the colder season), and in spring (Figure 3).

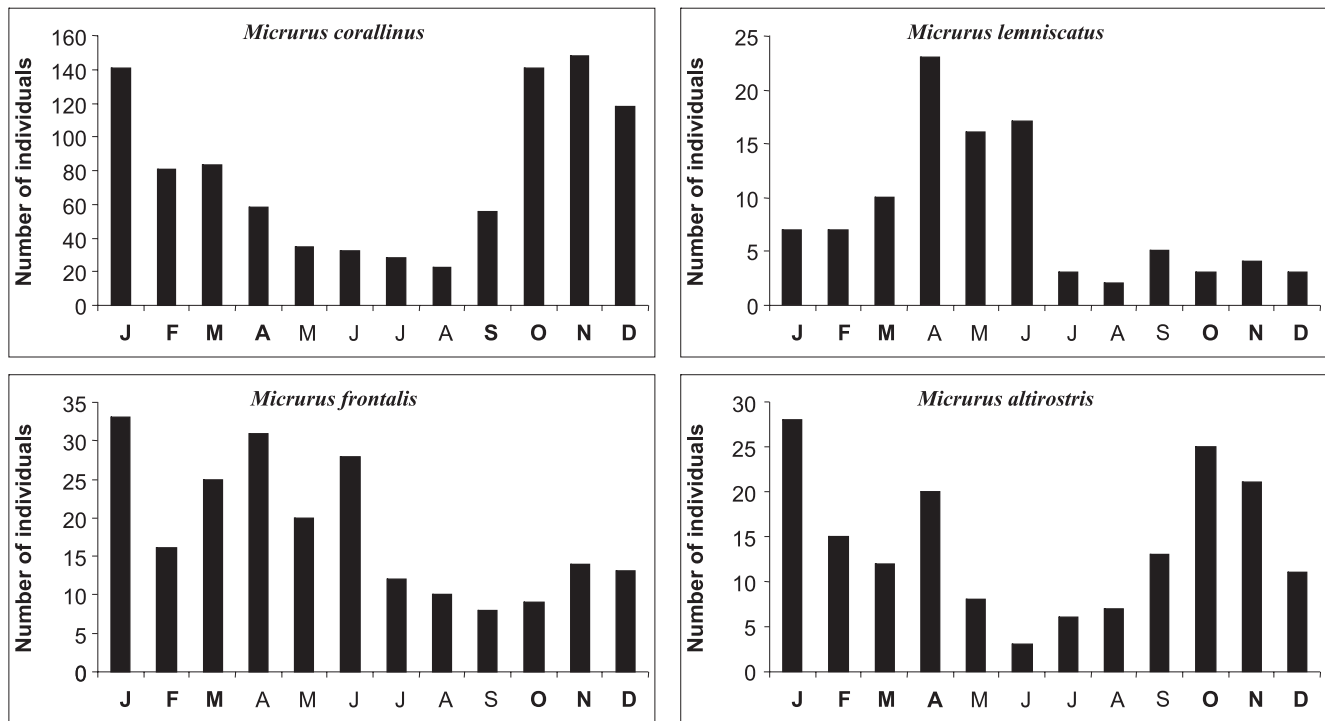


Figure 3: Seasonal activity of four species of *Micrurus*. The values represent the percentage of individuals collected each month and sent to Instituto Butantan from 1982 to 1990 (excluding 1986, see text for details). Bold letter represents rainy season.

DISCUSSION

Activity patterns throughout the year have already been described for *Micrurus fulvius*, in Florida, United States, and *M. corallinus*, from Southeastern Brazil. Both species have a highly seasonal activity, lower during autumn and winter. Lower values of temperatures and precipitation are most likely responsible for the decrease in activity during these periods (Marques, 1996). Climate variation also seems to influence the activity patterns of the other species of *Micrurus* studied here, since most show a decrease in activity during the colder and less rainy months. Temperature directly influences the metabolic rate of snakes (Lillywhite, 1987), which must limit the amount of movement they can make. This factor may be more important for *M. altirostris*, a species that occurs in higher latitudes, where temperatures are much lower in the dry season (autumn and winter) and rainfall is less variable in this period.

In addition to the higher temperature, a greater availability of food during the rainy periods may enhance coral snake activity. These snakes feed mainly on amphisbaenians and caecilians (Marques and Sazima, 1997; Greene, 1973) which live predominantly underground, but come up to the surface after heavy rains

(*cf.* Marques and Sazima, 2004; L.C. dos Santos, pers. comm.). Individuals of *Micrurus* can capture these preys either in their underground shelters or on the ground (Marques and Sazima, 1997). They are able to find the subterranean galleries built by amphisbaenians following chemical signals left on the surface (Marques, 1992; Roze, 1996; Jared *et al.*, 1999). These signals (chemical tracks) may be more evident in the soil during rainy periods (when amphisbaenians move more frequently to the surface), and probably enhance the foraging activity of *Micrurus* in the rainy season (spring and summer). Alternatively, coral snakes may be more active during the warmer period of the year because amphisbaenians and caecilians, which feed upon invertebrates, may be more active in spring and summer, when their prey are more abundant (*e.g.*, Janzen and Schoener, 1968).

The annual activity patterns of *M. corallinus* and *M. fulvius* are very similar (Jackson and Franz, 1981; Marques, 1996; present study) and seem to be influenced by the reproductive cycle of males and females (Jackson and Franz, 1981; Marques, 1996; Almeida-Santos *et al.*, 2006). In both species there is an increase in activity in spring, when males are actively searching for females to mate with (Jackson and Franz, 1981; Marques, 1996). Vitellogenesis of females of both

M. fulvius and *M. corallinus* takes place during spring (Jackson and Franz, 1981; Marques, 1996); however, activity levels of females *M. fulvius* are low in this period, whereas females of *M. corallinus* are more active and exposed (Jackson and Franz, 1981; Marques, 1996). Therefore, the peak of activity of *M. corallinus* at the onset of the rainy season (spring) must include both males (which are searching mates) and females (which are carrying vitellogenic follicles and need to bask more often; see Bonnet and Naulleau, 1996; Marques, 1996; Ladyman, 2003). Their activity remains intense in December and January (summer). In December many females still have vitellogenic follicles, while others already have eggs and may become more exposed looking for nesting sites (Marques, 1996). In January, while there are still females with eggs, those that have already laid their eggs may remain active because of their need to forage and replenish the energy used during reproduction (Almeida-Santos et al., 2006).

The activity patterns of *M. frontalis* and *M. lemniscatus* are similar, especially regarding the apparently high activity at the end of the rainy season and onset of the dry season (autumn and early winter) and the absence of capture peak at the beginning of the rainy season (spring). The activity patterns of these species are considerably different from that of *M. corallinus*. In the latter, the period of vitellogenesis is very short and females become more active on the surface when they are carrying vitellogenic follicles (cf. Bonnet and Naulleau, 1996; Marques, 1996; Ladyman et al., 2003), at the onset of the rainy season (spring) (Marques, 1996; see above). *Micrurus frontalis* and *M. lemniscatus*, nevertheless, have a longer period of vitellogenesis, which begins before the rainy season (O.A.V. Marques, S.M. Almeida-Santos e L. Pizzatto, unpublished data). Consequently, the basking activity of these females is probably distributed more evenly throughout the year. The activity pattern of *M. altirostris* seems to be more correlated to climatic variation, since there is an increase in activity at the beginning of the rainy season (spring). Many snakes from Southern Brazil have a more pronounced reproductive seasonality (cf. Di-Bernardo, 1999; Hartmann et al., 2004), which probably reflects the lower temperatures in the dry season (winter; cf. Pizzatto and Marques, 2006). It is likely that in this region the period of vitellogenesis of *M. altirostris* is more restricted (like *M. corallinus*) because of the very low tempera-

tures in winter. Thus, female activity (with vitellogenic follicles) would only increase at the beginning of the rainy season (spring). A study characterizing the reproductive cycle of this species would help to elucidate this assumption.

The activity peak of *M. altirostris* in April seems to be related to the reproductive traits of this species. Ritual combat between two individuals of *M. altirostris* in nature was recorded in April (Almeida-Santos et al., 1998). On two occasions, during the same season of the year, Almeida-Santos et al. (1998) observed two captive males fighting. Recently, two additional fighting males were observed in nature, also in April (A. Tozzetti, pers. comm.). Ritual combat is related to the dispute between males for a single female (Gillingham, 1987; Shine, 1993) and copulation in this species has also been recorded in April (S. Cechin, pers. comm.). Therefore, the activity peak of *M. altirostris* in April seems to be related to an increase of activity of males in this period due male-male combat and courtship.

Coralsnakes of the genus *Micrurus* are composed by two distinct monophyletic lineages, recognized by their color pattern: one has black rings arranged in monads and the other has black rings in triads (cf. Slowinsky, 1995; Campbell and Lamar, 2004). Two of the species mentioned above (*M. corallinus* and *M. fulvius*) belong to the same phylogenetic group (black rings in monads), while the other three (*M. altirostris*, *M. frontalis* and *M. lemniscatus*) belong to another clade (black rings in triads). Available data suggests that the mating season of *M. corallinus* is different from that of *M. altirostris*; the former mating early in the rainy season (spring) and the latter at the end of the rainy season (autumn). *Micrurus frontalis* and *M. lemniscatus* are most active at the end of the rainy season and early in the dry season (from late autumn to early winter), which corresponds to the mating period of *M. altirostris*. Apparently, the mating period of *M. altirostris* is shorter (April) than that of *M. frontalis* and *M. lemniscatus* (autumn and early winter) due to lower temperatures in Southern Brazil. These three species with black rings in triads (*M. altirostris*, *M. frontalis* and *M. lemniscatus*) share several common characteristics and belong to the same clade (Slowinsky, 1995). It is therefore reasonable to assume that their mating period occurs at the same time of the year (autumn and early winter). Moreover, the occurrence of a distinct mating period for the species with black rings in monads (spring) suggests distinct

reproductive strategies between the two lineages of *Micrurus*. A comparative study including additional species of *Micrurus*, as well as a reliable phylogeny of the genus, would be helpful to identify the factors responsible for the interspecific variations in activity described here.

RESUMO

A atividade sazonal de quatro espécies de *Micrurus* do sul e sudeste do Brasil foi inferida por meio de dados de exemplares trazidos ao Instituto Butantan ao longo de oito anos. Para a maioria das espécies, a atividade na superfície foi significativamente menor no período mais seco e frio. Baixas temperaturas podem reduzir a taxa metabólica de serpentes e, conseqüentemente, limitar sua atividade. A disponibilidade de presas ao longo do ano pode explicar este padrão de atividade. A condição reprodutiva (extensão do ciclo vitelogênico e acasalamento) também deve influenciar no padrão de atividade e pode explicar diferenças observadas entre as espécies. Uma das espécies (*M. corallinus*) tem o período de vitelogênese e acasalamento restrito à primeira metade da estação chuvosa (primavera). O padrão de atividade e observações na natureza indicam que o acasalamento ocorra do final da estação chuvosa à primeira metade da estação seca (outono) nas outras três espécies (*M. altirostris*, *M. frontalis*, *M. lemniscatus*), as quais pertencem a uma mesma linhagem filogenética. Os resultados do presente trabalho indicam que estratégias reprodutivas distintas ocorrem nas duas linhagens filogenéticas de *Micrurus*.

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LITERATURE CITED

- ALMEIDA-SANTOS, S.M., L.F.S.A. AGUIAR & R.L. BALESTRIN. 1998. *Micrurus frontalis* (Coral Snake). Male Combat. *Herpetological Review*, 29:242.
- ALMEIDA-SANTOS, S.M. & M.G. SALOMÃO. 2002. Reproduction in neotropical pitvipers, with an emphasis on species of the genus *Bothrops*, pp. 445-462. In: *Biology of the Vipers*, G.W. Schuett, M. Höggren, M.E. Douglas & H.W. Greene (Eds.). Eagle Mountain Publishing, LC, Utah.
- ALMEIDA-SANTOS, S.M., L. PIZZATO & O.A.V. MARQUES. 2006. Intra-Sex Synchrony and Inter-Sex Coordination in the Reproductive
- Timing of the Coral Snake *Micrurus corallinus* (Elapidae). *Herpetological Journal*, in press.
- BONNET, X. & G. NAULEAU. 1996. Catchability in snakes: consequences for estimates of breeding frequency. *Canadian Journal of Zoology*, 74:233-239.
- CAMPBELL J.A. & W.W. LAMAR. 2004. *The Venomous Reptiles of Western Hemisphere*. Cornell University Press, Ithaca, vol. I, 475 pp.
- DI-BERNARDO, M. 1999. História natural de uma comunidade de serpentes da borda oriental do Planalto das Araucárias, Rio Grande do Sul, Brasil. Ph.D. dissertation, Universidade Estadual Paulista, Rio Claro, Brasil, 119 pp.
- GIBBONS, J.W. & R.D. SEMLITSCH. 1987. Activity Patterns, pp. 396-421. In: R.A. Seigel; J.T. Collins & S.S. Novak (Eds.), *Snakes: ecology and evolutionary biology*. Macmillan Publishing Company, New York.
- GILLINGHAM, J.C. 1987. Social behavior, pp. 184-209. In: R.A. Seigel, J.T. Collins & S.S. Novak (Eds.), *Snakes: Ecology and Evolutionary Biology*. Macmillan Publishing Company, New York.
- GREENE, H.W. 1973. Defensive tail display by snakes and amphisbaenians. *Journal of Herpetology*, 7:143-161.
- GREGORY, P.T. 1982. Reptilian hibernation, pp. 53-154. In: C. Gans & F.H. Pough (Eds.). *Biology of Reptilia*, vol. 13. Academic Press, New York.
- HARTMANN, M.T., O.A.V. MARQUES & S.M. ALMEIDA-SANTOS. 2004. Reproductive biology of the southern Brazilian pitviper *Bothrops meuwiedi pubescens* (Serpentes: Viperidae). *Amphibia-Reptilia*, 25:77-85.
- HENDERSON, R.W., J. DIXON & P. SOINI. 1978. On the seasonal incidence of tropical snakes. *Milwaukee Public Museum Contributions in Biology and Geology* 17:1-15.
- JACKSON, D.R. & R. FRANZ. 1981. Ecology of the eastern coral snake (*Micrurus fulvius*) in northern peninsular Florida. *Herpetologica*, 37:213-228.
- JANZEN, D.H. & T.W. SCHOENER. 1968. Differences in insect abundance and diversity between wetter and drier sites during a tropical dry season. *Ecology*, 49:96-110.
- JARED, C., ANTONIAZZI, M.M., SILVA, J.R.M.C. & FREYMÜLLER, E. 1999. Epidermal glands in Squamata: microscopical examination of pre-cloacal glands in *Amphisbaena alba* (Amphisbaenia, Amphisbaenidae). *Journal of Morphology*, 241:197-206.
- LADYMAN, M., X. BONNET, O. LOURDAIS, D. BRADSHAW & G. NAULLEAU. 2003. Gestation, thermoregulation, and metabolism in a viviparous snake *Vipera aspis*: evidence for fecundity-independent costs. *Physiological and Biochemical Zoology*, 74:497-510.
- LILLYWHITE, H.B. 1987. Circulatory adaptations of snakes to gravity. *American Zoologist*, 27:81-95.
- MARQUES, O.A.V. 1992. História natural de *Micrurus corallinus* (Serpentes, Elapidae). MSc dissertation, Universidade de São Paulo, São Paulo, Brasil, 80 p.
- MARQUES, O.A.V. 1996. Reproduction, seasonal activity and growth of the *Micrurus corallinus* (Serpentes, Elapidae). *Amphibia Reptilia*, 17:277-285.
- MARQUES, O.A.V., A. ETEROVIC & W. ENDO. 2000. Seasonal activity of snakes in the Atlantic forest in southeastern Brazil. *Amphibia-Reptilia*, 22:103-111.
- MARQUES, O.A.V. & G. PUERTO. 1998. Feeding, reproduction and growth in the crowned snake *Tantilla melanocephala* (Colubridae), from southeastern Brazil. *Amphibia-Reptilia*, 19:311-318.

- MARQUES, O.A.V. & I. SAZIMA. 1997. Diet and feeding behavior of the coral snake, *Micrurus corallinus*, from the Atlantic forest of Brazil. *Herpetological Natural History*, 5:88-93.
- MARQUES, O.A.V. & I. SAZIMA. 2004. História natural dos répteis da Estação Ecológica Juréia-Itatins; pp. 257-277. In: O.A.V. Marques & W. Duleba (Eds.), Estação Ecológica Juréia-Itatins: Ambiente Físico, Flora e Fauna. Editora Holos, Ribeirão Preto.
- NIMER, E. 1989. Climatologia do Brasil. 2º Ed. IBGE Departamento de Recursos Naturais e estudos Ambientais, Rio de Janeiro, RJ.
- OLIVEIRA, M.E. & M. MARTINS. 2002. 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.
- PIZZATTO, L. & O.A.V. MARQUES. 2006. Interpopulational variation in reproductive cycles and activity of the water snake *Liophis miliaris* (Colubridae) in Brazil. *Herpetological Journal*, in press.
- REINERT, H.K. 1987. Habitat variation within sympatric snake populations. *Ecology*, 65:1673-1682.
- ROZE, J.A. 1996. Coral Snakes of the America: Biology, Identification, and Venoms. Krieger Publishing Co, Florida, 262 pp.
- SHINE, R. 1979. Activity patterns in Australian elapid snakes (Squamata: Serpentes: Elapidae). *Herpetologica*, 35:1-10.
- SHINE, R. 1993. Sexual dimorphism in snakes; pp. 49-86. In: R.A. Seigel, & J.T. Collins (Eds.), Snakes: Ecology and Behavior. MacGraw-Hill, New York.
- SILVA JR, N.J. & J.W. SITES JR. 1999. Revision of the *Micrurus frontalis* complex (Serpentes: Elapidae). *Herpetological Monographs*, 13:142-194.
- SLOWINKY, J.B. 1995. A phylogenetic analysis of the new world coral snakes (Elapidae: *Leptomicrurus*, *Micruroides* and *Micrurus*) based on the allozymic and morphological characters. *Journal of Herpetology*, 29:325-338.

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