

Reproductive Strategies of New World Coral Snakes, Genus *Micrurus*

Author(s): Otavio A. V. Marques , Lígia Pizzatto , and Selma M. Almeida Santos

Source: Herpetologica, 69(1):58-66. 2013.

Published By: The Herpetologists' League

DOI: <http://dx.doi.org/10.1655/HERPETOLOGICA-D-12-00091>

URL: <http://www.bioone.org/doi/full/10.1655/HERPETOLOGICA-D-12-00091>

BioOne (www.bioone.org) is a nonprofit, online aggregation of core research in the biological, ecological, and environmental sciences. BioOne provides a sustainable online platform for over 170 journals and books published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Web site, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/page/terms_of_use.

Usage of BioOne content is strictly limited to personal, educational, and non-commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

REPRODUCTIVE STRATEGIES OF NEW WORLD CORAL SNAKES, GENUS *MICRURUS*

OTAVIO A. V. MARQUES^{1,4}, LÍGIA PIZZATTO^{1,2,3}, AND SELMA M. ALMEIDA SANTOS¹

¹Laboratório de Ecologia e Evolução, Instituto Butantan, Avenida Dr. Vital Brazil, 1500, São Paulo, 05503–900, SP, Brazil

²Departamento de Zoologia CP 6109, Instituto de Biologia, Universidade Estadual de Campinas, 13083–970, Campinas, SP, Brazil

ABSTRACT: New World Coral Snakes (genus *Micrurus*) occur from North to South America in a wide range of climates and habitats. Using both original and published data, we show that reproductive patterns diverge in the two phylogenetic lineages of *Micrurus* within the subtropical regions. Species with black rings arranged in triads are characterized by males larger than or equal in size to females, male combat behavior, and a broader season of vitellogenesis and oviposition. In these species, mating in autumn is synchronous with both spermatogenesis and vitellogenesis. Thus, females need to store sperm until ovulation in spring. In species with black rings arranged in monads, females are generally larger than males, there is no male–male combat, and seasonal vitellogenesis occurs in spring synchronous with mating. Egg laying occurs from late spring to summer, and hatchlings emerge from late summer to autumn. Spermatogenesis peaks during autumn, and males store sperm in the deferent duct over winter, until the mating season. Despite these phylogenetic trends, climatic influence on the extension of reproductive cycles was evident, with equatorial species exhibiting more continuous cycles and species from cold areas exhibiting more seasonal cycles. These two disparate reproductive strategies may be considered another differential trait between these two clades of *Micrurus* showing the high divergence between them.

Key words: Coral Snake; *Micrurus*; Phylogenetic lineage; Reproduction; Subtropical area

THE DIVERSITY of reproductive tactics among snakes has always attracted considerable attention (Shine, 2003). The amplitude of such variation, especially of the reproductive cycles, is even more pronounced in tropical areas, making the recognition of patterns much harder (Seigel and Ford, 1987; Greene, 1997). Recent studies have expanded our knowledge of the reproductive cycles of tropical snakes (Mathies, 2011). However, with such a high species richness, lineage diversity, and climatic and ecological complexity, there is still an absence of data regarding basic reproductive aspects in many species, making generalizations about reproductive strategies of tropical snakes premature.

The semifossorial Coral Snakes are the only representatives of the family Elapidae in the New World, comprising at least 70 species in the monotypic genus *Micruroides*, and the

speciose genus *Micrurus* (including *Leptomicrurus*; Slowinski, 1995; Campbell and Lamar, 2004). *Micrurus* species occur in a wide range of climates and habitats from the southeastern United States to South America (Campbell and Lamar, 2004). The genus includes two distinct phylogenetic lineages: one lineage includes approximately 40 species that possess black rings arranged in monads (BRM—one black ring in between two white/yellow rings and these rings in between red rings), and the other lineage with approximately 20 species possessing black rings in triads (BRT—three black rings separated by white/yellow rings, and this set of rings in between red rings; Slowinski, 1995, Campbell and Lamar, 2004). The two clades of *Micrurus* are similar ecologically, and the species from different lineage can be sympatric in several regions where they usually seem to live in syntopy and use the same type of food resource (Martins and Oliveira, 1998; Argôlo, 2004; Marques et al., 2004).

The reproductive biology within *Micrurus* is still not well known, but data are available for some species. Among the BRM species, data on sexual dimorphism, male and female

³ PRESENT ADDRESS: University of Newcastle, School of Environmental and Life Sciences, University Drive, Callaghan, 2308, NSW, Australia

⁴ CORRESPONDENCE: e-mail, otaviomarques@butantan.gov.br

reproductive cycles, and seasonal activity are available for *M. fulvius* and *M. tener* from North America (Quinn, 1979; Jackson and Franz, 1981) and for *M. corallinus* from South America (Marques, 1996; Almeida-Santos et al., 2006). Information on reproductive biology is also available for *M. nigrocinctus* from Central America (Solórzano and Cerdas, 1988; Goldberg, 2004). Data on BRT species are more scarce, with fragmentary information on the reproduction of *M. altirostris*, *M. decoratus*, and *M. pyrrocryptus* (Almeida-Santos et al., 1998; Marques, 2002; Marques et al., 2006; Ávila et al., 2010).

Males of most species of the BRT group reach a larger size than females (Roze, 1996; Marques, 2002), whereas in BRM group the females usually attain larger body size (Jackson and Franz, 1981; Marques, 1996; Roze, 1996). In addition, the species of the two lineages from subtropical regions differ in seasonal surface activity, a difference that may be related to reproduction events, including mating (Marques et al., 2006). These data and record of combat only in the Coral Snakes of the BRT group (Almeida-Santos et al., 1998) indicate that differential reproductive strategies may occur between these two distinct phylogenetic lineages of *Micrurus*. The purpose of this study is to assess this hypothesis by using original and published data on reproductive cycles, reproductive behavior, and body sizes of *Micrurus* species from both groups.

MATERIALS AND METHODS

Our original data are based on the analyses of four species of Coral Snakes with BRT pattern, from seasonal subtropical areas (between 20 and 30°S): 148 *M. altirostris* (43 females, 81 males, 24 immature; this species was included in *M. frontalis* in previous taxonomic classification), 60 *M. decoratus* (52 mature males, 8 immature), 126 *M. frontalis* (41 females, 58 males, 27 immature), and 149 *M. lemniscatus* (49 females, 45 males, 55 immature). Our sample was restricted to preserved snakes that were killed at the time of (or soon after) collection. All specimens were collected in southern and southeastern Brazil and belong to the Instituto Butantan (IB) and Museu de História Natural da

Universidade Estadual de Campinas (ZUEC) collections. For each specimen, we measured the snout–vent length (SVL, in millimeters), and after dissection we recorded sex, diameter of the largest ovarian follicle or oviductal egg, length of the right testis, and diameter of the distal portion of deferent ducts (cf. Almeida-Santos et al., 2006). Females were considered sexually mature if they had enlarged follicles (> 5 mm) and oviductal eggs or folded oviducts, and males were considered mature if they had opaque and convoluted deferent ducts (Shine 1977a, 1980; Marques, 1996). Immature individuals < 300 mm in SVL were considered to be newborns (or at least a couple of months old, based on our own experience with these species), and data on dates of collection were used to infer recruitment periods.

Mean body sizes of mature males and females were compared using *t*-tests, and we calculated the index of sexual size dimorphism (SSD: [mean size of the larger sex/mean size of the smaller sex] – 1; this index is expressed as negative if males are the larger than females, Shine 1994). We described the female reproductive cycles by plotting the size of the largest follicle or egg by the date of collection, and we compared the length of the right testis and diameter of deferent ducts among the seasons by using ANOVA. Because both testis size and deferent duct diameter were related to SVL in all species, we used the residuals of the regression of these variables by SVL in all analyses, except for the deferent duct of *M. lemniscatus* in which there was no such correlation.

We compared our original data with published data for BRM Coral Snakes also from subtropical areas (approximately between 20 and 30°S and 25 and 30°N): *M. corallinus* from the Southern Hemisphere in eastern Brazil (Marques, 1996; Almeida-Santos et al., 2006) as well as *M. fulvius* and *M. tener* from the Northern Hemisphere in the southern United States (Quinn, 1979; Jackson and Franz, 1981). For comparison on sexual dimorphism, we also used data on adult body sizes of *M. nigrocinctus* from tropical regions in Northern Hemisphere (Solórzano and Cerdas, 1988; Goldberg, 2004). Information on male–male combat and courtship for

TABLE 1.—Mean snout-vent length (SVL, in mm) \pm SD, range (in parentheses) and degree of sexual size dimorphism (SSD) in Coral Snakes from the New World. BRM = black rings arranged in monads, and BRT = black rings in triads.

Species	Female SVL	Male SVL	SSD	Reference
BRM				
<i>Micrurus corallinus</i>	672 \pm 125 (425–950, n = 194)	563 \pm 73 (440–740, n = 125)	0.19	Marques, 1996
<i>M. fulvius</i>	727 \pm ? ^a (250–970, n = 52)	547 \pm ? ^a (260–700, n = 73)	0.33	Jackson and Franz, 1981
<i>M. tener</i>	620 \pm ? ^a (494–971, n = 71)	539 \pm ? ^a (400–685, n = 64)	0.15	Quinn, 1979
<i>M. nigrocinctus</i>	606 \pm 86 (490–793, n = 19)	530 \pm 54 (450–640, n = 15)	0.14	Goldberg, 2004
<i>M. n. nigrocinctus</i>	588 \pm 145 (327–1000, n = ?? ^b)	530 \pm 83 (331–692, n = ?? ^b)	0.11	Solórzano and Cerdas, 1988
<i>M. n. mosquitensis</i>	696 \pm 115 (382–887, n = ?? ^b)	510 \pm 97 (363–474, n = ?? ^b)	0.36	Solórzano and Cerdas, 1988
BRT				
<i>M. altirostris</i>	606 \pm 98 (409–977, n = 45)	704 \pm 128 (459–1036, n = 93)	-0.16	Present work
<i>M. decoratus</i>	516 \pm 41 (465–570, n = 6)	510 \pm 92 (360–802, n = 51)	0.01	Marques, 2002; present work
<i>M. frontalis</i>	757 \pm 115 (500–957, n = 41)	953 \pm 201 (641–1425, n = 58)	-0.26	Present work
<i>M. lemniscatus</i>	806 \pm 188 (500–1172, n = 36)	824 \pm 196 (488–1297, n = 45)	-0.02	Present work

^a Single question mark (?) indicates information missing from reference

^b Double question mark (??) indicates studies used 150 specimens in total of *Micrurus n. nigrocinctus* and 119 specimens of *M. n. mosquitensis*, but they did not specify the number of females and males.

snakes from both lineages was summarized from observations by fellow researchers, our own, and published literature.

RESULTS

BRT Coral Snakes

Body sizes and sexual dimorphism.—Male SVL was larger than female SVL in *M. altirostris* ($t = 4.55$, $df = 136$, $P < 0.0001$) and *M. frontalis* ($t = 5.64$, $df = 97$, $P < 0.0001$), but no significant difference was found for *M. lemniscatus* ($t = 0.41$, $df = 80$, $P = 0.681$) and *M. decoratus* ($t = 0.16$, $df = 55$, $P = 0.875$; Table 1). SSD was negative or close to zero for all BRT species (Table 1).

Mating and combat behavior.—In addition to previous records of combat behavior in captive males *M. altirostris* (cf. Almeida-Santos et al., 1998), three additional fighting males were observed in nature during the same season of the year (in April and May; A. Tozzetti and J. L. Ucha, personal communication; Fig. 1). Copulation in this species also was recorded in April (S. Cechin, personal communication; Table 2).

Female reproductive cycles.—Records of enlarged follicles (> 5 mm) started during autumn and progressed through spring when ovulation occurred for *M. altirostris*, *M. frontalis*, and *M. lemniscatus*. The female reproductive cycle was strictly seasonal in *M. altirostris*, but *M. frontalis* and probably *M. lemniscatus* (based on the broad dispersion of enlarged follicles) seem able to produce eggs



FIG. 1.—Record of ritual combat in the field in *Micrurus* Coral Snakes with black rings arranged in triads (BRT), *M. altirostris*. Photograph by João L. Ucha; used with permission.

TABLE 2.—Time of the different events of the reproductive cycle in Coral Snakes from subtropical areas. BRM = black rings arranged in monads, and BRT = black rings in triads. Data from ¹Almeida-Santos et al., 1998; ²Jackson and Franz, 1981; ³Marques, 2002; ⁴Marques, 1996; ⁵Marques, 2002; ⁶Marques et al., 2006; ⁷Quinn, 1979; and ⁸present work.

Species/predominant season	Latitude	Follicles >5 mm	Ovulation/oviposition	Hatching	Mating	Peak of sperm production	Sperm in the deferent duct
BRM							
<i>Micrurus corallinus</i> ^{1,3}	20–30°S	September–December	November–January	February–May	October–November ^a	April–June ^{b,c}	July–December ^{b,c}
<i>M. fulvius</i> ²	25–30°N	March–June	June–July	October–November	—	September–December ^b	—
<i>M. tener</i> ⁶	25–30°N	March–April	May–July	—	October ^d –May ^{a,c}	September–May ^{b,c}	August–June ^c
Season		Spring	Late spring	Autumn	Spring	Autumn	Winter–spring
BRT							
<i>M. altirostris</i> ^{5,7}	25–30°S	June–January	November	March–April	April	January–March ^c	January–December ^c
<i>M. decoratus</i> ^{4,7}	22–27°S	October–November	—	May	—	January–December ^b	January–December ^b
<i>M. frontalis</i> ⁷	20–24°S	February–September	August, January	November–March	—	January–December ^c	January–December ^c
<i>M. lemniscatus</i> ⁷	20–22°S	May–October	—	January–June	—	January–March ^c	January–December ^c
Season		Spring or autumn–spring	Spring	Autumn	Autumn	Extended or summer	Any

^a Behavioral observations.
^b Inferred by maximum testis size or mass and deferent duct diameter.
^c Evidenced by histology.
^d Single question mark (?) indicates uncertain data.

for a longer period (Fig. 2). Because published data show mating occurs in autumn, females may have to store sperm until ovulation in spring.

Male reproductive cycles.—No seasonal variation was detected in the size of the testes in *M. decoratus* ($F_{3,36} = 0.68$, $P = 0.570$, $n = 40$, Fig. 3A) and *M. frontalis* ($F_{3,44} = 0.85$, $P = 0.476$, $n = 48$; Fig. 3C). In *M. altirostris*, testes were larger during the summer and gradually decreased in size toward winter ($F_{3,70} = 3.16$, $P = 0.030$, $n = 74$; Fig. 3B), and this same pattern was detected in *M. lemniscatus* ($F_{3,35} = 4.83$, $P = 0.006$, $n = 39$; Fig. 3D). There was no seasonal variation in the diameter of the deferent duct for *M. decoratus* ($F_{3,38} = 0.36$, $P = 0.785$, $n = 42$), *M. altirostris* ($F_{3,72} = 0.68$, $P = 0.564$, $n = 76$), *M. frontalis* ($F_{3,47} = 0.07$, $P = 0.975$, $n = 51$), or *M. lemniscatus* ($F_{3,40} = 2.15$, $P = 0.108$, $n = 44$). Thus, males either produce sperm more aseasonally or they have a peak of sperm production in the summer and mating may be synchronous with spermatogenesis.

Newborns and recruitment.—The smallest individuals in our samples measured 244, 234, 278, and 339 mm SVL for *M. altirostris*, *M. frontalis*, *M. lemniscatus*, and *M. decoratus*, respectively. Newborn *M. altirostris* < 300 mm in SVL were recorded from late summer to early autumn, *M. frontalis* from late spring to summer, and *M. lemniscatus* from summer to autumn (Fig. 4).

BRM Coral Snakes

Summary of data.—Females were larger and attained larger maximum body size than males (Table 1). SSD were positive for all species and higher than those of BRT Coral Snakes (Table 1). There are no records of combat behavior in these snakes throughout many years of observation in nature and in captivity, although there are many records of interactions between males and females on species of this group (see Quinn, 1979; Jackson and Franz, 1981; Marques, 1996; Argôlo, 2004; Almeida-Santos et al., 2006; O. A. V. Marques and S. M. Almeida-Santos, personal observation). Females had a highly seasonal reproductive cycle with vitellogenesis restricted to spring, oviposition occur-

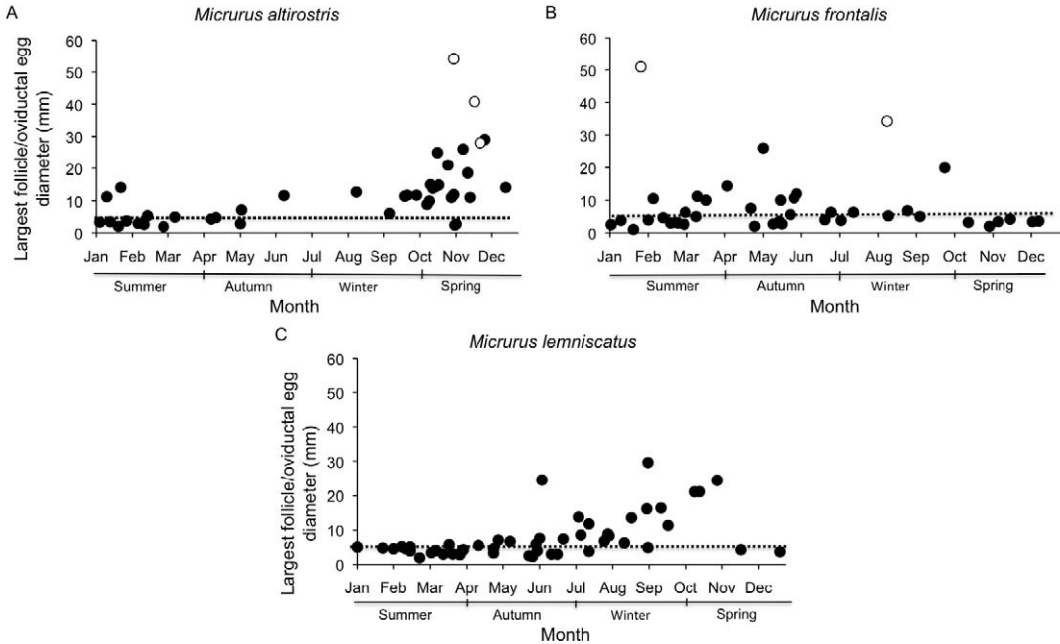


FIG. 2.—Seasonal variation in the largest follicle diameter (black circles) and oviductal egg (white circles) in *Micrurus* spp. with black rings arranged in triads, from southern and southeastern Brazil.

ring from late spring to early summer, and hatchlings emerging from late summer to early autumn. Mating was recorded only in the spring (Table 2). Spermatogenesis peaked during autumn, and males have to store sperm in the deferent duct over winter until the mating season. For this reason, an increase in the diameter of the deferent duct was observed from winter until spring (Table 2).

DISCUSSION

The data presented here indicate that reproductive strategies differ greatly between the two *Micrurus* lineages. The reproductive differences include sexual dimorphism, as is related to the presence or absence of combat, a behavioral trait widespread among snakes (Shine, 1994). Male–male combat was never recorded for any BRM species, consistent with the female-biased SSD (Shine, 1978, 1994). In contrast, male–male combat behavior has been observed in *M. altirostris* (Almeida-Santos et al., 1998; Marques et al., 2006), and the low SSD in the other BRT species suggests that this behavior may occur in the group (cf. Shine, 1978, 1994). Phyloge-

netic analyses based on morphological and molecular characters support a close relationship between northern Asian Coral Snakes (*Sinomicrurus*) and American Coral Snakes (*Micrurus* and *Micruroides*; Slowinski et al., 2001). This study suggests that snakes of the genera *Micrurus* and *Micruroides* are derived from an ancestor that dispersed from Asia into the Americas. Thus, the genera *Sinomicrurus*, *Micruroides*, and *Micrurus* form a monophyletic group (Slowinski et al., 2001; Castoe et al., 2007). Male–male combat is recorded in at the least one Asian Coral Snake, *Sinomicrurus japonicus* (Ota and Iwanaga, 1996). Combat was never observed for *Micruroides*, but the low SSD (−0.01; data from Goldberg, 1997) suggests the existence of this behavior in this genus. The monophyletic group of Coral Snakes formed by *Sinomicrurus*, *Micruroides*, and *Micrurus* share a common ancestor with Afro–Asian cobras in the genera *Naja* and *Ophiophagus* (Heise et al., 1995; Keogh 1998; Slowinski et al., 2001; Fry et al., 2003) in which combat also has been documented (Shine, 1978, 1994). Phylogenetic distribution of male–male combat suggests that this trait

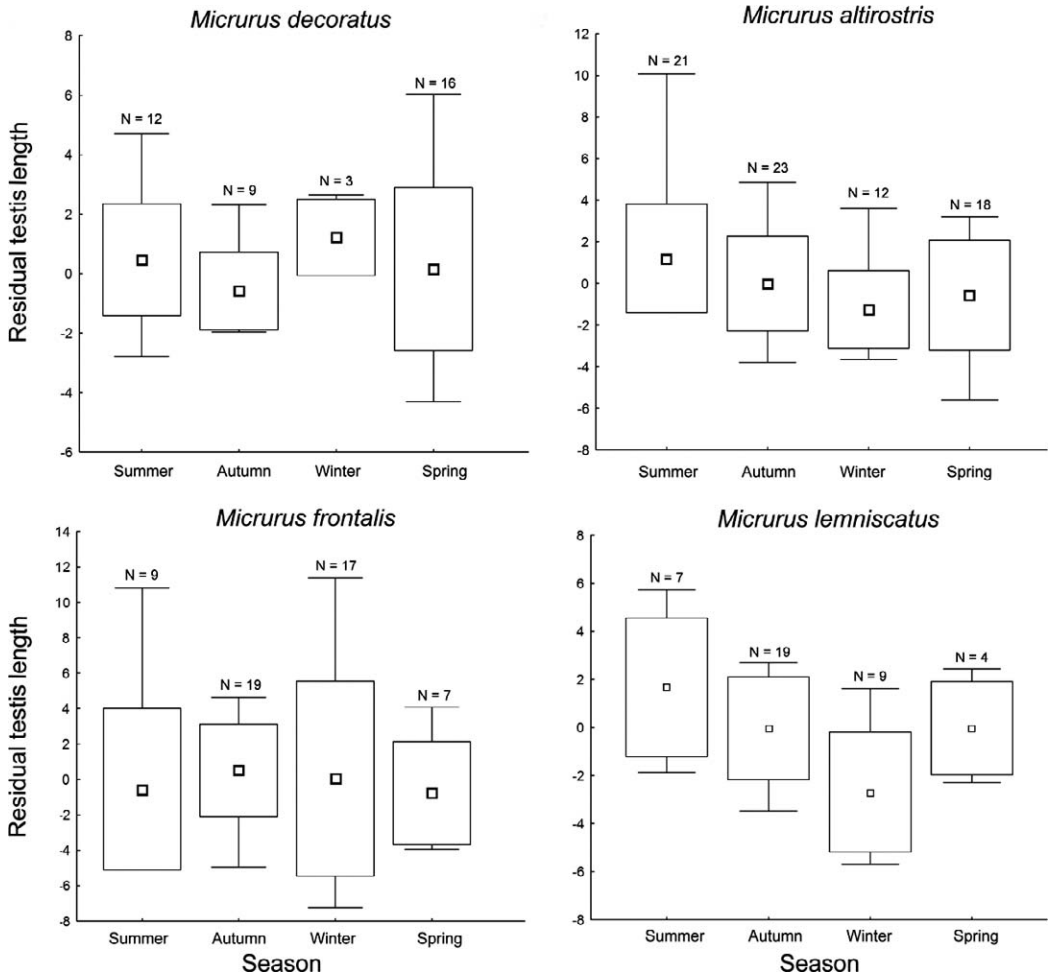


FIG. 3.—Seasonal variation in testis length in *Micrurus* spp. from southern and southeastern Brazil. Squares represent means, boxes are ± 1 standard deviation, and bars are maximum and minimum values.

has evolved or has been lost many times within snake phylogeny (Shine, 1994). However, because behavior is often hard to observe in snakes, it is probable that combat is even more widespread than our current records indicate. The hypothesis of evolutionary relationships among elapids (e.g., Keogh, 1998; Fry et al., 2003) and reports of combat in many species (Shine, 1994) also suggest a similar scenario within elapid phylogeny, and it is possible the BRM Coral Snakes of the New World have lost this behavior.

In addition to differences in sexual dimorphism and combat behavior, the reproductive cycles in both males and females differ

between the two *Micrurus* lineages. These differential reproductive cycles can explain differences in surface activity patterns between the two phylogenetic lineages of *Micrurus* in subtropical regions. The BRT Coral Snakes have a longer period of vitellogenesis, and the surface activity of these snakes is usually distributed more evenly throughout the year (see Marques et al., 2006). In addition, mating and ritual combat, behaviors that are related to the dispute between males for a single female (see Gillingham, 1987; Shine, 1994), in BRT Coral Snakes also have been recorded in autumn (Marques et al., 2006). Therefore, the surface

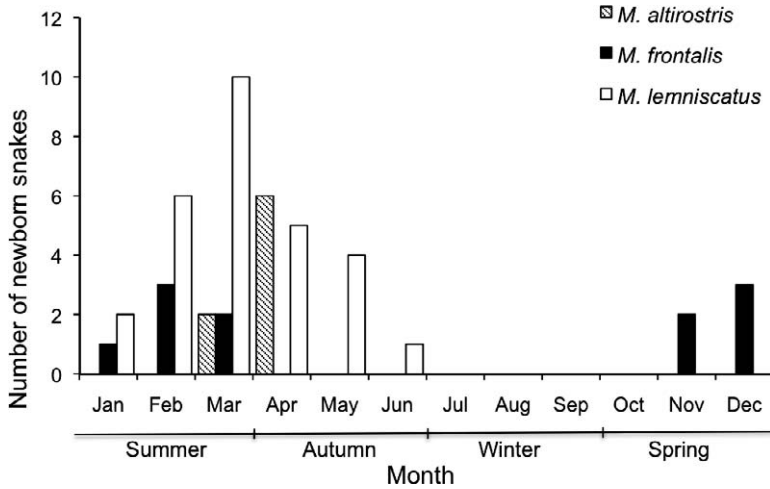


FIG. 4.—Number of newborn (SVL < 300 mm) *Micrurus* spp. from southern and southeastern Brazil.

activity peak in autumn verified for BRT Coral Snakes seems to be related to an increase of activity of males in this period (Marques et al., 2006). In contrast, vitellogenesis in the BRM Coral Snakes is very short and takes place in spring, simultaneously with mating. Thus, males searching for females in this period probably accounts for the male surface activity peak in spring recorded for BRM Coral Snakes (cf. Jackson and Franz, 1981; Marques, 1996).

Reproductive cycles in elapid snakes are highly variable (see Shine, 1977a,b), but detailed information is absent for various elapid clades, including other Coral Snakes such as the Asian *Sinomicrurus*. In addition, the species belonging to the two clades of *Micrurus* are ecologically similar and often coexist within a region. Thus, it is not easy to trace how these two strategies have evolved within the genus *Micrurus* as well as which factors may lead to the differences between the two lineages. The climate has a great influence on the reproductive cycles of snakes (Saint-Girons, 1982). The Earth's climate has changed continually since the middle Miocene (Hay et al., 2002) when the *Micrurus* genus probably evolved (Rage, 1987). There are many possible climate zones where each lineage of *Micrurus* may have emerged that may have been determinants of this differentiation.

Phylogenetic constraints are observed in a wide range of life-history traits, including several aspects of reproduction such as reproductive mode, reproductive seasonality, and clutch sizes (e.g., Pizzatto and Marques, 2007; Pizzatto et al., 2008a,b). Thus, phylogeny has an important role in reproductive cycles, but climate also can influence tropical and subtropical snakes (Pizzatto et al., 2008a,b). Our work shows that general reproductive strategy differs between the two *Micrurus* lineages and may be conservative within each lineage, but reproductive periods can be variable within a lineage. Climatic influence is obvious among the studied BRT species, because the species from higher latitudes (*M. altirostris*) exhibited more restricted cycles than species from lower latitudes (*M. frontalis* and *M. lemniscatus*). The BRM Coral Snakes *M. corallinus*, *M. fulvius*, and *M. tener* exhibit very similar timing of reproductive cycles. However, the areas where the populations were studied (southern and southeastern Brazil; Florida and Texas, USA) are similar in terms of climate (roughly between latitudes 20 and 30°). In contrast, data on the BRM *M. nigrocinctus* from a lower latitude region (Costa Rica, ≈10° N; see Solórzano and Cerdas, 1988; Goldberg, 2004) suggests an aseasonal cycle, different from that of the other BRM species studied. However, sample sizes for this species were limited, and more

studies dealing with tropical and equatorial Coral Snake species are essential to better understand climatic influences on the reproductive cycles of *Micrurus*.

The two lineages of *Micrurus* differ in color pattern and other morphological characteristics, such as hemipenial shape and size of tail (Slowinski, 1995; Campbell and Lamar, 2004). The distinction between these two groups is supported by biochemical characters as well (Slowinski, 1995). The two reproductive strategies described here may be considered additional characteristics that differentiate these two clades of *Micrurus*, and they must have been fixed over time when the two lineages diverged.

Acknowledgments.—We are thankful to the referees as well as the associate editor for valuable comments on the manuscript; to F. L. Franco (IB), V. Germano (IB), and P. R. Manzani (ZUEC) for permission and help with accessing specimens; to V. Copovilla and L. Parpinelli for help with data collection; to S. Cechin, A. Tozzetti, and J. L. Ucha for providing behavioral data; and to M. Crossland for language review. This work was supported by FAPESP and CNPq.

LITERATURE CITED

- Almeida-Santos, S., L.F.S.A. Aguiar, and R.L. Balestrin. 1998. *Micrurus frontalis* (Coral Snake). Male combat. *Herpetological Review* 29:242.
- Almeida-Santos, S.M., L. Pizzatto, and 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* 16:371–376.
- Argôlo, A.J.S. 2004. As serpentes dos cacauais do sudeste da Bahia. Editora Editus, Ilhéus, Brazil.
- Ávila, R.W., R.A. Kawashita-Ribeiro, V.L. Ferreira, and C. Strüßmann. 2010. Natural History of the Coral Snake *Micrurus pyrrhocryptus* Cope 1862 (Elapidae) from semideciduous forests of western Brazil. *South American Journal of Herpetology* 5:97–101.
- Campbell, J.A., and W.W. Lamar. 2004. *The Venomous Reptiles of the Western Hemisphere*. Cornell University Press, USA.
- Castoe, T.A., E.N. Smith, R.M. Brown, and C.L. Parkinson. 2007. Higher-level phylogeny of Asian and American coralsnakes, their placement within the Elapidae (Squamata), and the systematic affinities of the enigmatic Asian coralsnake *Hemibungarus calligaster* (Wiegmann, 1834). *Zoological Journal of the Linnean Society* 151:809–831.
- Fry, B.G., W. Wüster, R.M. Kini, V. Brusic, A. Khan, D. Venkataraman, and A.P. Rooney. 2003. Molecular evolution and phylogeny of elapid snake venom three finger toxins. *Journal of Molecular Evolution* 57:110–129.
- Gillingham, J.C. 1987. Social behavior, Pp. 184–209 in R. A. Seigel, J.T. Collins, and S.S. Novak (Eds.), *Snakes: Ecology and Evolutionary Biology*. Macmillan Publishing Company, USA.
- Goldberg, S.R. 1997. Reproduction in the western coral snake, *Micruroides euryxanthus* (Elapidae), from Arizona and Sonora, Mexico. *Great Basin Naturalist* 57:363–365.
- Goldberg, S.R. 2004. Notes on reproduction in the Central American coral snake, *Micrurus nigrocinctus* (Serpentes: Elapidae) from Costa Rica. *Caribbean Journal of Science* 40:420–422.
- Greene, H.W. 1997. *Snakes: The Evolution of Mystery in Nature*. University of California Press, USA.
- Hay, W.W., E. Soeding, R.M. DeConto, and C.N. Wold. 2002. The Late Cenozoic uplift: climate change paradox. *International Journal of Earth Sciences* 91:746–774.
- Heise, P.J., L.R. Maxson, H.G. Dowling, and S.B. Hedges. 1995. Higher-level snake phylogeny inferred from mitochondrial DNA sequences of 12S rRNA and 16S rRNA genes. *Molecular Biology and Evolution* 12:259–265.
- Jackson, D.R., and R. Franz. 1981. Ecology of the eastern coral snake (*Micrurus fulvius*) in northern peninsular Florida. *Herpetologica* 37:213–228.
- Keogh, J.S. 1998. Molecular phylogeny of elapid snakes and a consideration of their biogeographic history. *Biological Journal of the Linnean Society* 63:177–203.
- Marques, O.A.V. 1996. Growth of the coral snake, *Micrurus corallinus* (Elapidae), in southeastern Atlantic forest in Brazil. *Amphibia-Reptilia* 17:277–285.
- Marques, O.A.V. 2002. Natural history of the coral snake *Micrurus decoratus* (Elapidae) from the Atlantic forest in southeastern Brazil, with comments on mimicry. *Amphibia-Reptilia* 23:228–232.
- Marques, O.A.V., A. Eterovic, and I. Szazima. 2004. *Snakes of the Brazilian Atlantic Forest: An Illustrated Field Guide for the Serra do Mar Range*. Holos Editora, Ribeirão Preto, Brazil.
- Marques, O.A.V., S.M. Almeida-Santos, and M. Rodrigues. 2006. Activity patterns in coralsnakes genus *Micrurus* (Elapidae) in south and southeastern Brasil. *South American Journal of Herpetology* 2:99–105.
- Martins, M., and M.E. Oliveira. 1998. Natural history of snakes in forests of the Manaus Region, Central Amazonia, Brazil. *Herpetological Natural History* 6:78–150.
- Mathies, T. 2011. Reproductive cycles of tropical snakes, Pp. 511–550 in R.D. Aldridge, and D.M. Sever (Eds.), *Reproductive Biology and Phylogeny of Snakes*. Science Publishers, USA.
- Ota, H., and S. Iwanaga. 1996. Field observation of the combat dance in *Hemibungarus japonicus boettgeri* (Squamata: Elapidae). *Akamata* 13:13–14. [In Japanese.]
- Pizzatto, L., and O.A.V. Marques. 2007. Reproductive ecology of Boine snakes with emphasis on Brazilian species and a comparison to pythons. *South American Journal of Herpetology* 2:107–122.
- Pizzatto, L., M. Cantor, J.L. Oliveira, O.A.V. Marques, V. Capovilla, and M. Martins. 2008a. Reproductive ecology of dipsadine snakes, with emphasis on South American species. *Herpetologica* 62:168–179.
- Pizzatto, L., R.S. Jordão, and O.A.V. Marques. 2008b. Overview of reproductive strategies in Xenodontini

- (Serpentes: Colubridae: Xenodontinae) with new data for *Xenodon newwiedii* and *Waglerophis merremii*. 2008. *Journal of Herpetology* 42:153–162.
- Quinn, H.R. 1979. Reproduction and growth of Texas coral snake (*Micrurus fulvius tenere*). *Copeia* 1979:453–463.
- Rage, J.C. 1987. Fossil history, Pp. 51–76 in R.A. Seigel, J.T. Collins, and S.S. Novak (Eds.), *Snakes: Ecology and Evolutionary Biology*. Macmillan Publishing Company, USA.
- Roze, J.A. 1996. Coral Snakes of the Americas: Biology, Identification and Venoms. Krieger Publishing Company, USA.
- Saint-Girons, H. 1982. Reproductive cycles of male snakes and their relationships with climate and female reproductive cycles. *Herpetologica* 38:5–16.
- Seigel, R.A., and N.B. Ford. 1987. Reproductive ecology, Pp. 210–252 in R.A. Seigel, J.T. Collins, and S.S. Novak (Eds.), *Snakes: Ecology and Evolutionary Biology*. Macmillan Publishing Company, USA.
- Shine, R. 1977a. Reproduction in Australian elapid snakes. I. Testicular cycles and mating seasons. *Australian Journal of Zoology* 25:647–653.
- Shine, R. 1977b. Reproduction in Australian elapid snakes. II. Female reproductive cycles. *Australian Journal of Zoology* 25:655–666.
- Shine, R. 1978. Sexual size dimorphism and male combat in snakes. *Oecologia* 33:269–277.
- Shine, R. 1980. Comparative ecology of three Australian snake species of the genus *Cacophis* (Serpentes, Elapidae). *Copeia* 1980:831–838.
- Shine, R. 1994. Sexual dimorphism in snakes revisited. *Copeia* 1994:326–356.
- Shine, R. 2003. Reproductive strategies in snakes. *Proceedings of the Royal Society B: Biological Sciences* 270:995–1004.
- Slowinski, 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.
- Slowinski, J.B., J. Boundy, and R. Lawson. 2001. The phylogenetic relationships of Asian coral snakes (Elapidae: *Calliophis* and *Maticora*) based on morphological and molecular characters. *Herpetologica* 57:233–245.
- Solórzano, A., and L. Cerdas. 1988. Ciclos reproductivos de la serpiente coral *Micrurus nigrocinctus* (Serpentes: Elapidae) en Costa Rica. *Revista de Biología Tropical* 36:235–239.

Accepted: 12 October 2012

Associate Editor: Sarah Woodley