

# REPRODUCTION IN NEOTROPICAL PITVIPERS, WITH EMPHASIS ON SPECIES OF THE GENUS *BOTHROPS*

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**ABSTRACT:** Data on reproductive cycles, sperm storage by females, and parthenogenesis are presented for multiple species of Neotropical pitvipers of the genus *Bothrops*. Reproductive tracts of 13 species (*B. alternatus*, *B. ammodytoides*, *B. bilineatus*, *B. erythromelas*, *B. insularis*, *B. itapetiningae*, *B. jararaca*, *B. jararacussu*, *B. leucurus*, *B. moojeni*, *B. neuwiedi*, *B. pradoi*, and *B. taeniatus*) were examined for stage of follicular maturation (non-vitellogenic vs vitellogenic), presence of spermatozoa in the oviduct, and presence of muscular twisting and convolution of the uterus, referred to hereafter as uterine muscular twisting (UMT), which is hypothesized to have a similar function as copulatory plugs described in other species of snakes. These data, combined with published information, indicate that sexual activities (i.e., courtship, mating, and male-male fighting) occur primarily in austral autumn (April to June). In females, follicular growth (e.g., vitellogenesis) and long-term sperm storage (LTSS) occur in autumn and winter (July to September). Fertilization occurs in spring (October to December), and parturition in summer (January to March), which is the rainy season. This reproductive cycle, which has obligatory LTSS and suggests a biennial pattern in females, appears to be common in other species of viperid snakes. Our results show that similar reproductive patterns were found in six of the main lineages of the genus *Bothrops* in South America, as well as in pitvipers of other genera from temperate regions. Our preliminary conclusion indicates retention of an ancestral reproductive pattern, despite climatic changes in original and current habitats.

## INTRODUCTION

The reproductive biology of viperid snakes from temperate regions has been studied extensively (e.g., Saint Girons, 1957, 1975, 1982, 1985; Fitch, 1970; Blem, 1981; Duvall et al., 1982, 1992, 1993; Seigel and Ford, 1987; Schuett, 1992; Schuett et al., this volume), but few studies concern tropical taxa (e.g., Fitch, 1982). Of the Neotropical pitvipers, an overview of the natural history of *Bothrops asper* (Sólorzano and Cerdas, 1989), *B. jararaca* (Sazima, 1992), *B. moojeni* (Leloup, 1975, 1984), anecdotal data on the biology of *B. insularis* (Amaral, 1921; Hoge et al, 1959; Federsoni et al, 1987; Duarte et al, 1995), and recent information on *Crotalus durissus terrificus* (Salomão et al., 1995; Almeida-Santos and Salomão, 1997; Almeida-Santos et al., 1998; Salomão and Almeida-Santos, this volume) are among the few studies available. Consequently, lack of information on species of Neotropical pitvipers hinders robust comparative analyses of snake mating systems (Seigel and Ford, 1987; Duvall et al., 1992, 1993) and related topics such as population dynamics (Vitt, 1987).

Several reproductive events are used to classify (categorize) reproductive cycles. In females, the type (or pattern) and timing of follicular maturation (i.e., primary and secondary vitellogenesis) and ovulation are among the most important events (Aldridge 1979, 1982). Secondary vitellogenesis, the primary yolking phase, requires more time for completion than primary vitellogenesis (e.g., Dessauer and Fox, 1959). Further,

the occurrence and duration of secondary vitellogenesis are variable depending on species, time of year, duration of the active season, prey availability, and quantity of fat reserves (Blem, 1981, 1982; Diller and Wallace, 1984; Macartney and Gregory, 1988; Macartney et al., 1990; Duvall et al., 1992; Schuett, 1992; Naulleau and Bonnet, 1996; Beaupre, this volume; Bonnet et al., this volume).

Another important event used to classify reproductive cycles is seasonal timing of mating (Fitch, 1970; Shine, 1977a, b; Saint Girons, 1982; Schuett and Gillingham, 1986; Seigel and Ford 1987; Schuett, 1992; Schuett et al., 1997b, this volume). Information on mating periods has been used to infer onset and development of vitellogenesis, spermatogenesis, and hormonal production and secretion (Crews, 1984, 1991; Crews et al 1984; Crews and Gans, 1992), although these activities do not always coincide (Schuett, 1992). In many species of viperids, for example, females show the capacity of oviductal sperm storage for prolonged periods (long-term sperm storage, LTSS) prior to ovulation; hence, timing of certain reproductive events (e.g., mating and fertilization) can be highly asynchronous (Schuett, 1992). Finally, gestation and timing of parturition have been used to infer reproductive cycles in snakes, but their utility is limited due to the presence of LTSS by females (Saint Girons, 1975, 1982; Schuett and Gillingham, 1986; Gist and Jones, 1987, 1989; Schuett, 1992). As a result of climatic conditions and availability and abundance of resources (e.g., prey, shelter), some authors have reported that reproductive cycles of tropical snakes are (or may be) aseasonal (Fitch, 1982; Vitt, 1983; Seigel and Ford, 1987).

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**Table 1.** Seasonal reproductive condition and occurrence of uterine muscular twisting (UMT) in 13 species of *Bothrops*, *Crotalus durissus terrificus*, and three species of temperate pitvipers. Vitellogenic stage (S = secondary, P = primary). \* = temperate zone species. \*\* = see Figure 3 for austral seasons.

Species	Vitellogenic stage	UMT	Date**
<i>Bothrops ammodytoides</i>	S	Yes	No information
	P	Yes	October
<i>B. alternatus</i>	S	Yes	May to July
	P	Yes	March and November
<i>B. itapetiningae</i>	S	Yes	June
<i>B. neuwiedi</i>	S	Yes	October
	P	Yes	January
<i>B. erythromelas</i>	P	Yes	January
<i>B. jararaca</i>	S	Yes	April to September
	P	Yes	September
<i>B. insularis</i>	S	Yes	April to September
<i>B. jararacussu</i>	S	Yes	May to September
	P	Yes	July
<i>B. bilineatus</i>	S	Yes	September
<i>B. taeniatus</i>	S	Yes	July
<i>B. moojeni</i>	S	Yes	June
	P	Yes	February and March
<i>B. pradoi</i>	P	Yes	July and September
<i>B. leucurus</i>	S	Yes	April
	P	Yes	June
<i>Crotalus durissus terrificus</i>	S	Yes	April to September
<i>C. viridis</i> *	S	Yes	May
<i>Agkistrodon contortrix</i> *	P	Yes	March and May
<i>A. piscivorous</i> *	S	Yes	May

Furthermore, obligatory LTSS is presumed to be absent in tropical taxa (Saint Girons, 1982; but see Schuett, 1992). Aseasonal reproduction in pitvipers, however, is not supported by our data, and obligatory LTSS, for example, has recently been described in the Neotropical rattlesnake, *Crotalus durissus terrificus* (Almeida-Santos and Salomão, 1997).

Herein we review and describe reproductive patterns of Neotropical pitvipers, with emphasis on species of the genus *Bothrops*. We discuss timing of mating and obligate LTSS during austral winter by females. In addition, the evolutionary significance of LTSS is discussed in the context of other viperid snakes.

## METHODS

Female reproductive tracts of preserved museum specimens (N = 196) of species of the genus *Bothrops*, collected in different months, were inspected. We recorded the presence or absence of vitellogenic follicles in the ovary or mature oviductal ova, as well as the overall condition of the uterus (e.g., indication of past or recent activity). Live snakes (N = 162) brought to our institution were sacrificed and examined for

reproductive condition. Cloacal smears were performed to detect the presence of sperm (live or dead), and hence, recent mating. Additional snakes (N = 200) were maintained in captivity, either isolated or in groups, and reproductive tracts of females were examined following parturition. From 1986 to 1998, we recorded the number of juvenile and adult *Bothrops* (both sexes) brought to our institution to infer seasonal activity patterns. The seasonal frequency of animals was evaluated by a randomized block analysis of variance by rank (Friedman's Test), followed by Dunn's multiple comparison test (Zar, 1984). Most of the main lineages of *Bothrops* are included in this analysis (see Salomão et al., 1997, 1999). Information for 13 species of *Bothrops* was analyzed and compared to published data. Localities of specimens analyzed in this study are presented in Table 4.

## TIMING OF MATING AND MALE-MALE FIGHTING

In many species of viperids, timing of mating is dissociated from timing of fertilization (Table 2). This can occur, for example, when mating occurs in late

**Table 2.** Timing of mating, gestation (time from mating to parturition), and parturition dates for 12 species of the genus *Bothrops*. See Figure 3 for austral seasons.

Species	Mating	Gestation (days)	Parturition dates	Reference
<i>Bothrops alternatus</i>	May/June	173	March/April	Araujo and Ely, 1980
	February		July	Pezzano, 1986
<i>B. itapetiningae</i>	No information	300	March	Nascimento and Brandão, 1998
<i>B. neuwiedi</i>	May/June	283–356	March/April	Chaves et al. 1993; Alves et al., 1998; Almeida, 1999
<i>B. erythromelas</i>	April/May	400	January/February	Machado and Cotta, 1998
<i>B. bilineatus</i>	July/August	191–208	February	Argolo, 1996
<i>B. jararaca</i>	April/May	240–300	February/March/ April	Sazima, 1992; S. Almeida-Santos, unpublished
<i>B. insularis</i>	July/August/September	120–150	March/April/June	Amaral, 1921; M. Furtado and O. Marques, pers. comm.
<i>B. jararacussu</i>	May/June	200–300	March	Lula et al., 1993; Marques, 1998b
<i>B. moojeni</i>	March/April/May	200–300	December/January February	Leloup, 1975 S. Almeida-Santos, unpublished
<i>B. atrox</i>	March/April	161–343	April/May	Fernandes et al., 1993
<i>B. leucurus</i>	No information	80	January	Lira-da-Silva et al., 1994, 2000;
		147	January/April	S. Almeida-Santos, unpublished
<i>B. pradoi</i>	May	—	—	G. Puerto, pers. comm.

summer and/or autumn, and fertilization occurs in spring and/or summer (Schuett, 1992). In viperids, copulation can be preceded by certain social interactions, such as male-male fighting (MMF) and precopulatory guarding (Shine, 1978, 1994; Shine et al., 1981; Andrén and Nilson 1981; Carpenter, 1986; Andrén, 1986; Schuett and Gillingham, 1989; Duvall et al., 1992, 1993; Aldridge, 1993; Madsen et al., 1993; Schuett, 1997; Almeida-Santos et al., 1998).

Generally, MMF occurs only during the mating season(s), and its function, as we currently understand it, is to establish dominant-subordinate relations for priority-of-access to mates (Andrén, 1986; Madsen et al., 1993; Schuett, 1996, 1997). Evidence thus far indicates that MMF in viperids is activated and maintained by elevated levels of circulating sex steroids, such as androgens and estrogens (Schuett et al., 1997b, this volume), which are under the control of the hypothalamo-pituitary-gonadal (HPG) axis (see Salomão and Almeida-Santos, this volume). In South American taxa, autumnal and early winter MMF has been described in *C. d. terrificus* (Santos et al., 1990; Salomão et al., 1995; Almeida-Santos and Salomão, 1997; Almeida-Santos et al., 1998) and in several species of *Bothrops*. The species of *Bothrops* include *B. atrox* (late March and April; Cardoso et al., 1993) from the Amazon Basin, and *B. moojeni* (April and May; Leloup, 1975; S. Almeida-Santos and M. Furtado, unpublished) from central Brazil, and *B. leucurus* from the Atlantic forest (early May; S.

Cardoso, pers. comm). These three populations belong to the monophyletic *B. atrox* complex (Wüster et al., 1997, 1999, this volume).

Male-male fighting tends to be expressed in taxa where male-biased sexual size dimorphism occurs (e.g., *Agkistrodon*, *Bitis*, *Crotalus*, *Calloselasma*, *Sistrurus*, *Trimeresurus*, and *Vipera*) (Shine, 1978, 1994; Duvall et al., 1992; Greene, 1992; Almeida-Santos et al., 1998). In many species of *Bothrops*, however, there is a clear female-biased sexual size dimorphism, as is the case in *B. alternatus* (Haller and Martins, 1999), *B. asper* (Solórzano and Cerdas, 1989), *B. atrox* (W. Wüster, pers. comm.), *B. itapetiningae* (Valdujo et al., 1999), *B. jararaca* (Janeiro-Cinquini et al., 1992), *B. jararacussu* (Marques, 1998a), *B. moojeni* (Leloup, 1975; Nogueira and Valdujo, 1999), and *B. neuwiedi pauloensis* (Valdujo and Nogueira, 1999). Interestingly, MMF has been documented in *B. atrox* and *B. moojeni*, two species where adult females attain greater snout-vent length and mass than adult males. This size and mass correlation is similar to that found in European adders (e.g., *Vipera berus*; Andrén, 1986).

In many cases, the winner of a fight locates a nearby female and copulates with her (Madsen et al., 1993; Schuett, 1997). Mating has been recorded in late austral summer and/or autumn in *B. atrox* (March and April) (Fernandes et al., 1993), *B. erythromelas* (April and May) (Machado and Cotta, 1998), *B. jararaca* (April and May) (S. Almeida-Santos, unpublished) and *B. jararacussu* (May and June) (Lula et al., 1993),

**Table 3.** Mean litter size for 12 taxa of the genus *Bothrops* and *Bothriechis schlegelii*.

Species	Mean number of offspring	Reference
<i>B. alternatus</i>	6.6	Murphy and Mitchell, 1984
	8	Leitão-de-Araujo and Pezzarolo, 1974
	12	Pezzano, 1986
<i>B. neuwiedi</i>	3.5	Murphy and Mitchell, 1984
	13	Alves et al., 1998
<i>B. n. pubescens</i>	11.8	Almeida, 1999
<i>B. n. pauloensis</i>	9.3	Valdujo et al., 2002
<i>B. erythromelas</i>	11	Lira-da-Silva et al., 1994
<i>B. jararaca</i>	10.7	Sazima, 1992
	13.3	Breno et al., 1990
<i>B. insularis</i>	6.5	Hoge et al., 1959
<i>B. jararacussu</i>	13 to 37	Marques, 1998b
<i>B. atrox</i>	31	Alves et al., 1998
<i>B. moojeni</i>	14.4	Leloup, 1975
<i>B. leucurus</i>	15	Lira-da-Silva et al., 1994
	8.5	Sant'Anna et al., 2001
<i>B. asper</i>	8	Cruz et al., 1989
	15	Solórzano and Cerdas, 1989
<i>Bothriechis schlegelii</i>	20	Antonio, 1980

*B. moojeni* (April and May) (Leloup, 1975), and *B. neuwiedi* (March) (Almeida, 1999). In late autumn (May to early June) and the onset of winter, mating has been observed in *B. neuwiedi* (Chaves et al., 1993; Alves et al., 1998) and *B. pradoi* (G. Puerto, pers. comm.). In *B. bilineatus*, coitus has been observed in July and August (winter) (Argolo, 1996), and in *B. insularis* (Amaral, 1921), mating occurs from July to September (winter). In the former, however, observations were made in captivity, where temperature and humidity are often held constant, and in the latter it is not clear whether the observation occurred in nature or captivity (Amaral, 1921). A field observation of courtship between a male and an intersex (= female with hemiclitoris) individual of *B. insularis* was recorded in March, 2002 (M. Martins, pers. comm.; see Fig 1); another observation of courtship between a male and an intersex female, in a tree, was recorded on 25 July 1995 (mid-winter) (O. Marques, pers. comm.), which emphasizes the arboreal habits of this species (Amaral, 1921). Winter mating in *B. insularis* may be attributed to climatic conditions on Queimada Grande Island, where this species occurs; climatic conditions on the island are unusually constant, even in winter (July to September) (Duarte et al., 1995). Captive *B. alternatus* maintained outside Brazil (Northern Hemisphere) mated in mid winter (February) (Pezzano, 1986) (Table 2).

#### LONG-TERM SPERM STORAGE, UTERINE MUSCULAR TWISTING, AND DELAYED FERTILIZATION

Early reports inferred the existence of sperm storage in female snakes, based on birthing events by captive females after long periods of isolation from males (Fox, 1977). Sperm storage is a common phenomenon that occurs in lizards, snakes, turtles, and in other ectothermic vertebrates such as fishes (Woodward, 1933; Atsatt, 1953; Fox, 1956, 1963; Stewart, 1972; Gist and Jones, 1987; Kumari et al., 1990). In many species of snakes from temperate regions, sperm storage is an important (even obligate), mechanism that allows fertilization to be delayed (Fukada, 1986; Schuett, 1992). Nevertheless, parturition occurs during the most favorable time of the year for offspring survival (Shine, 1977b; Vitt, 1983).

In some species of reptiles, reproductive cycles are synchronized (e.g., maturation of male and female gametes) and ovulation occurs shortly following copulation (e.g., Duvall et al., 1982; Fitch, 1982). This pattern is commonly observed in birds and mammals, and characterizes a reproductive pattern where events between the sexes tend to be coupled. Long-term sperm storage (LTSS) and delayed fertilization, on the other hand, represent uncoupling of reproductive events between the sexes, and permit mating in one season and follicular development, fertilization,



**Fig. 1.** Courtship interaction between a male and an intersex (= female with hemiclitoris) *Bothrops insularis*, recorded *in situ*, in March 2002. Photo by Marcio Martins.

and parturition in another (Birkhead and Møller, 1993). Further, it may permit a female to lay several fertile clutches of eggs from a single mating (e.g., Tryon, 1984; Marques, 1996).

In species of snakes from temperate regions, particularly pitvipers, mating can be restricted to summer and/or autumn and sperm must be stored in the female reproductive tract through winter, six (or more) months prior to ovulation. When mating occurs only in spring, sperm is stored in the oviduct for two to five weeks prior to ovulation; this is categorized as short-term sperm storage (STSS) (Hoffman and Wimsatt, 1972; Halpert et al., 1982; Schuett, 1992).

The duration of successful sperm storage by female reptiles is, indeed, impressive. Nonetheless, few studies show the exact location of stored sperm, and descriptions of specialized structures in the oviduct of snakes are limited (Hoffman and Wimsatt, 1972; Gist and Jones, 1987, 1989; Saint Girons, 1982; Halpert et al., 1982; Kumari et al., 1990; Schuett, 1992; Perkins and Palmer, 1996; Almeida-Santos and Salomão, 1997). The specific location of sperm storage in the female differs among species and may include specialized

seminal receptacles located in the anterior uterus (infundibulum) (Fox, 1956, 1977; Saint Girons, 1962; Aldridge, 1992), or in the posterior regions of the uterus, which can be convoluted and contracted (referred to herein as uterine muscular twisting, UMT). It appears that the function of UMT is similar to that of a copulatory plug, which was first described in temperate colubrid snakes, *Nerodia* and *Thamnophis* (Devine, 1975, 1977).

In *C. d. terrificus*, ovulation in spring apparently stimulates UMT to relax and influences spermatozoa located in the posterior uterus to migrate anteriorly. Histological analyses show that UMT is present for ca. four months (winter; Almeida-Santos and Salomão, 1997). Uterine muscular twisting apparently permits *C. d. terrificus* to store sperm for only one season after mating, and thus might explain the observation that captive *C. d. terrificus* were unable to produce more than one litter after isolation from males (Almeida-Santos and Salomão, 1997).

The reproductive cycle of *Bothrops* is similar to that described for certain species of *Crotalus* with regard to the presence of obligatory LTSS in austral

**Table 4.** Localities of specimens examined in this study.

Species	Locality
<i>Agkistrodon contortrix</i>	North Carolina and Texas, USA
<i>A. piscivorus</i>	North Carolina and South Carolina, USA
<i>Bothrops ammodytoides</i>	Buenos Aires, Argentina
<i>B. alternatus</i>	Minas Gerais, Rio Grande do Sul, São Paulo, Brazil
<i>B. itapetiningae</i>	Distrito Federal, São Paulo, Brazil
<i>B. neuwiedi</i>	Goiás, Rio Grande do Sul, São Paulo, Brazil
<i>B. erythromelas</i>	Bahia, Pernambuco, Brazil
<i>B. jararaca</i>	Paraná, São Paulo, Brazil
<i>B. insularis</i>	Queimada Grande Island: São Paulo, Brazil
<i>B. jararacussu</i>	Paraná, Santa Catarina, São Paulo, Brazil
<i>B. bilineatus</i>	Amazonas, Espírito Santo, Rondônia, Brazil
<i>B. taeniatus</i>	Amazonas, Mato Grosso, Pará, Brazil
<i>B. moojeni</i>	Goiás, São Paulo, Brazil
<i>B. leucurus</i>	Bahia, Brazil
<i>B. pradoi</i>	Espírito Santo, Brazil
<i>Crotalus durissus terrificus</i>	Minas Gerais, São Paulo, Brazil
<i>C. viridis</i>	New Mexico and Texas, USA

winter (July to September), UMT (Fig. 2), and delayed fertilization until spring (October to December). We observed the presence of UMT in mated females of 12 species of *Bothrops* (*B. alternatus* (N = 17), *B. ammodytoides* (N = 6), *B. bilineatus* (N = 15), *B. insularis* (N = 7), *B. itapetiningae* (N = 7), *B. jararaca* (N = 16), *B. jararacussu* (N = 8), *B. leucurus* (N = 5), *B. moojeni* (N = 126), *B. neuwiedi* (N = 6), *B. pradoi* (N = 21), and *B. taeniatus* (N = 13). All females were examined in late autumn (June) and winter (Table 1). Microscopic examination of the right uterus showed the presence of live spermatozoa in all animals. In most cases, females had mature (yolked) follicles, evidence that secondary vitellogenesis was complete (or nearly complete). Early yolk deposition in *Bothrops* (e.g., *B. jararacussu*) can be observed in follicles as small as 10 mm diameter from late March to early September (Janeiro-Cinquini et al., 1993b). In all species of *Bothrops* our study, embryonic development was clearly visible from October to March (spring and summer).

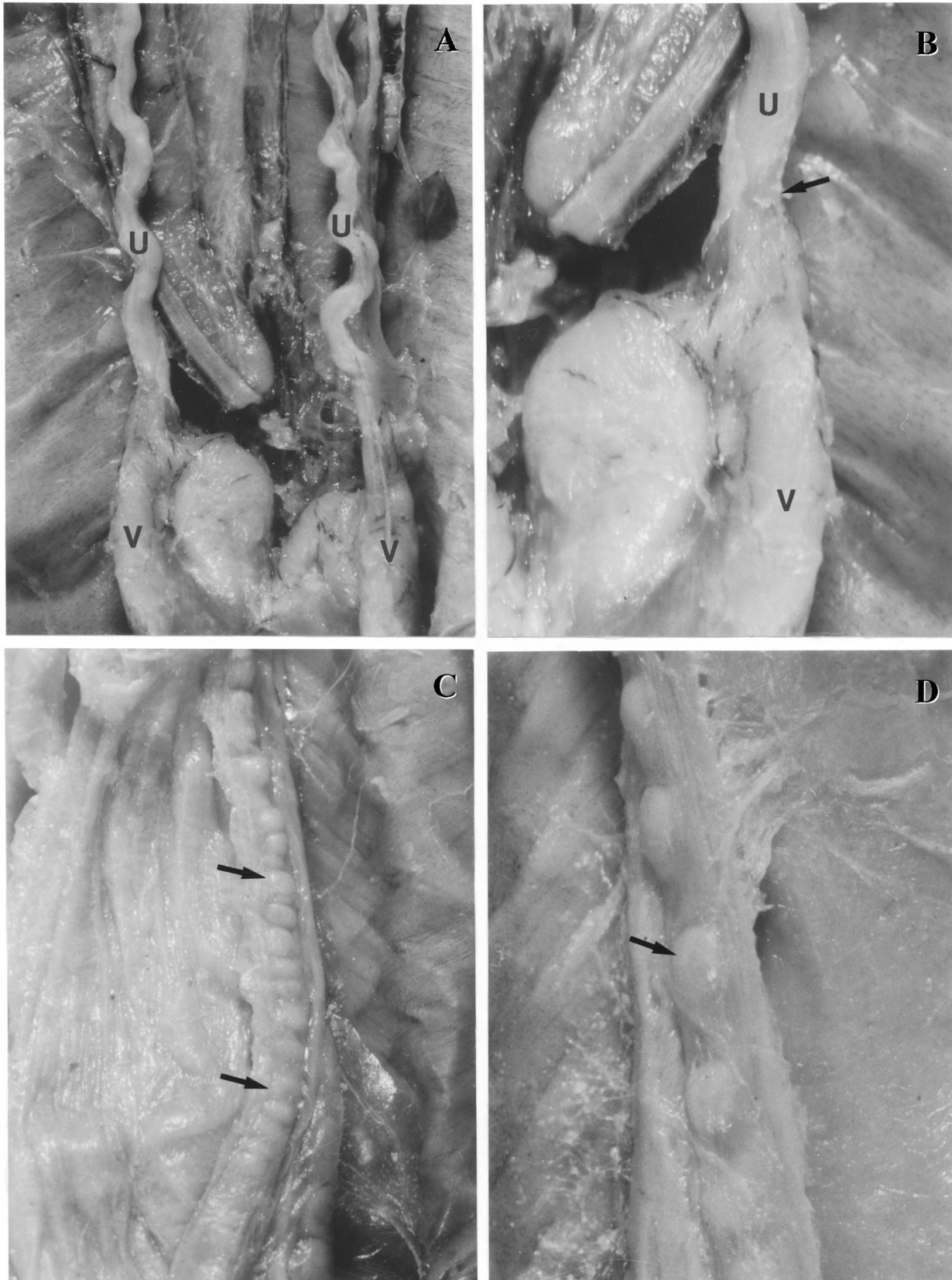
#### PARTHENOGENESIS

Parthenogenesis is a reproductive strategy documented in squamate reptiles, primarily in multiple lineages of all-female populations (or nearly so) of lizards and one species of typhlopoid snake, *Ramphotyphlops braminus* (Darevsky et al., 1985). Schuett et al. (1997a) provided evidence that production of embryos or offspring may occur in captivity by facultative automictic parthenogenesis (FAP) in four

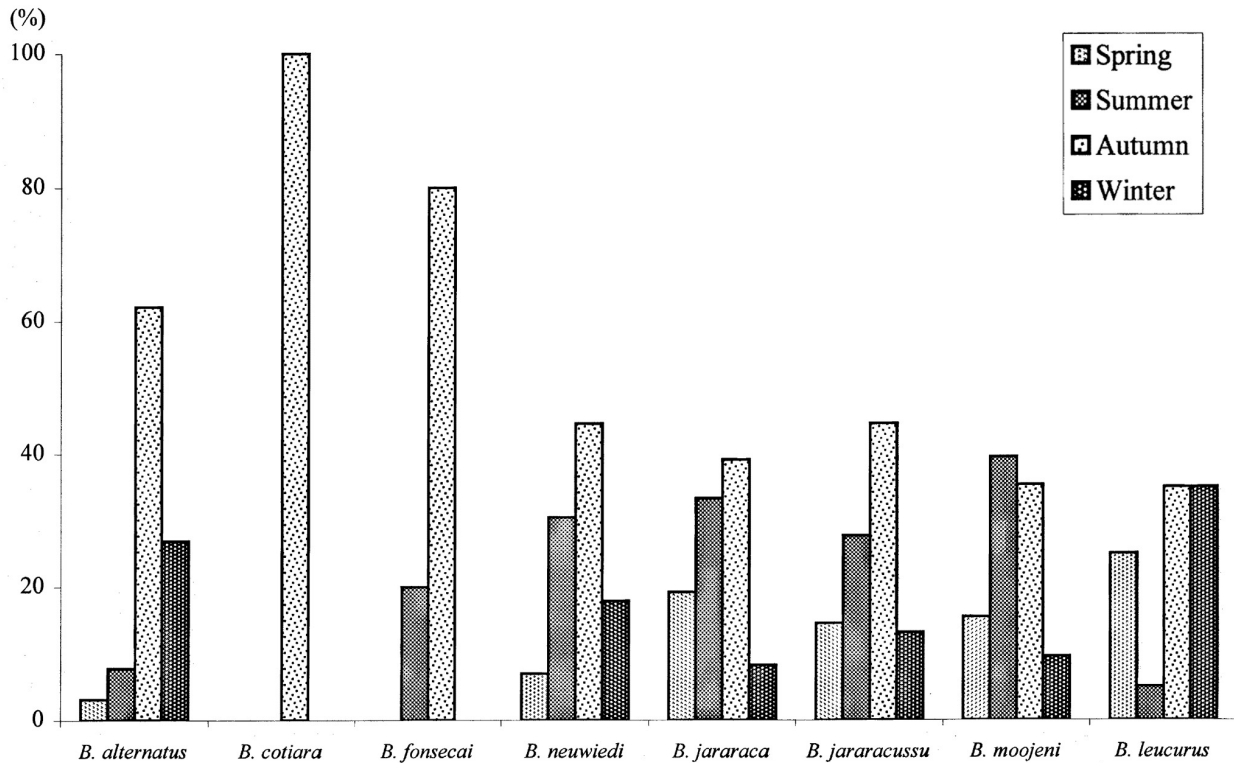
species of snakes in three different lineages. These included two species of viperids (*Crotalus horridus* and *C. unicolor*) and two species of natricine colubrids (*Thamnophis elegans* and *T. marcianus*). Also, Dubach et al. (1997) described a case of FAP in a species of acrochordid (*Acrochordus arafurae*). Extreme cases of supposed LTSS in snakes, ranging from four to seven years, may be examples of this unusual type of parthenogenesis (Dubach et al., 1997; Schuett et al., 1997a). Obviously, the results of these two studies strongly indicate that re-examination of published accounts of cases of LTSS in female reptiles is required (M. Salomão et al., unpublished).

Two species of *Bothrops* held in captivity produced embryos and offspring, highly suspected to be through FAP. In January 1998, a 6-year-old female *B. moojeni*, born in captivity and reared in the absence of males, gave birth to two males, one alive and one dead, three embryos in different stages of development, and 46 unfertilized eggs. Cytological studies carried out on both neonates showed that they were diploid (Batistic et al., 1999). Production of diploid males suggests that the mechanism is FAP (Schuett et al., 1997a).

In 1995, an individual *B. insularis* maintained in captivity at the Instituto Butantan for eight years and isolated from males produced unfertilized eggs. Two years later (April 1997) she produced a fully developed offspring of normal appearance and 13 unfertilized eggs. Unfortunately, data on karyotypes (to determine ploidy) and sex were not recorded. It is well known,



**Fig. 2.** Uterine muscular twisting (UMT) in *Bothrops*. (A) *B. jararacussu*: general view showing the uterus (U) and vagina (V) (x 2.0). (B) *B. jararacussu*: detail of the junction (arrow) between the uterus (U) and the vagina (V) (x 3.5). (C) *B. jararacussu*: segment of UMT (arrows) (x 2.2). (D) *B. jararaca*: detail of the UMT that retains sperm during the winter (arrow) (x 7.5).



**Fig. 3.** Percentage of juvenile snakes of the genus *Bothrops* that arrived at the Instituto Butantan between 1986 and 1998. *B. alternatus* (N = 193); *B. cotiara* (N = 2); *B. fonsecai* (N = 5); *B. newwiedi* (N = 298); *B. jararaca* (N = 4,675); *B. jararacussu* (N = 426); *B. moojeni* (N = 503) and *B. leucurus* (N = 20).

however, that *B. insularis*, endemic to Queimada Grande Island in the coastal area of the state of São Paulo, Brazil, is unique among reptiles in that intersex animals predominate (50%), males are less common (40%), and true females (10%) are infertile (Hoge et al., 1959; Mallmann-Franco and Franco, 1998). In this case, as in unisexual populations of lizards (Cole, 1984; Dawley and Bogart, 1989; Nussbaum, 1980; Volobouev et al., 1993), parthenogenesis would appear to confer evolutionary advantages, and the capacity to show FAP is highly plausible. Also, intersex females have been recorded in *B. jararaca*, *B. jararacussu*, and *B. moojeni* (Mallmann-Franco and Franco, 1998, 1999), which suggest that this condition is more widely present in *Bothrops* than previously thought. Of the species mentioned above, however, *B. insularis* is the only one to show a low degree of fecundity, since its litters are smaller than those of close relatives (Hoge et al., 1959; see Table 3).

Several questions remain unanswered regarding FAP. For example, if ovulation is stimulated by copulation, as is demonstrated in Old World vipers, (Volsøe, 1944; Nilson and Andrén, 1982; Andrén and Nilson, 1987; Bona-Gallo and Licht, 1983; Luiselli,

1993), what would trigger ovulation in a system where FAP occurs? Recently, we (Almeida-Santos and Salomão, 1999) showed that captive conditions do not interfere with follicular development (e.g., vitellogenesis) in *C. d. cascavella*. In animals maintained for 29 years in the absence of males, copulation was not an obligatory component for ovulation in this and other rattlesnakes (*C. d. collilineatus* and *C. d. terrificus*), and in *B. leucurus* (S. Almeida-Santos, unpublished).

#### TIMING OF PARTURITION

Activity patterns and parturition have been inferred based on the arrival of snakes (adults and neonates) at the Instituto Butantan (for details, see Fowler and Salomão, 1994; Reis-Duarte, 1995, 1997; Salomão et al., 1995; Marques et al., 2001). Data obtained over a 12-year period show a unimodal peak of activity of juveniles between late February (summer) and early May (autumn), indicating that those periods are primary birthing times in *B. alternatus*, *B. cotiara*, *B. fonsecai*, *B. itapetiningae*, *B. jararaca*, *B. jararacussu*, *B. leucurus*, *B. moojeni*, and *B. newwiedi* (Fig. 3). In all species investigated, there was a significant rate of



recruitment in autumn ( $\chi^2 = 14.47$ ,  $P < 0.0023$ ). These data also coincide with the incidence of snakebite, primarily *B. jararaca*, which peaks in late summer (March) (Ribeiro and Jorge, 1990; Cardoso et al., 1993).

In captivity, births were more frequent in summer and early autumn (Table 2). Parturition dates of *B. bilineatus* in February (Argolo, 1996), *B. erythromelas* in January and February (Machado and Cotta, 1998), *B. insularis* in March (Amaral, 1921), February and April (S. Almeida-Santos, unpublished) and early July (M. Furtado, pers. comm.), *B. itapetiningae* in March (Nascimento and Brandão, 1998), *B. jararaca* in January and April (Sazima, 1992) and February, March and April (S. Almeida-Santos, unpublished), *B. jararacussu* in March (Lula et al., 1993; Marques, 1998b), and *B. leucurus* in January, February, March and April (Lira-da-Silva et al., 1994, 2000; S. Almeida-Santos, unpublished), and *B. neuwiedi* include February, March, and April (Chaves et al., 1993; Alves et al., 1998; Leitão-de-Araujo et al., 1998).

In Brazil, austral summer coincides with the rainy season, whereas autumn is coincident with the dry season. During summer, climatic conditions (e.g., temperature, rain, humidity) and abundance of food are highly favorable for the survival of juvenile snakes (Fitch, 1987), which explains, in part, their increase in activity during these months. Adult *B. jararaca* were shown to be more active in summer (Sazima, 1988; 1992) as opposed to adult *C. durissus* from southeastern Brazil, which are more active in autumn (Salomão et al., 1995). Accordingly, differences in activity pattern may be related to feeding habits, since juveniles in most species of *Bothrops* feed on amphibians, but later show an ontogenetic dietary shift to rodents. An ontogenetic change in diet, however, was not observed in *C. d. terrificus* (Salomão et al., 1995; Sant'Anna, 1999) nor in *B. alternatus*, *B. cotiara* and *B. fonsecai*, species that may feed exclusively on mammals (Haller and Martins, 2000; Martins et al., this volume). Thus, mid summer and early autumn birthing appears to be temperature-dependent for normal development of embryos rather than as a consequence of food availability.

Litter size in *Bothrops* is variable, but it is positively correlated with the size of the mother as shown for *B. itapetiningae* (Valdujo et al., 1999), *B. moojeni* (Nogueira and Valdujo, 1999), and *B. neuwiedi* (Valdujo and Nogueira, 1999). Females likely grow larger than males due to fecundity advantages (Shine, 1994). Litter size in *B. jararacussu*, one of the largest members of the genus *Bothrops*, ranges from one to 73

(W. Fernandes, pers. comm.); average litter size in *Bothrops* and *Bothriechis* is shown in Table 3.

#### REPRODUCTIVE CYCLES

The female reproductive cycle of *Bothrops* is similar to that of several species of temperate vipers (e.g., Luiselli, 1993; Andrén et al., 1997) and pitvipers (e.g., Schuett, 1992). Briefly, the cycle in Brazil begins with courtship and mating in autumn, secondary vitellogenesis occurs from early autumn (April, dry season) to early spring (October), long-term sperm storage (LTSS) in winter (July to September), ovulation, fertilization, and embryogenesis in spring (October to December) but in some cases extends to early summer (January), and parturition in late summer (March), the rainy season (Fig. 4). These events agree with those recorded for snakes from temperate areas (Seigel and Ford, 1987, Shine, 1977b; Macartney and Gregory, 1988).

Biennial (or greater) reproduction in female snakes is a consequence of energy reserves (i.e., body fat) (Derickson, 1976; Plummer, 1983; Shine, 1986; Naulleau and Bonnet, 1996; Beaupre, this volume; Bonnet et al., this volume). Consequently, frequency of reproduction (Bull and Shine, 1979) is dependent, in part, on nutritional status (Blem, 1982; Macartney and Gregory, 1988; Stearns, 1992).

Despite favorable climatic conditions and abundance of food in many tropical regions (Fitch, 1982; Vitt, 1983), the period between parturition (late summer) and the potential onset of vitellogenesis (late autumn to early winter) is relatively short. As a result, this brief period prevents females from restoring body fats necessary to initiate follicular yolking the same year (Shiroma, 1993, Janeiro-Cinquini et al, 1995). In captives, low energy reserves do not prevent female *Bothrops* from mating soon after producing offspring and storing sperm for the following season. A female *B. neuwiedi* from Rio Grande do Sul copulated on 7 June 1995, and produced a litter on 21 February 1997 (Alves et al., 1998), which suggests LTSS. The capacity to store sperm for more than one season explains why some females examined soon after capture had UMT and live spermatozoa, but no yolked follicles. In many cases, the presence of corpora lutea (and the absence of secondary vitellogenesis) was an indication of parturition the previous summer. The ability to store sperm for more than one season might be related to the presence of seminal receptacles in the uterus (Graber, 1940; Fox, 1956; Darevsky, 1971; Hoffman and Wimsatt, 1972; Halpert et al., 1982).

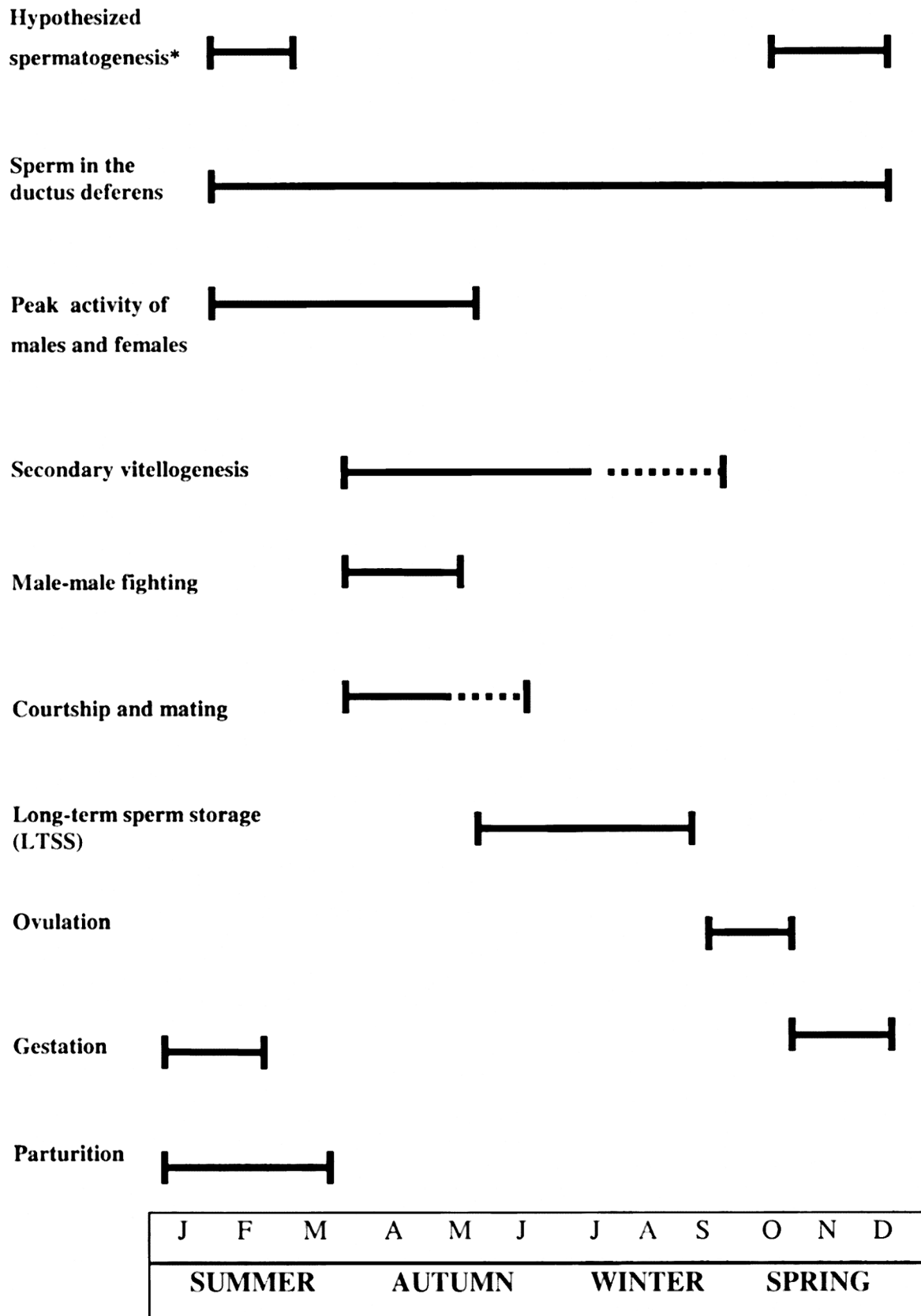
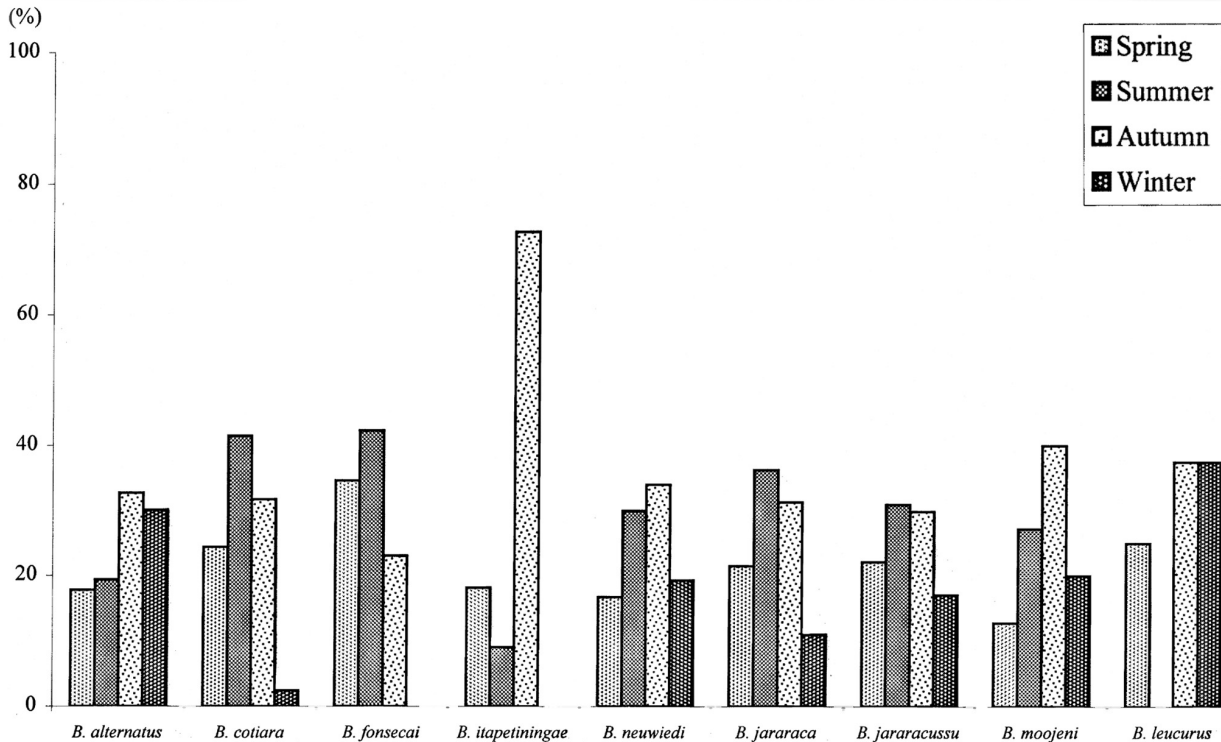


Fig. 4. Representation of reproductive events in the genus *Bothrops*. \* = data available only for *B. jararaca* (S. Almeida-Santos, unpublished).



**Fig. 5.** Percentage of adult snakes genus *Bothrops* that arrived at Instituto Butantan between 1986 and 1998. *B. alternatus* (N = 1156); *B. cotiara* (N = 41); *B. fonsecai* (N = 26); *B. itapetiningae* (N = 11); *B. jararaca* (N = 14,354); *B. neuwiedi* (N = 1,398); *B. jararacussu* (N = 1,008); *B. moojeni* (N = 2,840) and *B. leucurus* (N = 24).

Additional information on the morphology of the uterus of *Bothrops* is required to support this hypothesis. The possibility of yearly mating in *Bothrops* raises another question: what is the release for mating when females are not reproductively active (i.e., they are not undergoing secondary vitellogenesis)?

The above discussion reveals that LTSS is an obligatory component of reproduction in *Bothrops*, and that courtship, mating, and ovulation are dissociated (i.e., copulation occurs in autumn, and ovulation occurs in spring). The existence of LTSS in winter conveys an extended reproductive cycle, which is sometimes misinterpreted as a long gestation period [e.g., *B. jararaca* (Janeiro-Cinquini et al., 1993a; Marques, 1998b), *B. jararacussu* (Marques, 1998b), *B. moojeni* (Leloup, 1975), and *B. neuwiedi* (Almeida, 1999); see Table 2].

Due to the lack of detailed information on male reproductive cycles in tropical snakes some authors have tentatively proposed that they are aseasonal (Fitch, 1982; Seigel and Ford, 1987). The male cycle (or parts thereof) has been described in several temperate viperids (e.g., *Crotalus atrox*, *C. d. terrificus*, *C. scutulatus*, *C. viridis*, and *Agkistrodon piscivorus*; see Aldridge, 1975; 1979; Jacob et al., 1987; Johnson et al., 1982; Saint Girons, 1982; Goldberg and Rosen,

2000; Holycross and Goldberg, 2001; Schuett et al., this volume).

The onset of the spermatogenic cycle in *C. d. terrificus* occurs in early spring, spermatogenesis is completed in summer and early autumn, and spermatozoa are stored in the ductus deferens throughout the entire year (Almeida-Santos and Salomão, this volume), which suggests that males are capable of copulating at any time (Almeida-Santos et al., 1998). In *Bothrops jararaca*, testis mass is greatest in summer, and mobile spermatozoa in the ductus deferens is present year-round (Janeiro-Cinquini et al., 1993b). Tentatively, we suggest that this indicates a pattern of spermatogenesis similar to that of the Neotropical Rattlesnake, *Crotalus durissus*. Presence of mobile (live) spermatozoa in the ductus deferens year-round was also found in *B. neuwiedi* (Almeida, 1999).

Reproductive events such as male-male fighting and mating in *Bothrops* are seasonal. During periods of sexual activity, the number of snakes captured in nature and received at the Instituto Butantan increases (for details, see Salomão et al., 1995; Marques, 1996). In a 12-year period, our analyses show that (Fig. 5) autumn and summer are the predominant seasons when adult *Bothrops* are collected ( $\chi^2 = 11.02$ ;  $P < 0.01$ ), which is most likely due to increased activity

from reproduction and foraging. Moreover, as indicated above, the incidence of snakebite to humans is higher during this period (Ribeiro and Jorge, 1990; Lira-da-Silva and Carvalho, 1999). Autumnal and early winter activity peaks have been observed in *B. alternatus* (Mesquita and Brites, 1999) and *B. insularis* (Duarte, 1999), whereas in *B. atrox* the active season is in mid summer and autumn (Oliveira and Martins, 1999), and in *C. durissus* it is in autumn. For the above-mentioned species, these activity peaks coincide with mating and male-male fighting in captivity (Salomão et al., 1995; Almeida-Santos et al., 1998). Copulation in captivity, however, has been observed in winter (Table 2), but this is likely a consequence of captive conditions, such as constant temperature and abundance of food. Under stable (predictable) environmental conditions, captive snakes should be able to reproduce at times outside of their typical reproductive cycle (Vitt, 1983). Nonetheless, as in nature, mating occurs months prior to ovulation and obligate LTSS is present.

In conclusion, 13 of 30+ species of the genus *Bothrops* show seasonal reproduction, the presence of UMT and LTSS in winter. Species of *Bothrops*, such as *B. asper* in Costa Rica (Solórzano and Cerdas, 1989), and related genera, such as *Cerrophidion godmani* in Central America (Campbell and Solórzano, 1992), *Porthidium yucatanicum* in Mexico (McCoy and Censky, 1992), and captive *Bothriechis schlegelii* (Antonio, 1980) show similar patterns in reproduction. Widespread occurrence of similar reproductive characters indicates a pattern for the entire complex, which has been observed in true vipers that mate in autumn (e.g., *V. aspis*, *V. latastei*, *V. seoanei*; see Luiselli, 1993), and temperate pitvipers (e.g., *Agkistrodon*, *Crotalus*, and *Sistrurus*; see Schuett, 1992). Our discovery of UMT during winter in *Agkistrodon contortrix* (N = 5), *A. piscivorus* (N = 11), and *C. viridis* (N = 5) suggests that the timing of mating (summer and autumn, with subsequent obligatory LTSS) is a conserved ancestral trait in this group of snakes (Schuett, 1992). Accordingly, when sufficient data become available, comparative phylogenetic analyses will be performed to analyze this and similar problems.

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#### LITERATURE CITED

- ALDRIDGE, R. D. 1975. Environmental control of spermatogenesis in the rattlesnake *Crotalus viridis*. *Copeia* 1975:493–496.
- . 1979. Female reproductive cycles of the snakes *Arizona elegans* and *Crotalus viridis*. *Herpetologica* 35:256–260.
- . 1982. The ovarian cycle of the watersnake *Nerodia sipedon* and effects of hypophysectomy and gonadotropin administration. *Herpetologica* 38:71–79.
- . 1992. Oviductal anatomy and seasonal sperm storage in the south eastern crowned snake (*Tantilla coronata*). *Copeia* 1992:1103–1106.
- . 1993. Male reproductive cycle anatomy and seasonal occurrence of mating and combat behavior of the rattlesnake *Crotalus viridis viridis*. *J. Herpetol.* 27:481–484.
- ALMEIDA, M. T. 1999. História natural de *Bothrops pubescens* (Serpentes, Viperidae). Unpublished M.S. thesis, Universidade Estadual Paulista, Rio Claro, São Paulo.
- ALMEIDA-SANTOS, S. M., AND M. G. SALOMÃO. 1997. Long-term sperm storage in the Neotropical rattlesnake *Crotalus durissus terrificus* (Viperidae: Crotalinae). *Japanese J. Herpetol.* 17:46–52.
- , AND ———. 1999. Reproductive senescence of the Neotropical rattlesnake *Crotalus durissus cascavella* (Serpentes: Viperidae). *Bull. Chicago Herpetol. Soc.* 34:250.
- , ———, E. A. PENETI, P. S. SENA, AND E. S. GUIMARÃES. 1998. Predatory combat and tail wrestling in hierarchical contests of the Neotropical rattlesnake *Crotalus durissus terrificus* (Serpentes: Viperidae). *Amphibia-Reptilia* 20:88–96.

- ALVES, M. L. M., M. L. ARAUJO, AND E. CABERLON. 1998. Atividade reprodutiva de *Bothrops neuwiedi* em cativeiro (Serpentes, Viperidae). *Iheringia, Sér. Zool.* 84:185–191.
- AMARAL, A. 1921. Contribuição para o conhecimento dos ofídios do Brasil. A. Parte II. Biologia da nova espécie, *Lachesis insularis*. *Mem. Inst. Butantan* 1:39–44.
- ANDRÉN, C. 1986. Courtship, mating and agonistic behaviour in a free-living population of adders, *Vipera berus* (L.). *Amphibia-Reptilia* 7:353–383.
- , AND G. NILSON. 1981. Reproductive success and risk of predation in normal and melanistic colour morphs of the adder, *Vipera berus*. *Biol. J. Linn. Soc.* 15:235–246.
- , AND ———. 1987. The copulatory plug of the adder, *Vipera berus*: a reply. *Oikos* 49:232–233.
- , ———, M. HÖGGREN, AND H. TEGELSTRÖM. 1997. Reproductive strategies and sperm competition in the adder, *Vipera berus*. Pp. 129–142 *In* R. S. Thorpe, W. Wüster, and A. Malhotra (Eds.), *Venomous Snakes: Ecology, Evolution and Snakebite*. Clarendon Press, Oxford.
- ANTONIO, F. B. 1980. Mating behavior and reproduction of the eyelash viper (*Bothrops schlegeli*) in captivity. *Herpetologica* 36:231–233.
- ARAUJO, M. L., AND L. A. M. ELY. 1980. Notas sobre a biologia de tanatofídeos criados em cativeiro - 2ª parte. (Ophidia - Elapidae e Viperidae). *Iheringia* 55:9–26.
- ARGOLO, A. J. S. 1996. *Bothriopsis bilineata* (Serpentes: Viperidae): cópula e reprodução em cativeiro. XXI Congresso Brasileiro de Zoologia. Porto Alegre. Abstract:198.
- ATSATT, S. R. 1953. Storage of sperm in the female chameleon *Microsaura pumila pumila*. *Copeia* 1953:59.
- BATISTIC, R. F., P. A. FEDERSONI, JR., S. C. R. CALIXTO, AND N. VITIELLO. 1999. Partenogênese facultativa em *Bothrops moojeni*: um caso. *Publicação Extra do Museo Nacional de História Natural Montevideo* 50:36.
- BIRKHEAD, T. R., AND A. P. MØLLER 1993. Sexual selection and the temporal separation of reproductive events: sperm storage data from reptiles, birds, and mammals. *Biol. J. Linn. Soc.* 50: 295–311.
- BLEM, C. R. 1981. Reproduction of the eastern cottonmouth *Agkistrodon piscivorus* (Serpentes, Viperidae) at the northern edge of its range. *Brimleyana* 5:117–128.
- . 1982. Biennial reproduction in snakes: an alternative hypothesis. *Copeia* 1982:961–963.
- BONA-GALLO, A. AND P. LICHT. 1983. Effects of temperature on sexual receptivity and ovarian recrudescence in the garter snake *Thamnophis sirtalis parietalis*. *Herpetologica* 39:173–182.
- BRENO, M. C., N. YAMANOUYE, B. C. PREZOTO, M. F. M. LAZARI, O. TOFFOLETTO, AND Z. P. PICARELLI. 1990. Maintenance of the snake *Bothrops jararaca* (Wied, 1824) in captivity. *The Snake* 22:126–130.
- BULL, J. J., AND R. SHINE. 1979. Iteroparous animals that skip opportunities for reproduction. *Am. Nat.* 114:296–316.
- CAMPBELL, J. A., AND A. SOLÓRZANO 1992. Biology of the montane pitviper, *Porthidium godmani*. Pp. 223–250 *In* J. A. Campbell and E. D. Brodie, Jr. (Eds.), *Biology of the Pitvipers*. Selva, Tyler, Texas.
- CARDOSO, S. R. T., M. M. G. CHAVES, C. K. MIYAJI, S. S. SANTANA, L. A. B. LULA, AND W. FERNANDES. 1993. Descrição da dança combate entre machos de *Bothrops atrox* durante a corte. (Serpentes, Viperidae). III Congresso Latino-Americano de Herpetologia Instituto de Biologia da Universidade Estadual de Campinas. Abstract: 64.
- CARDOSO, J. L. C., F. BUCARETCHI, F. O. DE S. FRANÇA, G. PUORTO, L. A. RIBEIRO, M. M. DE A. MARQUES, M. T. JORGE, P. CUPO, R. H. P. DE MORAES, S. E. HERIG, S. M. LUCAS, AND V. F. B. GUALTIERI. 1993. Manual de Vigilância Epidemiológica. Acidentes por animais peçonhentos: Identificação, diagnóstico e tratamento. Secretaria de Estado da Saúde.
- CARPENTER, C. C. 1986. An inventory of combat rituals in snakes. *Smithsonian Herpetol. Inform. Serv.* 69:11–18.
- CHAVES, M. M. G., W. FERNANDES, S. R. T. CARDOSO, C. K. MIYAJI, S. S. SANTANA, L. A. B. LULA. 1993. Observações em cativeiro da reprodução de *Bothrops neuwiedi* (Serpentes, Viperidae). III Congresso Latino-Americano de Herpetologia Instituto de Biologia da Universidade Estadual de Campinas. Abstract:66.
- COLE, C. J. 1984. Unisexual lizards. *Sci. Amer.* 250:94–100.
- CREWS, D. 1984. Gamete production, sex hormone secretion and mating behavior uncoupled. *Horm. Behav.* 18:22–28.
- . 1991. Trans-seasonal action of androgen in the control of spring courtship behavior in male red-sided snakes. *Proc. Natl. Acad. Sci. U.S.A.* 88:3545–3548.

- , AND C. GANS. 1992. The interaction of hormones, brain, and behavior: an emerging discipline in herpetology. Pp. 1–23 *In* C. Gans and D. Crews (Eds.) *Biology of the Reptilia*, Vol. 18. The University of Chicago Press, Chicago.
- , B. CAMAZINE, M. DIAMOND, R. MASON, R. R. TOKARZ, AND W. R. GARSTKA. 1984. Hormonal independence of courtship behavior in the male garter snake. *Horm. Behav.* 18:29–41.
- CRUZ, G. A., A. SOTO, AND R. V. BERMÚDEZ. 1989. Reproducción de *Bothrops asper* y *Bothrops nummifer* en Honduras (Serpentes, Viperidae). *Revta. Biol. Trop.* 37:201–202.
- DAREVSKY, I. S. 1971. Delayed fertilization in the colubrid snake *Xenodon merremii* (Wagler). *J. Herpetol.* 5:82–83.
- , L. A. KUPRIYANOVA, AND T. UZZELL. 1985. Parthenogenesis in reptiles. Pp. 411–526 *In* C. Gans and T. Billet (Eds.), *Biology of the Reptilia*, Vol. 15. John Wiley & Sons, New York.
- DAWLEY, R. M., AND J. P. BOGART (Eds.). 1989. *Evolution and Ecology of Unisexual Vertebrates*. Bulletin 466, New York State Museum, Albany.
- DERICKSON, W. K. 1976. Lipid storage and utilization in reptiles. *Amer. Zool.* 16:711–723.
- DESSAUER, H. C., AND W. FOX. 1959. Changes in ovarian follicle composition with plasma levels of snakes during oestrus. *Am. J. Physiol.* 197:360–366.
- DEVINE, M. C. 1975. Copulatory plug in snakes: enforced chastity. *Science* 187:844–845.
- . 1977. Copulatory plugs, restricted mating opportunities, and reproductive competition among male garter snake. *Nature* 267:345–346.
- DILLER, L. V., AND R. L. WALLACE. 1984. Reproductive biology of the northern Pacific rattlesnake (*Crotalus viridis oreganus*) in northern Idaho. *Herpetologica* 40:182–93.
- DUARTE, M. R. 1999. Microhabitat e relações térmicas da jararaca ilhoa, *Bothrops insularis* (Serpentes, Viperidae). Unpublished M.S. thesis, Universidade Estadual Paulista, Botucatu.
- , G. PUERTO, AND F. L. FRANCO 1995. A biological survey of the pitviper *Bothrops insularis* Amaral (Serpentes, Viperidae): an endemic and threatened offshore island snake of southeastern Brazil. *Studies on Neotropical Fauna and Environment* 30:1–13.
- DUBACH, J., A. SAJEWICZ, AND R. PAWLEY. 1997. Parthenogenesis in the Arafuran file snake (*Acrochordus arafurae*). *Herpetol. Nat. Hist.* 5:11–18.
- DUVALL, D., L. J. GUILLETTE, JR., AND R. E. JONES. 1982. Environmental control of reptilian reproductive cycles. Pp. 201–231 *In* C. Gans, C. and F. H. Pough (Eds.), *Biology of Reptilia*, Vol. 13. Academic Press, New York.
- , S. J. ARNOLD, AND G. W. SCHUETT. 1992. Pit viper mating systems: ecological potential, sexual selection and microevolution. Pp. 321–336 *In* J. A. Campbell and E. D. Brodie, Jr. (Eds.), *Biology of Pitvipers*. Selva, Tyler, Texas.
- , G. W. SCHUETT, AND S. J. ARNOLD. 1993. Ecology and evolution of snake mating systems Pp. 165–200 *In* R. A. Seigel and J. T. Collins (Eds.), *Snakes: Ecology and Behavior*. McGraw-Hill, New York..
- FEDERSONI, P. A., JR., M. BUONONATO, G. PUERTO, AND P. DE BIASI. 1987. *Bothrops insularis* - exame de conteúdo estomacal de um jovem (Serpentes: Viperidae). XIV Congresso Brasileiro de Zoologia, Juiz de Fora, Minas Gerais. Abstract:138.
- FERNANDES, W., S. R. T. CARDOSO, M. M. G. CHAVES, C. K. MIYAJI, S. S. SANTANA, AND L. A. B. LULA. 1993. Aspectos reprodutivos de *Bothrops atrox*: Período de cópula e dados sobre a ninhada. (Serpentes, Viperidae). III Congresso Latino-Americano de Herpetologia Instituto de Biologia da Universidade Estadual de Campinas. Abstract:68.
- FITCH, H. S. 1970. Reproductive cycles of lizards and snakes. *Univ. Kansas Mus. Nat. Hist. Misc. Publ.* 52:1–247.
- . 1982. Reproductive cycles in tropical reptiles. *Occas. Pap. Mus. Nat. Hist. Univ. Kansas* 96:1–53.
- . 1987. Collecting and life-history techniques. Pp. 143–164 *In* R. A. Seigel, J. T. Collins, and S. S. Novak (Eds.), *Snakes: Ecology and Evolutionary Biology*. Macmillan, New York.
- FOWLER, I. R., AND M. G. SALOMÃO. 1994. Activity patterns in the colubrid snake genus *Philodryas* and their relationship to reproduction and snakebite. *Bull. Chicago Herpetol. Soc.* 29:229–232.
- FOX, W. 1956. Seminal receptacles of snakes. *Anat. Rec.* 124:519–539.
- . 1963. Special tubules for sperm storage in female lizards. *Nature* 198:500–501.
- . 1977. The urogenital system of reptiles. Pp. 1–157 *In* C. Gans and T. S. Parsons (Eds.), *Biology of the Reptilia*, Vol. 6. Academic Press, New York.

- FUKADA, H. 1986. Delayed fertilization in the Japanese mamushi. *Japanese J. Herpetol.* 11:156–157.
- GARSTKA, W. R., AND D. CREWS. 1982. Female control of male reproductive function in a Mexican snake. *Science*, 217:1159–1160.
- GIST, D., AND J. M. JONES. 1987. Storage of sperm in the reptilian oviduct. *Scanning Microscopy* 1:1839–1849.
- , AND J. M. JONES. 1989. Sperm storage within the oviduct of turtles. *J. Morphol.* 199:379–384.
- GOLDBERG, S. R., AND P. ROSEN. 2000. Reproduction in the Mojave rattlesnake, *Crotalus scutulatus* (Serpentes, Viperidae). *Texas J. Sci.* 52:101–109.
- GRABER, R. 1940. Beobachtungen an *Ophis* (syn. *Xenodon*) *merremi* und *O. severus*. *Wochenschr. Aquar. – und Terrark.* 37:291–292.
- GREENE, H. W. 1992. The ecological and behavioral context for pitviper evolution. Pp. 107–118 *In* J. A. Campbell and E. D. Brodie, Jr. (Eds.), *Biology of the Pitvipers*. Selva, Tyler, Texas.
- HALLER, E. C. P., AND M. MARTINS. 1999. História natural da urutu, *Bothrops alternatus* (Serpentes: Viperidae: Crotalinae). *Publicação Extra do Museo Nacional de História Natural Montevideo* 50:69.
- HALPERT, A. P., W. R. GARSTKA, AND D. CREWS. 1982. Sperm transport and storage and its relation to the annual sexual cycle of the female red-sided garter snake, *Thamnophis sirtalis parietalis*. *J. Morphol.* 174:149–159.
- HOFFMAN, L. H., AND W. A. WIMSATT. 1972. Histochemical and electron microscopic observations on the sperm receptacles in the garter snake oviduct. *Amer. J. Anat.* 134:71–96.
- HOGUE, A. R., H. E. BELLUOMINI, G. SCHREIBER, AND A. M. PENHA. 1959. Sexual abnormalities in *Bothrops insularis* (Amaral) (Serpentes). *Mem. Inst. Butantan* 29:17–88.
- HOLYCROSS, A. T., AND S. R. GOLDBERG. 2001. Reproduction in northern populations of the ridgenose rattlesnake, *Crotalus willardi* (Serpentes, Viperidae). *Copeia* 2001:473–481.
- JACOB, J. S., S. R. WILLIAMS, AND R. P. REYNOLDS. 1987. Reproductive activity of male *Crotalus atrox* and *Crotalus scutulatus* (Reptilia: Viperidae) in northeastern Chihuahua, Mexico. *Southwest. Nat.* 32:273–276.
- JANEIRO-CINQUINI, T. R. F., E. C. FARIAS, AND F. F. LEINZ. 1995. Relation between the quantity of abdominal fat and reproductive state of the snake *Bothrops jararaca*. *The Snake* 27:21–14.
- , F. F. LEINZ, AND E. C. FARIAS. 1993a. Ovarian cycle of the snake *Bothrops jararaca*. *Mem. Inst. Butantan* 55:33–36.
- , ———, AND ———. 1993b. Seasonal variation in weight and length of the testicles and the quantity of abdominal fat of the snake *Bothrops jararaca*. *Mem. Inst. Butantan* 55:15–19.
- , ———, AND V. C. F. FIGUEIREDO. 1992. Sexual dimorphism in adult *Bothrops jararaca*. *Bull. Chicago Herpetol. Soc.* 27:94–95.
- JOHNSON, L. F., J. S. JACOB, AND P. TORRANCE. 1982. Annual testicular and androgenic cycles of the cottonmouth (*Agkistrodon piscivorus*) in Alabama. *Herpetologica* 38:6–25.
- KUMARI, T. R. S., H. B. D. SARKAR, AND T. SHIVANANDAPPA. 1990. Histology and histochemistry of the oviductal sperm pockets of agamid lizard *Calotes versicolor*. *J. Morphol.* 203:97–106.
- LEITÃO-DE-ARAUJO, M., AND M. PEZZAROLO. 1974. Nota prévia sobre a biologia de tanatofídeos em cativeiro (Ophidia, Elapidae e Viperidae). *Iheringia Sér. Zool.*, Porto Alegre 45:55–66.
- , M. L. M. ALVES, R. L. BALESTRIM, AND L. F. S. DE AGUIAR. 1998. Nascimento e desenvolvimento de *Bothrops neuwiedi* em cativeiro (Serpentes, Viperidae). *Iheringia Sér. Zool.*, Porto Alegre 85:3–10.
- LELOUP, P. 1975. Observation sur la reproduction de *Bothrops moojeni* en captivité. *Acta Zool. Path. Antverpiensia* 62:173–201.
- . 1984. Various aspects of venomous snake breeding on a large scale. *Acta Zool. Path. Antverpiensia* 78:177–198.
- LIRA-DA-SILVA, R. M., AND F. M. CARVALHO. 1999. Estudo clínico-epidemiológico dos acidentes por *Bothrops leucurus* (Serpentes; Viperidae). XXII Congresso Brasileiro de Zoologia, Universidade Federal de Pernambuco Sociedade Brasileira de Zoologia, Recife. Abstract:76.
- , T. K. BRAZIL, AND S. PASSOS. 2000. Acompanhamento de uma ninhada de *Bothrops leucurus* (Serpentes; Viperidae) em cativeiro. XXIII Congresso Brasileiro de Zoologia, Cuiabá, Mato Grosso. Abstract:524.
- , L. L. CASAS-DE-SILVA, I. B. DE QUEIROZ, AND T. B. NUNES. 1994. Contribuição à biologia de serpentes da Bahia, Brasil. I. Vivíparas. *Revta bras. Zool.* 11:187–193.

- LUISELLI, L. 1993. Are sperm storage and within-season multiple mating important components of the adder reproductive biology? *Acta Oecol.* 14:705–710.
- LULA, L. A. B. M., S. S. SANT'ANNA, C. K. MIYAJI, M. M. G. CHAVES, S. R. T. CARDOSO, AND W. FERNANDES. 1993. Técnicas para reprodução de serpentes do gênero *Bothrops* mantidas em cativeiro. III Congresso Latino Americano de Herpetologia, Campinas, SP. Abstract:65.
- MACARTNEY, J. M., AND P. T. GREGORY. 1988. Reproductive biology of female rattlesnakes (*Crotalus viridis*) in British Columbia. *Copeia* 1988:47–57.
- , ———, AND M. B. CHARLAND. 1990. Growth and sexual maturity of the western rattlesnake *Crotalus viridis*, in British Columbia. *Copeia* 1990:528–542.
- MACHADO, L., AND G. A. COTTA. 1998. Observações sobre o comportamento reprodutivo da jararaca da seca *Bothrops erythromelas* em Cativeiro. XXII Congresso Brasileiro de Zoologia, Universidade Federal de Pernambuco Sociedade Brasileira de Zoologia, Recife. Abstract:285.
- MADSEN, T., R. SHINE, J. LOMAN, AND T. HÅKANSSON. 1993. Determinants of mating success in male adders, *Vipera berus*. *Anim. Behav.* 45:491–499.
- MAGNUSSON, W. E. 1979. Production of an embryo by an *Acrochordus javanicus* isolated for seven years. *Copeia* 1979:744–745.
- MALLMANN-FRANCO, M. T. O., AND F. FRANCO. 1998. Primeiro caso de intersexualidade em *Bothrops jararaca* (Crotalinae; Viperidae; Serpentes). XXII Congresso Brasileiro de Zoologia, Universidade Federal de Pernambuco Sociedade Brasileira de Zoologia, Recife. Abstract:284.
- , AND ———. 1999. Presença de hemiclitoris em *Bothrops jararacussu* (Serpentes; Viperidae; Crotalinae). Publicação Extra do Museu Nacional de História Natural Montevideo 50:62.
- MARQUES, O. A. V. 1996. Biologia reprodutiva da cobra-coral *Erythrolamprus aesculapii* (Colubridae), no sudeste do Brasil. *Rev. Bras. Biol.* 13:747–753.
- . 1998a. Reprodução e hábitos alimentares de *Bothrops jararacussu* (Serpentes, Viperidae), na Estação Ecológica Juréia-Itatins, litoral sul de São Paulo. XXII Congresso Brasileiro de Zoologia, Recife, Pernambuco. Abstract:271.
- . 1998b. Composição faunística, história natural e ecologia de serpentes da Mata Atlântica, na região da Estação Ecológica Juréia-Itatins, São Paulo, SP. Unpublished Ph.D. dissertation, Universidade de São Paulo.
- , A. ETEROVIC, AND W. ENDO. 2001. Seasonal activity of snakes in the Atlantic forest in south-eastern Brazil. *Amphibia-Reptilia* 22:103–111.
- MCCOY, C. J., AND E. J. CENSKY. 1992. Biology of the Yucatan hognosed pitviper, *Porthidium yucatanicum*. Pp. 217–222 In J. A. Campbell and E. D. Brodie, Jr. (Eds.). *Biology of the Pitvipers*. Selva, Tyler, Texas.
- MESQUITA, D. O., AND V. L. C. BRITES. 1999. Aspectos ecológicos da população de *Bothrops alternatus* (Serpentes: Crotalinae) da zona geográfica do Triângulo e Alto Paranaíba - MG. Publicação Extra do Museu Nacional de História Natural Montevideo 50:84.
- MURPHY, J. B., AND L. A. MITCHELL. 1984. Miscellaneous notes on the reproductive biology of reptiles. 6. Certain varieties of the genus *Bothrops* (Serpentes, Crotalidae). *Acta Zool. Path. Antverpiensia* 1:199–214.
- NASCIMENTO, C.L.A., AND R. A. BRANDÃO. 1998. Sobre a reprodução da cotiarinha (*Bothrops itapetiningae*) no Distrito Federal. XXII Congresso Brasileiro de Zoologia, Universidade Federal de Pernambuco Sociedade Brasileira de Zoologia, Recife. Abstract:285.
- NAULLEAU, G., AND X. BONNET. 1996. Body condition threshold for breeding in a viviparous snake. *Oecologia* 107:301–306.
- NILSON, G., AND C. ANDRÉN. 1982. Function of renal sex secretion and male hierarchy in the adder, *Vipera berus*, during reproduction. *Horm. Behav.* 16:404–413.
- NOGUEIRA, C., AND P. H. VALDUJO. 1999. Ecologia de viperídeos do cerrado: *Bothrops moojeni* Hoge, 1965 (Serpentes: Viperidae). Publicação Extra do Museu Nacional de História Natural Montevideo 50:90.
- NUSSBAUM, R. A. 1980. The brahminy blind snake (*Ramphotyphlops braminus*) in the Seychelles Archipelago: distribution, variation, and further evidence for parthenogenesis. *Herpetologica* 36:215–221.
- OLIVEIRA, M. E., AND M. MARTINS. 1999. Atividade e utilização de ambiente em *Bothrops atrox* na Amazônia Central. Publicação Extra do Museu Nacional de História Natural Montevideo 50:92.



- PERKINS, M. J., AND B. D. PALMER. 1996. Histology and functional morphology of the oviduct of an oviparous snake, *Diadophis punctatus*. *J. Morphol.* 227:67–79.
- PEZZANO, V. 1986. Reproduction of *Bothrops alternatus* (Duméril, Bibron & Duméril, 1854) in captivity. *Litteratura Serpentina* 6:13–18 (English edition).
- PLUMMER, M. V. 1983. Annual variation in stored lipids and reproduction in green snakes (*Opheodrys aestivus*). *Copeia* 1983:741–745.
- . 1942. The reproductive cycle of the prairie rattlesnake. *Copeia* 1942:233–240.
- REIS-DUARTE, R. M. 1995. Resposta sazonal do gênero *Bothrops* (Ophidia: Viperidae) do Estado de São Paulo. Unpublished M.S. thesis, Universidade Guarulhos, SP.
- , AND M. S. GALVÃO-BUENO. 1997. Frequências de distribuição de serpentes do gênero *Bothrops* (Viperidae: Crotalinae) no Estado de São Paulo, Brasil. *Rev. Univ. Guarulhos, Série Pós-Graduação II*: 44–52.
- RIBEIRO, L. A., AND M. T. JORGE. 1990. Epidemiologia e quadro clínico dos acidentes por serpentes *Bothrops jararaca* adultos e filhotes. *Rev. Inst. Med. Trop. São Paulo* 32:436–442.
- SAINT GIRONS, H. 1957. Le cycle sexuel chez *Vipera aspis* (L.) dans l'Ouest de la France. *Bull. biol. Fr. Belg.* 91:284–350.
- . 1962. Présence de réceptacles séminaux chez les caméléons. *Beaufortia* 9:165–172.
- . 1975. Sperm survival and transport in the female genital tract of reptiles. Pp. 106–113 *In* E. S. E. Hafez and C. G. Thibault (Eds.), *The Biology of Spermatozoa*. S. Karger, Basel, Switzerland.
- . 1982. Reproductive cycles of male snakes and their relationships with climate and female reproductive cycles. *Herpetologica* 38: 5–16.
- . 1985. Comparative data on lepidosaurian reproduction and some time tables. Pp. 35–58 *In* C. Gans and F. Billett (Eds.), *Biology of the Reptilia*, Vol. 15. John Wiley & Sons, New York.
- SALOMÃO, M. G., S. M. ALMEIDA-SANTOS, AND G. PUERTO. 1995. Activity pattern of the rattlesnake *Crotalus durissus* (Viperidae: Crotalinae): feeding, reproduction and snakebite. *Studies on Neotropical Fauna and Environment* 30:101–106.
- , WÜSTER, W., R. S. THORPE, AND BBBSP. 1997. DNA evolution of South American pit vipers of the genus *Bothrops*. Pp. 89–98 *In* R. S. Thorpe, W. Wüster, and A. Malhotra (Eds.), *Venomous Snakes: Ecology, Evolution and Snakebite*. Symposia of the Zoological Society of London 70. Clarendon Press, Oxford.
- , ———, AND BBBSP. 1999. MtDNA evolution in Neotropical pitvipers of the genus *Bothrops* (Squamata: Serpentes: Viperidae). *Kaupia* 8:127–134.
- SANT'ANNA, S. S. 1999. Hábito Alimentar da cascavel *Crotalus durissus* No Sudeste Brasileiro (Serpentes, Viperidae). Unpublished M.S. thesis, Universidade Estadual Paulista, Rio Claro, São Paulo.
- , K. F. GREGO, AND W. FERNANDES. 2001. *Bothrops leucurus* (White-tailed Lancehead), Reproduction. *Herpetol. Rev.* 32:45–46.
- SANTOS, S. M. A., I. L. LAPORTA FERREIRA, AND G. PUERTO. 1990. Ritual de combate em *Crotalus durissus*. *An. Acad. Bras. Ciências* 62:418.
- SAZIMA, I. 1988. Um estudo de biologia comportamental de jararaca, *Bothrops jararaca*, com uso de marcas naturais. *Mem. Inst. Butantan* 50:83–99.
- . 1992. Natural history of the jararaca pitviper *Bothrops jararaca* in southeastern Brazil. Pp.199–216 *In* J. A. Campbell and E. D. Brodie, Jr. (Eds.), *Biology of the Pitvipers*. Selva, Tyler, Texas.
- SCHUETT, G. W. 1992. Is long-term sperm storage an important component of the reproductive biology of temperate pitvipers? Pp. 169–184 *In* J. A. Campbell and E. D. Brodie, Jr. (Eds.), *Biology of the Pitvipers*. Selva, Tyler, Texas.
- . 1996. Fighting dynamics of male copperheads *Agkistrodon contortrix* (Serpentes, Viperidae): stress-induced inhibition of sexual behavior in losers. *Zoo Biol.* 15:209–221.
- . 1997. Body size and agonistic experience affect dominance and mating success in male copperheads. *Anim. Behav.* 54:213–224.
- , P. J. FERNANDEZ, W. F. GERGITS, N. J. CASNA, D. CHISZAR, H. M. SMITH, J. B. MITTON, S. P. MACKESSY, R. A. ODUM, AND M. J. DEMLONG. 1997b. Production of offspring in the absence of males: evidence for facultative parthenogenesis in bisexual snakes. *Herpetol. Nat. Hist.* 5:1–10.
- , AND J. C. GILLINGHAM. 1986. Sperm storage and multiple paternity in the copperhead (*Agkistrodon contortrix*). *Copeia* 1986:807–811.

- , AND ———. 1989. Male-male agonistic behaviour of the copperhead, *Agkistrodon contortrix*. *Amphibia-Reptilia* 10:243–266.
- , H. J. HARLOW, J. D. ROSE, E. A. VAN KIRK, AND W. J. MURDOCH. 1997a. Annual cycle of plasma testosterone in male copperheads, *Agkistrodon contortrix* (Serpentes, Viperidae): relationship to timing of spermatogenesis, mating, and agonistic behavior. *Gen. Comp. Endocrinol.* 105:417–424.
- 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, New York.
- SHINE, R. 1977a. Reproduction in Australian elapid snakes. I. Testicular cycles and mating seasons. *Aust. J. Zool.* 25:647–653.
- . 1977b. Reproduction in Australian elapid snakes. II. Female reproductive cycles. *Aust. J. Zool.* 25:655–666.
- . 1978. Sexual dimorphism and male combat in snakes. *Oecologia* 33:269–277.
- . 1986. Ecology of a low-energy specialist: food habits and reproductive biology of the Arafura filesnake (Acrochordidae). *Copeia* 1986:424–437.
- . 1994. Sexual size dimorphism in snakes revisited. *Copeia* 1994:326–346.
- , G. C. GRIGG, T. G. SHINE, AND P. HARLOW. 1981. Mating and male combat in Australian blacksnakes, *Pseudechis porphyriacus*. *J. Herpetol.* 15:101–107.
- SHIROMA, H. 1993. Follicular growth and fat body cycle of female habus, *Trimeresurus flavoviridis*, in the Okinawa Islands. *Japanese J. Herpetol.* 15:53–58.
- SOLÓRZANO, A., AND L. CERDAS. 1989. Reproductive biology and distribution of the terciopelo, *Bothrops asper* Garman (Serpentes: Viperidae) in Costa Rica. *Herpetologica* 45:444–450.
- STEARNS, S. C. 1992. *The Evolution of Life Histories*. Oxford University Press, New York.
- STEWART, G. R. 1972. An unusual record of sperm storage in a female garter snake (genus *Thamnophis*). *Herpetologica* 28:346–347.
- TRYON, B. W. 1984. Additional instances of multiple egg-clutch production in snakes. *Trans. Kansas Acad. Sci.* 87:98–104.
- VALDUJO, P. H., AND C. NOGUEIRA. 1999. Ecologia de viperídeos do cerrado: *Bothrops neuwiedi pauloensis* Amaral 1925 (Serpentes: Viperidae). *Publicação Extra do Museo Nacional de História Natural Montevideo* 50:115.
- , ———, AND R. A. BRANDÃO. 1999. Ecologia de viperídeos do cerrado: *Bothrops itapetingae* (Boulenger 1907) (Serpentes: Viperidae). *Publicação Extra do Museo Nacional de História Natural Montevideo* 50:116.
- , ———, AND M. MARTINS. 2002. Ecology of *Bothrops neuwiedi pauloensis* (Serpentes: Viperidae: Crotalinae) in the Brazilian Cerrado. *J. Herpetol.* 36:169–176.
- VALOBOUEV, V., G. PASTEUR, I. INEICH, AND B. DUTRILLAUX. 1993. Chromosomal evidence for a hybrid origin of diploid parthenogenetic females from the unisexual-bisexual *Lepidodactylus lugubris* complex (Reptilia, Gekkonidae). *Cytogenet. Cell Genet.* 63:194–199.
- VITT, L. J. 1983. Ecology of an anuran eating guild of terrestrial tropical snakes. *Herpetologica* 39:52–66.
- . 1987. Communities. Pp. 335–365 *In* R. A. Seigel, J. T. Collins, and S. S. Novak (Eds.), *Snakes: Ecology and Evolutionary Biology*. Macmillan, New York.
- VOLSØE, H. 1944. Structure and seasonal variation of the male reproductive organs of *Vipera berus* (L.). *Spolia Zool. Mus. Haun.* 5:1–157.
- WOODWARD, S. F. 1933. A few notes on the persistence of active spermatozoa in the African night-adder, *Causus rhombeatus*. *Proc. Zool. Soc. London* 1933:189–190.
- WÜSTER, W., M. G. SALOMÃO, R. S. THORPE, AND BBBSP. 1997. Systematics of the *Bothrops atrox* species complex: insights from multivariate analysis. Pp. 99–113 *In* R. S. Thorpe, W. Wüster, and A. Malhotra (Eds.), *Venomous Snakes: Ecology, Evolution and Snakebite*. Symposia of the Zoological Society of London 70.
- , ———, AND BBBSP. 1999. Mitochondrial DNA evolution of the *Bothrops atrox* complex (Squamata: Serpentes: Viperidae). *Kaupia* 8:135–144.
- ZAR, J. H. 1984. *Biostatistical Analysis*. Prentice-Hall, Englewood Cliffs, New Jersey.