NATURAL HISTORY OF THE JARARACA PITVIPER, *BOTHROPS JARARACA,* IN SOUTHEASTERN BRAZIL

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ABSTRACT: *Bothrops jararaca* is a terrestrial, medium-sized (ca 120 cm TL) pitviper widespread in southeastern Brazil, where it occurs in a variety of forested habitats including scrubs, and even cultivated fields. The natural history of this snake has been studied in the Campinas region, State of São Paulo, over five years. *Bothrops jararaca* is mainly nocturnal and is active most of the year. Females tend to be larger and heavier than males. Gravid females tend to keep within certain areas and usually bask in shaded sites and sun-shade mosaics nearby a shelter. A biennial female reproductive cycle is inferred. Births occur from the middle to the end of the rainy season. Number of offspring, and size and mass of neonates approach those known for other crotalines of comparable size. Prey are mostly rodents for adult snakes and frogs for juveniles, indicating an ontogenetic shift in diet. Feeding on mammals consists of the "strike-release-trail" tactic known for most ambush hunting, rodent-eating viperids. Frog prey is held until swallowed. Caudal luring behavior occurs in juveniles. Predators of *B. jararaca* include birds of prey and also presumably opossums and ophiophagous snakes. Defensive tactics escalate from immobility and locomotor escape to threat and bite. Certain sympatric colubrids seem to form a mimetic assemblage with *B. jararaca* as the dangerous model.

INTRODUCTION

Southeastern Brazil harbors a rich snake fauna of about 130 species, including 12 or 13 pitvipers (Peters and Orejas-Miranda, 1970; Hoge and Romano-Hoge, 1981; Vanzolini, 1986; Campbell and Lamar, 1989). Data on the natural history of these viperids are scarce and the biology of most species remains unknown. An overview of the natural history of *Bothrops moojeni* exists (Leloup, 1975, 1984), and scattered data are available on the biology of *B. insularis,* an island endemic (e.g. Amaral, 1921; Hoge, 1950; Mertens, 1955; Hoge et al., 1960; De Biasi et al., 1986; Federsoni et al., 1987).

Notwithstanding its wide occurrence, local abundance, and medical importance (Fonseca, 1949; Rosenfeld, 1971; Campbell and Lamar, 1989; Ribeiro and Jorge, 1990), *Bothrops jararaca* remained almost unstudied until recently (Sazima, 1987, 1989a). This terrestrial snake is a medium-sized (ca 120 cm total length), relatively slender species of *Bothrops* with variable color pattern and markings (description and photographs in Campbell and Lamar, 1989).

My aim is to survey the natural history of the jararaca pitviper, *B. jararaca,* in southeastern Brazil. This review is based on my studies over the past five years, as well as on published and original data supplied by colleagues working on this or related snakes. Most of my observations were done in nature and the general procedure and study sites have been described elsewhere (Sazima, 1989a, 1989b, 1991; Morellato, 1992). Some of the data presented here are partial results of studies in progress and the uneven treatment of topics reflects both the available information and my preference for a given subject (e.g. feeding, defense).

DISTRIBUTION AND HABITAT

The distribution of Neotropical pitvipers, although imperfectly known is nevertheless covered by the distributional maps in Campbell and Lamar (1989). Much less is known about the habitats of most species (Campbell and Lamar, 1989). A characterization of the habitats of five crotaline species (including *B. atrox* and *B. brazili*) was

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attempted by Cunha and Nascimento (1975) in northern Brazil. Aside from literature data, here I present limited information on elevational range and some habitats of *B. jararaca.*

Range and Elevational Distribution

Bothrops jararaca occurs in southeastern South America, from the State of Bahia southward to the State of Rio Grande do Sul in Brazil, and to northern Argentina (Hoge and Romano-Hoge, 1981; Campbell and Lamar, 1989). Its vertical range remains unreported. I have found this snake at localities from sea level (Praia Grande, State of São Paulo) to about 900 m (Atibaia, also in São Paulo). Adão J. Cardoso and J. P. Pombal, Jr. (pers. comm.) caught an adult female (ZUEC 728) at about 1200 m (Serra dos Orgãos, State of Rio de Janeiro).

Habitats

The distribution of *B. jararaca* in southeastern Brazil mostly coincides with the Tropical Atlantic Morphoclimatic Domain or the Atlantic Forest realm (cf. Ab'Saber, 1977; Vanzolini, 1988). *Bothrops jararaca* apparently is a forest dweller able to live in disturbed habitats, and it may be found from evergreen or semideciduous broadleaf forest to closed scrub, including highly degraded formations and even cultivated fields, habitually in close proximity to vegetational cover (see Eiten, 1970 for vegetational types, and Prance and Campbell, 1988 for present state of southeastern Brazil's forests). This snake may occasionally use open areas; I found an adult *B. jararaca* basking in a soybean field, ca 250 m from a small forest tract (Campinas, São Paulo), and another adult was moving in a marsh near the seashore, ca 80 m from a scrub (Praia Grande, São Paulo). Most of my observations on *B. jararaca* come from the Reserva Mata de Santa Genebra, a small (250 ha) remnant of broadleaf, semideciduous subtropical forest surrounded mostly by cultivated land (Fig. 1a, b) in Campinas, State of São Paulo, southeastern Brazil (ca 22° 49'S, 47° 06'W, 640 m; see Sazima, 1989a for further information).

Bothrops jararaca may be found close to or even within large Brazilian cities; in a two-year survey of snakes (307 individuals belonging to 25 species) found in the capital of São Paulo, the second largest and most populous city in Latin America, *B. jararaca* represented 12% of the sample

(Puorto et al., 1990). In this city *B. jararaca* was found mainly in larger "green areas", i.e. highly degraded remnants of forest tracts within the urban area (parks, vacant lots).

Another forest pitviper able to occupy disturbed habitats is *Bothrops atrox* (Campbell and Lamar, 1989); in northern Brazil, this snake was found in several habitats including cleared land and cultivated fields (Cunha and Nascimento, 1975, 1978). Due to their catholic habits and abundance, both *B. atrox* and *B. jararaca* are major sources of snakebite envenomations in Brazil (Rosenfeld, 1971; Cunha and Nascimento, 1975; Ribeiro and Jorge, 1989, 1990). March (1928a) reported on a similar situation for *B. asper* in Honduras (see also Scott, 1983).

ACTIVITY AND MOVEMENT PATTERNS

The activity of snakes is notoriously difficult to assess and knowledge of movements of Neotropical snakes is particularly scarce (recent reviews in Gregory et al., 1987 and Gibbons and Semlitsch, 1987). Information on Neotropical viperids include a short-term study of a radio-tagged female *B. atrox* in Peru (Henderson et al., 1976), observational studies on daily and seasonal activities of *B. moojeni* in southeastern Brazil (Leloup, 1984), and radiotelemetric studies on movements of *Lachesis muta* in Costa Rica (Greene and Santana, 1983; Greene, 1986). Comments on the activity of several species are found in general studies (e.g. Amaral, 1921; March, 1928a; Beebe, 1946; Cunha and Nascimento, 1978).

Data on activity and movements of *B. jararaca* are found in Sazima (1987, 1989a). Here I present data on capture or sightings of additional individuals that either confirm or contradict my previous suggestions.

Daily Activity

Ninety one active individuals of *B. jararaca* (39 males, 52 females) were recorded at the Santa Genebra reserve over a period of 54 months, from October 1985 to April 1990 (Sazima, 1989a and unpubl. data). From these, 72 snakes (79.12%) were moving at dusk or early night (1820-2030 h), the remainder being found from late night to dawn (n=12) or at various times throughout the day (n=7). Therefore *B. jararaca* is largely nocturnal. This also seems true for *B. moojeni* in southeastern Brazil (Leloup, 1984) and *B. atrox* in northern Brazil (Cunha and Nascimento, 1975, 1978), although some individuals of these two species were recorded also during daytime. Among species of *Bothrops* [sensu stricto], only *B. insularis* is claimed to be a largely diurnal snake (Amaral, 1921; Hoge, 1950).

Seasonal Activity

At the Santa Genebra reserve, active individuals of *B. jararaca* were found over most of the year, from October through May, at air temperatures ranging from 17 to 31°C, and relative air humidity from 68 to 100% (Sazima, 1989a and unpubl. data). Half of 122 snakes (43 males, 79 females) found over 54 months was from December to February (n=62), the three wettest months with 50.40% of the total annual average rainfall (1,365 mm, see Fig. 2; also Fig. 4 in Sazima, 1989a). I found no snakes from June to August, the
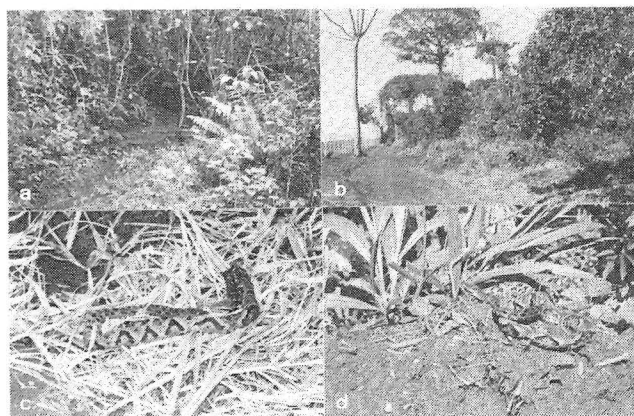

Fig. 1. Habitat and basking sites of *Bothrops jararaca* at the Santa Genebra reserve, Campinas, State of São Paulo, southeastern Brazil: (a) spring in the semideciduous broadleaf forest; (b) forest edge with bare ground strip, wire fence, and adjacent cultivated field; (c) conspicuously gravid female (ca 120 cm TL) basking on recently cut vegetation at the forest edge; (d) adult female (105 cm SVL) basking on an earth mound fully exposed to sunlight in early morning.

three driest and coldest months at the study area (Sazima, 1989a). Most snakebite cases in southeastern Brazil occur during the rainy season (Rosenfeld, 1971; Ribeiro and Jorge, 1990), this epidemiological factor clearly being related to snakes' increased activity (Sazima, 1989a). As previously suggested (Sazima, 1989a), the seasonal activity pattern of *B. jararaca* tends to conform to the unimodal type (cf. Gibbons and Semlitch, 1987).

Movements Assessed from Recaptures

All but one recapture of females (16 adults and 1 juvenile) were within 1 to 30 m from the site of the first sighting, within periods ranging from 1 to 24 months. One adult female was recaptured while basking at mid-morning, 30 days after and about 200 m from the site where it was originally found at night while moving (Sazima, 1989a and unpubl. data). The additional data support the previously suggested sedentary tendencies for females of *B. jararaca* (Sazima, 1989a).

Only three males were recaptured. One young adult was found after 25 days about 1 km from the site at which it was first seen (Sazima, 1989a); a second young adult was moving about 20 m from the original site but 15 days later; and a third individual was recaptured about 60 m from the site at which it was found 24 months earlier (I. Sazima and P. R. Manzani, unpubl. data). This third male was a juvenile that measured 47 cm TL when first caught, and was probably nearly mature when recaptured (75 cm TL; see "Growth"). Although inconclusive, these additional recapture data may not support the previously suggested wandering for male *B. jararaca* (Sazima, 1989a).

Gravid females of several snake species are more sedentary than non-gravid females or males (Fitch, 1960; Reinert, 1984; Gibbons and Semlitch, 1987; Reinert and Zappalorti, 1988). Radiotelemetric studies on the activity of females of *Lachesis muta* and *Bothrops asper* also indicate sedentary habits (Greene and Santana, 1983; Greene, 1986).
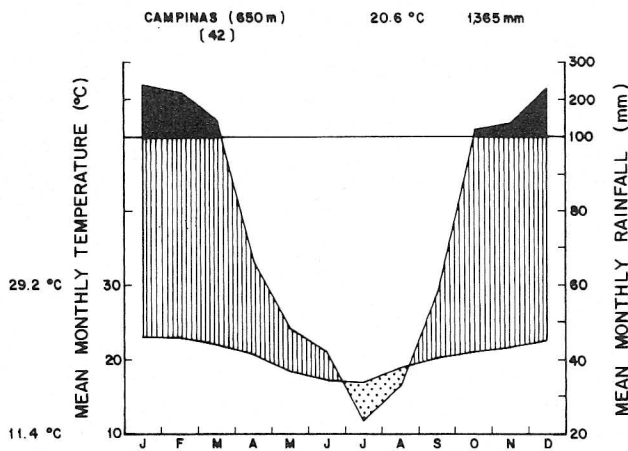
Fig. 2. Climatic diagram (after Walter, 1973) of Campinas, State of São Paulo, southeastern Brazil (ca 22° 49′S, 47° 06′W, 654 m). Curve of mean monthly rainfall (upper); curve of mean monthly temperature (lower). Relatively dry period (dotted), humid period (hatched), and hydric excess (black). Mean annual temperature 20.6°C; mean annual rainfall 1,365 mm; mean minimum air temperature of coldest month 11.4°C; mean maximum air temperature of warmest month 29.2°C. Meteorological data from 1929 to 1971 (42 years). Most data on natural history of *B. jararaca* were obtained at the region of Campinas (see Sazima, 1989a, b).

BASKING AND TEMPERATURE RELATIONS

Thermal biology of Neotropical snakes is poorly known (e.g. Huey, 1982; Lillywhite, 1987), and that of pitvipers in the genus *Bothrops* seems unreported. Here I give information on basking sites and postures (see also Sazima, 1989a), and data on body temperatures of basking and moving individuals of *B. jararaca*.

Basking Sites and Postures

Twenty eight snakes (1 male, 27 females) were found basking during daytime, 24 of them in the morning (0905-1130 h) and 4 in the afternoon (1325-1730 h). Three additional males seemingly were basking at night (see below). All but one snake found basking during daytime were females, including one immature, and most of them were visibly gravid (e.g. Fig. 1c). Seventeen gravid females used particular basking sites for periods variable from 3 to 78 days (Sazima, 1989a and unpubl. data), and two of these were recaptured two years later, gravid again, within a few meters of the same sites they basked in previously (I. Sazima and P. R. Manzani, unpubl. data; see also Reinert, 1984; Reinert and Zappalorti, 1988, for Nearctic crotalines).

Basking *B. jararaca* were found mostly at the forest edge and clearings (Fig. 1b), on sites where sun flecks penetrated the vegetation (sun-shade mosaics), and on shaded sites previously exposed to sunlight. Six individuals were found wholly exposed to direct sunlight (Fig. 1d) during early morning (0905-0930 h). Basking was evident mostly after periods of rain and occurred on vegetation (one snake up to 2 m above ground), leaf-litter and logs; rarely on bare ground.

Individuals on vegetation were often partly concealed. Snakes frequently basked in coiled posture (Fig. 3) but "bent" posture or loose loops also were used (Figs. 1c, d, and 13; see also Sazima, 1989a). Most basking sites had a shelter nearby (hole, heap of vegetation, stump, or log; see Fig. 3), and some females were observed to use these retreats in the afternoon, at night, or during rains.

Three males found during early night (1840-1920 h) were outstretched or sprawled, and dorsoventrally flattened on bare ground sites previously exposed to late afternoon sunlight. This behavior is suggestive of active use of these surfaces for thermoregulation (see Sullivan, 1981 for similar behavior in the colubrid *Pituophis melanoleucus*).

Data on basking indicate that *B. jararaca* may thermoregulate to some extent by diurnal basking and nocturnal use of warm surfaces. *Bothrops moojeni* was reported to behave in a similar way in southeastern Brazil (Leloup, 1984), and most basking individuals of both *B. jararaca* and *B. moojeni* were gravid females (see Fitch, 1960; Brown et al., 1982; Reinert 1984; and Reinert and Zappalorti, 1988, for similar behavior in Nearctic crotalines, and Huey, 1982 for comments on thermoregulation in tropical forest species).

Body Temperatures of Basking and Moving Snakes

Body (cloacal) temperatures, and concurrent air and substrate temperatures opportunistically taken with a digital quick reading thermometer are available for 17 snakes (Fig. 4). These data seem to indicate active thermoregulation for *B. jararaca* (but see Avery, 1982 for a critique of field studies on body temperature of reptiles). I think that a more accurate assessment of thermal activity of *B. jararaca* must await radiotelemetric studies (e.g. Brown et al., 1982; Shine, 1987).

POPULATIONAL DATA

Studies on population ecology of snakes still struggle with basic issues, and data on Neotropical species range from sparse to almost nonexistent (an exception are some data on

Fig. 3. Gravid female of *B. jararaca* (86 cm SVL) basking on a partly shaded site near its shelter, a log overgrown by vegetation at the forest edge.
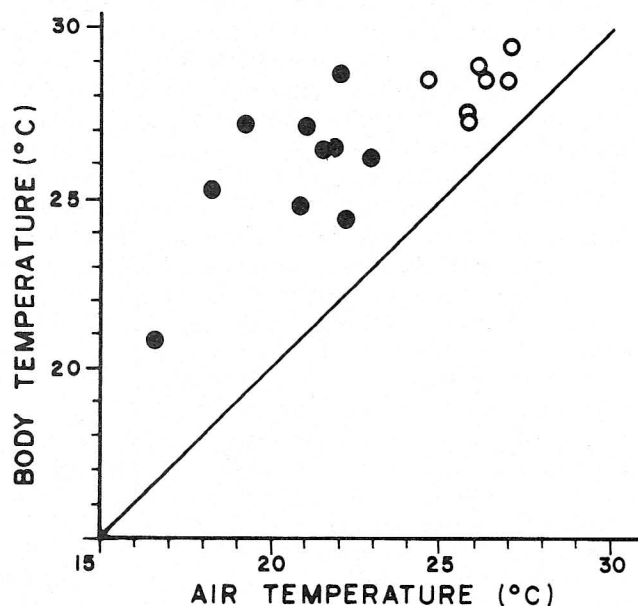
Fig. 4. Body temperatures of *B. jararaca* plotted against air temperature. Solid line = Tb = Ta; open circles = basking snakes; solid circles = moving snakes. Temperatures recorded from 1010 to 1050 h for basking snakes, and from 1825 to 1925 h for moving snakes, except the lowermost individual, recorded at 0510 h.

colubrid snakes in northeastern Brazil, see Vitt, 1983). No populational study on Brazilian viperids seems available although data on length-weight relationship of *B. jararaca* (Vanzolini, 1946), and on sex ratio and several bodily measures and counts of *B. insularis* (Hoge et al., 1960) exist. Here I present limited data on abundance, sex ratio, growth, and length-weight relationship of *B. jararaca* at the Santa Genebra reserve in Campinas.

Abundance

Bothrops jararaca may be locally abundant (Fonseca, 1949; Sazima, 1989a; Puorto et al., 1990). Out of 121 snakes belonging to 10 species sighted in the Santa Genebra reserve over 29 months, 77 individuals (63.63%) were *B. jararaca;* the second most frequent snake, *Dipsas indica* (14 individuals) represented 11.57% of the sightings (see Sazima, 1989a and c for methods). This abundance may be due to a kind of "Belém Park effect" (cf. Vanzolini, 1981), as Santa Genebra is surrounded by cultivated and semi-urbanized land.

From a total of 488,489 snakes received by the Instituto Butantan over 40 years (1906-1945), 188,869 individuals (38.66%) were *B. jararaca,* followed by the rattlesnake, *Crotalus durissus* (115,114 individuals; 23.56%) within the same period (Fonseca, 1949), a ratio of 1.6:1. However, during the years 1988, 1989, and 1990, a total of 3068, 3208, and 2323 *B. jararaca,* compared to 3625, 3829, and 2782 *C. durissus* respectively, entered the Instituto Butantan (G. Puorto, pers. comm.), a combined ratio of 0.84:1. These recent numbers may indicate a trend: due to continuous deforestation in southeastern Brazil (Prance and Campbell, 1988), suitable habitats for *B. jararaca* are shrinking while open habitats, favored by the rattlesnake, are expanding.

Sex Ratios

Only snakes found active at night are included to estimate sex ratios. Basking habits of gravid females would strongly bias the estimates due to their predictable occurrence at the forest edge and consequent ease of sighting (see also Reinert, 1984). From a total of 84 snakes found over 54 months (October 1985 to April 1990), 36 were males and 48 were females, an observed sex ratio of 0.75:1. However, when only adult individuals are counted, the ratio approaches 1:1 (25 males, 28 females). For a discussion on snake sex ratios, see Parker and Plummer (1987).

Size and Weight

A sample of 13 males (juveniles and adults) and 20 females (juveniles and either apparently non-gravid or post-partum adults) indicates that, on average, females of *B. jararaca* tend to be larger and heavier than males (Fig. 5). Vanzolini (1946) related this trend in his sample to pregnancy, but since some of the heaviest females in the Santa Genebra sample were post-partum individuals, and detectably gravid females were not included in fig. 5, pregnancy seems not be the sole cause. Eight large, post-partum females from unknown localities in the State of São Paulo ranged 89-109 cm SVL and weighed 243-414 g (W. Fernandes, unpubl. data). Females larger than males were recorded for *B. moojeni* from central Brazil (Leloup, 1975), and *B. asper* in Costa Rica (Solórzano and Cerdas, 1989), this trend appearing in most species of snakes (Shine, 1978; Fitch, 1981).
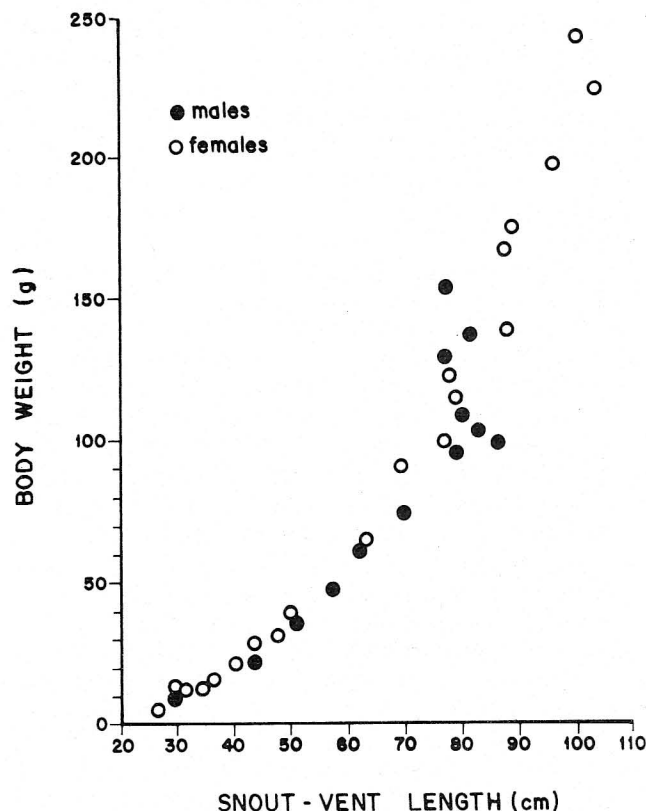

Fig. 5. Weight-length relationship in 33 individuals (13 males, 20 females) of *B. jararaca* at the Santa Genebra forest.

Maturity

The size at maturity for *B. jararaca* is unknown but I estimate that males ca 65 cm SVL and females ca 75 cm SVL are mature. These are approximately the sizes where the length-weight relationship tends to become linear, especially for females (Fig. 5). At the Santa Genebra reserve, the smallest gravid female measured 82 cm SVL. As most snakes mature at 60 to 75% of their maximum length (Parker and Plummer, 1987), I think these estimates are reasonable.

Growth

Data on growth of *B. jararaca* are based on five individuals, juveniles and adults, measured and recaptured after periods from 14 to 24 months (I. Sazima and P. R. Manzani, unpubl. data). Growth rates ranged from 0.5 to 1.8 cm/mo. These values are within the range found by Fitch (1960) for the crotaline *Agkistrodon contortrix* (see greater growth rates of captive *Bothrops atrox* in Hoge and Federsoni, 1978).

Based on limited data of growth rates, estimated minimum adult sizes, and sizes of large and presumably old individuals, my guess is that *B. jararaca* attains adult size by its third or fourth year, reproduces the next season, and its life span surpasses 10-12 years. (Dunham et al, 1988a; Campbell and Solórzano-Lopez, this volume, presented estimates for other crotaline snakes).

REPRODUCTION

Knowledge of the reproductive biology of Neotropical pitvipers in the genus *Bothrops* is meager and based mostly on observations of captive specimens (e.g. March, 1928a; Leloup, 1975; Melgarejo, 1977; Murphy and Mitchell, 1984), an exception being the recent study on *B. asper* in Costa Rica (Solórzano and Cerdas, 1989). Data on reproductive habits including male combat, courtship, and gestation period of captive *B. moojeni* (Leloup, 1975), and seasonal variation of testes mass of *B. jararaca* (Vanzolini, 1947) are available for southeastern Brazil. Courtship and mating seem unreported for *B. jararaca,* except for heterologous copulations between captives of this species and *Crotalus durissus* (e.g. Amaral, 1933a; Belluomini and Hoge, 1959).

Here I present initial information on birth season and female reproductive cycle, litter size, sex ratio and body size of neonates, as well as data on presumed hybrids between *B. jararaca* and three sympatric species of *Bothrops.*

Birth Season and Reproductive Cycle

In the Campinas region, I found the first visibly gravid females of *B. jararaca* from October-November through February-March (Sazima 1989a and unpubl. data). Times of births were assessed from observations of a few conspicuously gravid females (e.g. Fig. 1c) and subsequent notice of their post-partum condition. Some females were maintained captive for periods of up to two weeks before parturition. Under these conditions, births occurred from early January to middle April. Wilson Fernandes (pers. comm.) found that timing may vary from year to year. Births are spread over about 4 mo for *B. moojeni* in central Brazil (Leloup, 1975), 3 mo for *B. asper* in Costa Rica (Solórzano and Cerdas, 1989), and 2 mo for *Porthidium yucatanicum* in Mexico (McCoy and Censky, this volume).

The wet season in the Campinas region usually extends from October through March (Fig. 2). Most births of *B. jararaca* occur when prey availability for young snakes is high, as most frogs (see "Prey Items") reproduce during the rainy season in southeastern Brazil (e.g. Haddad and Sazima, 1992; pers. obs.). However, since frog activity decreases sharply after March (pers. obs.) and there is little or no activity of *B. jararaca* after May (Sazima, 1989a), I presume there is little growth of juvenile *B. jararaca* during their first year.

Based on collections of *B. atrox* in northern Brazil, Cunha and Nascimento (1975) stated that births occur during the rainy season, a result similar to that found for *B. moojeni* in central Brazil (Leloup, 1975), *B. asper* in Costa Rica (Solórzano and Cerdas, 1989), *Porthidium godmani* in Central America (Campbell and Solórzano, this volume), and *P. yucatanicum* in Mexico (McCoy and Censky, this volume). Occurrence of births during the wet season may be a trend for most tropical snakes (Seigel and Ford, 1987).

The frequency of reproduction in *B. jararaca* remains unknown but I suspect that individual females produce litters in alternate years; this assumption is based mostly on the recapture of two gravid females at the same sites but in alternate years (see "Basking"). Additionally, none of four recaptured females was gravid for two consecutive seasons during a five-year study (unpubl. data). Although admittedly inferred from scant evidence, the postulated biennial reproductive cycle for *B. jararaca* females agrees with the data obtained in southeastern Brazil for another crotaline, the rattlesnake *Crotalus durissus* (Langlada, 1972). Moreover, a biennial cycle seems consistent with the presumably lengthy pregnancy: Leloup (1975, 1984) found 7 mo for *Bothrops moojeni,* Solórzano and Cerdas (1989) found 6-8 mo for *B. asper,* Murphy and Mitchell (1984) estimated 6 mo for *Porthidium barbouri,* and Langlada (1972) also found 6 mo for *Crotalus durissus.* Very limited data on the female reproductive cycle indicate that *B. jararaca* has a seasonal, somewhat extended reproduction (about 4-6 mo) in southeastern Brazil (T.R.F. Janeiro-Cinquini, unpubl. data), and this may also be the case for *B. asper* in Costa Rica (Solórzano and Cerdas, 1989).

Based on the occurrence of the first visibly gravid females, time of births, and presumed pregnancy period, I submit that mating of *B. jararaca* occurs in April-June, at the beginning of the dry period (see Fig. 2). Leloup (1975, 1984) indicated a similar pattern for *B. moojeni* in southeastern Brazil.

Litter Size, Sex Ratio, and Body Size of Offspring

Data were obtained from eight females with unknown origin but mostly from the state of São Paulo (W. Fernandes, unpubl. data). This is far from ideal, since climatic differences have a distinct influence on the reproductive strategies of reptiles (see Shine, 1989 for the elapid *Pseudonaja* in Australia, and Solórzano and Cerdas, 1989, for *B. asper* in Costa Rica).

Litter size of *B. jararaca* varied from 5 to 16 young

($\bar{x}$ =10.75, sd=3.83), but extremes of 3 to 34 are known (W. Fernandes, pers. comm.). Sex ratio in these 8 litters was 0.56:1 (31 males, 55 females) but the ratio was about 1:1 in 424 young (211 males and 213 females) from an additional 32 litters (W. Fernandes, unpubl. data). Sizes and masses of neonate *B. jararaca* (Table 1) are roughly similar to those of *B. asper* (Solórzano and Cerdas, 1989), notwithstanding the much larger adult size of the latter (Campbell and Lamar, 1989) which, however, also has a much larger litter size (Solórzano and Cerdas, 1989).

Litter size of *B. jararaca* is within the range found for most other snakes, and approaches the highest average known for viperids (Seigel and Ford, 1987). Clutch size and clutch mass are positively correlated with female size in *B. asper* (Solórzano and Cerdas, 1989), and also in *B. jararaca* (W. Fernandes, unpubl. data), an apparently usual trend in snakes (Seigel and Ford, 1987; Dunham et al., 1988a).

Natural Hybrids

Presumed natural hybrids have been observed between *B. jararaca* and: *B. cotiara* (Vellard, 1929; O. Pesantes and A. S. Abe, unpubl. data), *B. neuwiedi* (Fernandes et al., 1987; pers. obs.), and *B. jararacussu* (A. S. Abe, unpubl. data-see Fig. 6a). These hybrid specimens show some traits intermediate between the two presumed parents, including color pattern, pholidosis, hemipenial features, and electrophoretic variation in plasma proteins, and apparently also nucleolar organizers (Vellard, 1929; Fernandes et al., 1987; A. S. Abe and O. Pesantes, unpubl. data; pers. obs.).

A presumed hybrid between *B. jararaca* and *B. neuwiedi* (Fig. 6b) gave birth to 21 young whose color patterns and markings ranged from those typical for *B. jararaca* to a pattern reminiscent of *B. neuwiedi* (Fig. 7). An analysis of the offspring, including of their plasma proteins (Fernandes et al., 1987), showed both a *B. jararaca* pattern and a mixture of *B. jararaca* with *B. neuwiedi*. Fernandes et al. (1987) concluded that the offspring resulted from the mating, in the wild, between the hybrid female with a male *B. jararaca* and warned about the possibility, in some species of *Bothrops,* of the occurrence of introgression hardly detectable by phenotypic methods.

From the species of *Bothrops* presumed to mate with *B. jararaca* and produce hybrids, only *B. jararacussu* is believed to be closely related to it (e.g. Janeiro-Cinquini et al., 1987; Campbell and Lamar, 1989). *Bothrops neuwiedi,* together with *B. erythromelas,* may form a distinct group found in open areas, whereas *B. cotiara,* together with the closely related *B. fonsecai* and *B. alternatus,* may form a group of stout vipers found both in forested and open areas (Amaral, 1923; Hoge and Belluomini, 1959; Janeiro-Cinquini et al., 1987; Campbell and Lamar, 1989; Pesantes and Fernandes, 1989; but see Werman, this volume, for another interpretation). Thus the supposed lesser affinities and the differences in hemipenial size and morphology (Segura, 1989) do not seem to constitute a barrier for interspecific matings in *B. jararaca* (Fernandes et al., 1987).

Interspecific matings may occur in relatively undisturbed environments, as *B. jararaca* sometimes is found in syntopy with some other species of *Bothrops* (e.g. *B. jararacussu,* pers. obs.), or may result from encounters due to environ-mental disturbance, nowadays a rule over most of south-eastern Brazil. Fernandes et al. (1986) reported on a presumed natural hybrid between *B. alternatus* and *B. cotiara,* and commented that habitat disturbance is a factor favorable to interspecific matings between these two viperids.

FEEDING HABITS

Information on feeding habits of most snakes has accumulated mainly from examination of preserved snakes; direct observations and field studies are scarce (recent review in Mushinsky, 1987). Nevertheless, food items for several crotaline species are known with some detail (e.g. Fitch, 1960; Klauber, 1972; Mushinsky, 1987), although Neotropical pitvipers remain poorly studied (e.g. Beebe, 1946; Sexton, 1956-57; Cunha and Nascimento, 1975, 1978; Dixon and Soini, 1986). Here I present data on feeding habits of *B. jararaca* including prey items, feeding behavior, caudal luring, and scavenging.

Prey Items

The diet of *B. jararaca* remains largely unstudied, although Amaral (1933b) and Vanzolini (1948) mentioned rodent-eating habits for this snake. An initial analysis of stomach contents of 33 individuals from several localities mainly in São Paulo State, southeastern Brazil (I. Sazima and G. Puorto, unpubl. data), revealed a diversified diet with a preponderance of rodents for adult snakes and frogs for juveniles.

Adult snakes (652-1110 mm SVL, 95-796 g, n=16) preyed mainly on medium-sized rodents (130-220 mm head and body length - HBL, 140-250 g, n=9), mostly murids including the water rat *(Nectomys squamipes)* and the Norway rat *(Rattus norvegicus),* and less often young and adult caviids *(Cavia aperea),* and echimyids (the spiny rats *Echimys* and *Proechimys).* Small murid rodents (60-120 mm HBL, 10-60 g, n=5), such as the field mouse *(Bolomys lasiurus),* the rice rat *(Oryzomys* cf. *nigripes),* and the house mouse *(Mus musculus),* were also eaten. Other prey items included a leptodactylid frog *(Thoropa miliaris)* eaten by a young female, and a quail *(Coturnix japonica* - probably an escapee from a poultry farm).

Food items of juvenile snakes (265-375 mm SVL, 11-35 g, n = 17) consisted mainly of frogs (32-51 mm SVL, 1-6 g, n = 9), such as the hylids *Hyla fuscovaria, H. leucopygia,* and *Hyla prasina,* and the leptodactylid *Physalaemus cuvieri.* Less frequent were small murid rodents (n=4), including the rice
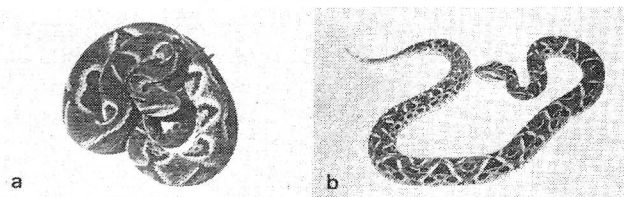

Fig. 6. Presumed natural hybrids between *B. jararaca* and two other species of *Bothrops:* (a) unsexed adult (female?) hybrid between *B. jararaca* and *B. jararacussu,* no further data (photo courtesy of A. S. Abe); (b) adult female hybrid between *B. jararaca* and *B. neuwiedi paranaensis* (see Fernandes et al., 1987 for further data.).

TABLE 1. Snout-vent length and weight of neonate *Bothrops jararaca* from the State of São Paulo, southeastern Brazil.

			$\overline{x}$	sd	range	n
Length	(cm)	Males	24.5	2.01	19.0-27.0	31
SVL		Females	25.3	1.76	19.0-27.5	55
Weight	(g)	Males	9.38	2.47	4.5-13.0	31
		Females	10.61	2.42	5.0-14.0	55

rat *(Oryzomys* cf. *nigripes)* and the house mouse *(Mus musculus)*. Two snakes ate lizards *(Hemidactylus mabouia)*, one juvenile ate a nestling passerine bird (probably Emberizidae), and another juvenile (ca 30 cm TL) upon capture disgorged two scolopendrid centipedes *(Otostigmus* sp., ca 5 cm) in different stages of digestion.

Centipedes were reported as prey of juveniles of other species of *Bothrops,* such as *B. insularis* (Hoge et al., 1960; Federsoni et al., 1987), *B. atrox* (Dixon and Soini, 1986), and *B. neuwiedi* (Achaval et al., n.d.), and also of adult *B. itapetiningae* (Prado, 1945). This latter snake is a very small species, ca 30-40 cm TL (Campbell and Lamar, 1989; pers. obs.). Centipedes may be a common prey item for juvenile *Bothrops,* given the abundance of these arthropods during the wet season and their nocturnal activity.

The differences in the diet of the young and adult *B. jararaca* are indicative of an ontogenetic shift in feeding habits, a trend already reported for several viperid species (Mushinsky, 1987). Reports on *B. "atrox"* in Venezuela (Beebe, 1946; Sexton, 1956-57) and Peru (Dixon and Soini, 1986) also indicate a diet with an ontogenetic shift, from anurans and lizards to rodents.

Mass of Prey

Bothrops jararaca is a relatively slender-bodied species within the genus (see Campbell and Lamar, 1989 for comparisons). For the food items eaten by *B. jararaca,* the ratio of prey mass relative to snake mass (WR cf. Greene, 1983; see also Pough and Groves, 1983) ranged from 0.09 to 0.41 ($\overline{x}$= 0.21, sd=0.11, n=8) for adults, and from 0.04 to 1.30 ($\overline{x}$=0.44, sd=0.36, n=9) for juveniles (I. Sazima and G. Puorto, unpubl. data). The data on mass ratios for adult *B. jararaca* are within the limits reported for other viperids (up to 0.36 of their own masses, Pough and Groves, 1983). For juvenile jararacas, the average mass ratio is greater but (except for one individual) near the values found by Pough and Groves (1983); Greene (1983) found a *B. atrox* juvenile with the exceptional WR of 1.56. The comparison between the mass ratios of juvenile and adult *B. jararaca* indicates that the former feed on a wider prey relative size range, a trend probably found in other snake species (Mushinsky, 1987).

Feeding Behavior

Observations on feeding behavior of most predators are fortuitous, the more so for snakes (Fitch, 1987) whose feeding modes are therefore largely unknown (Mushinsky, 1987). I observed only two instances of feeding behavior of *B. jararaca* in the field: a large female trailing an already
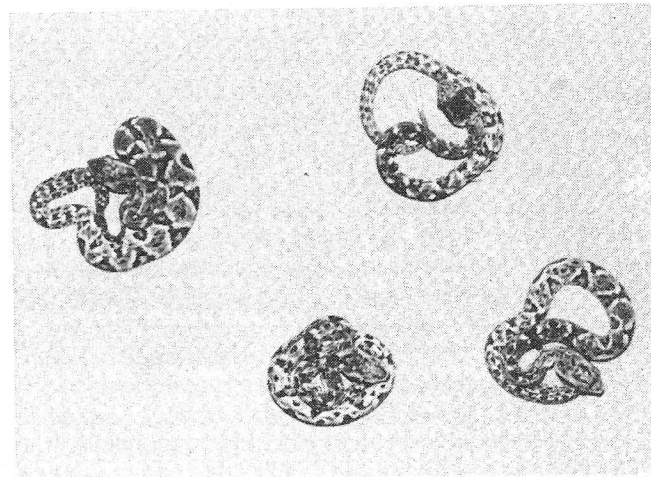
Fig. 7. Four of the offspring of the hybrid female shown on figure 6b. The upper left snake has the dorsal pattern typical for *B. jararaca,* whereas the lower middle one has a pattern reminiscent of *B. neuwiedi.* These juveniles supposedly resulted from the mating, in the wild, of the hybrid female with a male *B. jararaca* (see Fernandes et al., 1987).

envenomated water rat, *Nectomys squamipes,* on a stream bank (Pirassununga, March 1976), and an adult male swallowing an unidentified rat at the forest edge (Campinas, April 1987). Célio F. B. Haddad (pers. comm.) found a young male swallowing a treefrog, *Hyla prasina* (Fig. 9a), at the edge of a pond near the forest (Jundiaí, March 1989).

In order to study the feeding behavior of this pitviper under field conditions, I staged 17 encounters between 11 individuals of *B. jararaca* (83-120 cm TL) and small rodent prey such as house mice *(Mus musculus)* and rice rats *(Oryzomys* sp.) at the Santa Genebra reserve (Sazima, 1989b). Prey was released 10-100 cm in front of a moving or a stationary snake (basking or in ambush) by day or at night. Sometimes offered prey was restrained by a catgut or cotton collar attached to a fishing line tied to a 2.5 m fishing pole allowing independent movement (see Harlow and Shine, 1988; Hayes and Duvall, 1991, for similar techniques); on other occasions prey was released free, thus approaching the procedure to a natural encounter (Sazima, 1989b). Here I briefly describe and comment on the feeding sequences, and compare them to the growing body of literature on feeding behavior in captive viperid snakes (review in Chiszar et al., this volume).

The feeding behavior of *B. jararaca* on small rodents may be characterized by the following main components: orientation towards prey, approach, strike - with bite and release, trailing, inspection, and swallowing (Sazima, 1989b; see also

Fig. 8). The "strike-release-trail" tactic is known for most rodent-eating viperids and some elapids, and is viewed as a method to deal with dangerous prey (Chiszar et al., 1982; Kardong, 1986a).

Orientation towards prey appeared to be elicited mainly by the prey movements (see Cock Buning, 1983; Graves and Duvall, 1985). During this stage, tongue flicking rate was about 10-20/min (see Chiszar et al., 1982). The approach stage and the predatory strike were essentially the same as those described for pitviper species in the genera *Agkistrodon* and *Crotalus* (Kardong, 1975, 1986a, b; see also Fig. 2 in Sazima, 1989b). Coiled snakes advanced only the neck or part of the forebody (Fig. 8b), or less often waited for the prey to approach. The jararaca struck from a distance of 5 to 20 cm, mainly at the shoulder of the prey (72.72% n=11; see also Fig. 10, and Kardong, 1986a). Only once did a snake miss a strike (see Kardong, 1986b; Hayes and Duvall, 1991). Habitually a single envenomating strike was delivered, and the rodent was released by widely opening the jaws and disengaging the fangs from the prey's body. Following the release tongue flicking increased to about 40-50/min (see Chiszar et al., 1982, this volume).

Envenomated mice travelled a distance from 10 to 150 cm ($\bar{x}$=55.0, sd=40.1, n=13). Trailing of prey was initiated by the snake within 15 to 140 s after the strike ($\bar{x}$=101.7, sd=80.8, n=9), time enough for the injected venom to immobilize the prey (Estep et al., 1981; Kardong, 1986a), and perhaps also an adequate period for the snake to inspect the immediate surroundings for potential predators. During the trailing, the forebody of the snake made almost symmetrical, sidewards scanning movements while approaching the prey (Fig. 9b; also part of a trailing sequence in Sazima, 1989b). The amplitude of this scanning often increased with the distance from the strike site, especially when the prey travelled by jumping (Sazima, 1989b). Presumably this scanning behavior allows the snake to locate the scent trail left by the envenomated prey (Golan et al., 1982). During the trailing, tongue flicking rate varied from 30 to 60/min (Sazima, 1989b), within the range found among several other viperids (e.g. Chiszar et al., 1982, but see comments on thermal dependence of tongue-flicking in Cooper and Vitt, 1986). This strike induced chemosensory searching (SICS) occurs in all viperid snakes studied so far and seems to be an important component of the "strike-release-trail" tactic found among ambush hunting vipers (Chiszar et al., 1982, 1985, this volume; but see Cooper et al., 1989 for the occurrence of SICS also in colubrid snakes). Trailing episodes in *B. jararaca* lasted 70-140 s ($\bar{x}$=105.0, sd=31.1, n=4).

Inspection of prey was done by tongue flicking and snout touching (Fig. 8e), with more frequent and longer bouts on the nasal-oral and ano-genital regions of the prey (Sazima, 1989b). Presumably, the snake was searching for chemical cues to swallow the prey headfirst (Duvall et al., 1980; Cock Buning, 1983). The snout touching may serve both to assess the hair position (Diefenbach and Emslie, 1971) or, perhaps, to assess whether the prey is dead or alive (W. Fernandes, pers. comm.). Swallowing in *B. jararaca* occurred in essentially the same sequence described by Kardong (1977) for the cottonmouth, *Agkistrodon piscivorus*. The jararacas swallowed the prey headfirst in all but one instance, and
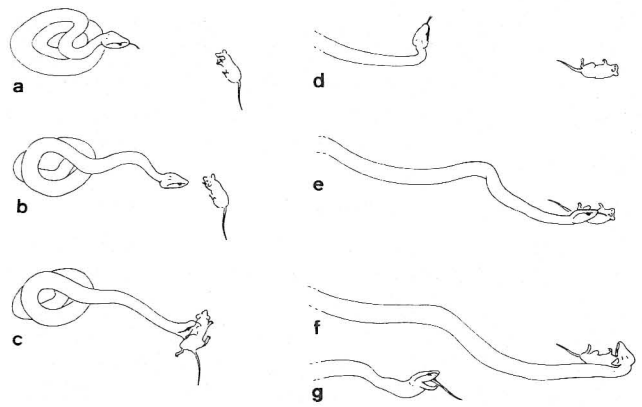

Fig. 8. Feeding behavior of *B. jararaca* on small rodents includes orientation towards prey (a), approach (b), striking with bite and release (c), trailing with sideways scanning movements (d), inspection with tongue-flicking and snout-touching (e), and swallowing, usually head-first (f,g).

Fig. 9. Feeding behavior of *B. jararaca*: (a) juvenile male (32 cm SVL; ZUEC 788) swallowing the treefrog, *Hyla prasina*, at the edge of a pond; note pale (yellowish) tail tip probably used to lure frog prey (photo courtesy of C. F. B. Haddad); (b) adult female (114 cm TL) trailing an envenomated rodent (arrow), at the forest edge.

ingestion lasted 125-300 s ($\bar{x}$=191.1, sd=55.9, n=9), a time considerably shorter than that reported by Duvall et al. (1980) for *Crotalus durissus* swallowing mice ($\bar{x}$=345.8 s). The single tailfirst swallowing by *B. jararaca* lasted ca 12 min. The whole feeding sequence, from the initial orientation towards the prey to the end of swallowing, lasted 8-20 min (Sazima, 1989b).

Caudal Luring

The behavior known as caudal luring was reported for several viperid, boid, and elapid snakes (reviews in Neill, 1960 and Heatwole and Davison, 1976). Among species of *Bothrops* (sensu stricto), caudal luring is disputably reported for juvenile *B. atrox* (see comments in Heatwole and Davison, 1976), and was recently recorded for juvenile *B.*

Fig. 10. Predatory strike of *B. jararaca* on a house mouse during an encounter staged in the field; same snake as in figure 9b (after Sazima, 1989b).

jararaca and *B. jararacussu* (Sazima, 1991; see also Fig. 11).

Caudal luring in *B. jararaca* was observed twice in the field, both instances during early night, 1930-2100 h (Sazima, 1991). In captive snakes, tail luring was induced by placing small frogs (25-45 mm SVL) in the snakes' terraria. Successful luring, i.e. the frog approaching the moving tail tip and the snake seizing the prey, was observed twice for *B. jararaca* and once for *B. jararacussu* (Sazima, 1991). Frog prey was struck and held between the jaws usually until immobilized and then swallowed (see Fitch, 1960; Klauber, 1972, for comments on this behavior in other viperids, in contrast to release of rodents).

The venom properties of juvenile *B. jararaca* differ from those of adult individuals in coagulant and fibrinolytic activities (e.g. Rosenfeld et al., 1959; Ribeiro and Jorge, 1989, 1990). These differences along with the caudal luring behavior may be related to dietary specialization of juvenile jararacas (see "Prey items"). Caudal luring behavior and the diet of juvenile *B. jararaca* are consistent with the suggestion that snake species which lure only as juveniles shift to other prey types as they grow (Greene and Campbell, 1972; Heatwole and Davison, 1976). It is probable that caudal

luring behavior occurs among some other Brazilian species of *Bothrops*, such as *B. moojeni*, *B. neuwiedi*, and *B. pradoi*, whose juveniles usually have conspicuous, pale tail tips (pers. obs.).

Scavenging

Bothrops jararaca occasionally may scavenge, as demonstrated by an episode staged in the field (Sazima and Strüssmann, 1990). A moving, adult female *B. jararaca* was offered a dead house mouse (killed 6 h earlier), placed on the leaf litter ca 50 cm in front of the snake as to intersect its path. The snake found and tongue flicked the mouse briefly, swallowing it afterwards. Necrophagic habits have been demonstrated for some species of rattlesnakes (e.g. Patten and Banta, 1980; Gillingham and Baker, 1981), and occasional scavenging may be a widespread habit among snakes (Sazima and Strüssmann, 1990).

Foraging Tactics

The feeding behavior of adults and the caudal luring of juvenile *B. jararaca* are consistent with the ambush hunting tactic suggested for most viperids (Chiszar et al., 1982; Mushinsky, 1987). Field observations on foraging tactics of pitvipers are scarce, the studies on *Crotalus horridus* (Reinert et al., 1984) and *Lachesis muta* (Greene and Santana, 1983; Greene, 1986) being notable exceptions. Both of these large pitvipers are typical ambushers, coiling adjacent to runways or feeding sites of small mammals. However, *B. jararaca* is a relatively slender, medium-sized pitviper, and based on two instances of moving and apparently foraging individuals (an adult snake in a maize field, and a juvenile on bushes and trees up to 3m, followed for up to 130 min —Sazima, 1989b; pers. obs.), I submit that this species may also occasionally forage by active searching. There remains the possibility that these two individuals were merely searching for a suitable ambush site (see Reinert et al., 1984; Duvall et al., 1985), although moving individuals of *B. jararaca* accepted prey readily during staged encounters (Sazima, 1989b), which seems consistent with active foraging. Also, the nestling bird eaten by one juvenile snake (see "Prey items") certainly was not ambushed. The occasional scavenging by *B. jararaca* (Sazima and Strüssmann, 1990) also lends support to the suggestion that this snake sometimes employs active searching for prey besides its habitual ambush tactic.

Based on the bodily proportions of *B. atrox*, another relatively slender viper (see Cunha and Nascimento, 1975; Campbell and Lamar, 1989), and on its diversified diet (e.g. Beebe, 1946; Cunha and Nascimento, 1975, 1978; Dixon and Soini, 1986) I suspect that this species also employs ambush and occasional active searching; indeed, this may apply to several other slender-bodied, terrestrial pitvipers.

PREDATORS, PARASITES, AND INJURIES

I found few published records of predation on species of *Bothrops*. Wagler (1824) described *B. leucostigma* (possibly a juvenile *B. jararaca*) based on a specimen recovered from the stomach contents of a laughing falcon, *Herpetotheres cach-*
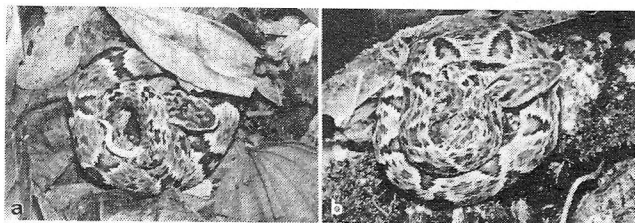
Fig. 11. Two juvenile females of *B. jararaca* in coiled postures shortly after displaying caudal luring behavior: (a) pale, yellowish tail tip (29 cm SVL; ZUEC 862); (b) barred, brownish tail tip (32 cm SVL).

innans. Beebe (1946) found two *B. atrox* in the stomach contents of the colubrid *Clelia clelia*, and Hoge (1953) mentioned cannibalism in *B. neuwiedi*. I found no records of predation on *B. jararaca* other than those based on captive animals (e.g. Brazil, 1911; Hermann, 1921; Amaral, 1934; Jackson, 1979; but see Wagler, 1824).

Here I present data on predators of *B. jararaca,* based both on field records and observations of captive animals. Also, I summarize literature data on parasites of *B. jararaca,* and present data on injuries found in snakes at the Santa Genebra reserve.

Observed and Presumed Predators

I found a roadside hawk, *Buteo magnirostris,* at roost with a young specimen of *B. jararaca* (ca 40 cm TL) in the Santa Genebra reserve (March 1986), and Antonio J. F. Cabral (pers. comm.) found a partly eaten *B. jararaca* (ca 45 cm TL) under another roost of this hawk in the same area in April 1987. As *B. magnirostris* is not known to take dead prey and is able to catch snakes up to 1 m in length (Stiles and Janzen, 1983; pers. obs.) the above instances probably were actual episodes of predation on *B. jararaca.* Augusto S. Abe (pers. comm.) found remains of two adult *B. jararaca* (one a male ca 80 cm TL; ZUEC 957) presumably preyed on by the laughing falcon, *H. cachinnans,* in the Rio Claro region, State of São Paulo (February 1990). This falcon is reputedly a snake-eater (Sick, 1985; also references in Brugger, 1989).

In staged encounters in the field eight individuals of *B. magnirostris* were offered juvenile *B. jararaca* (ca 35 cm TL). Five birds did not approach the snake (although they probably saw it), two birds approached but made no attempt to attack the snake, and one bird approached and attacked the jararaca. Several times this hawk spread its wings and approached with its wingtips within striking range of the snake. Due to this spreading of the wings I was unable to observe how the snake was attacked. *Buteo magnirostris* is a widespread, opportunistic predator able to catch snakes (Stiles and Janzen, 1983; Sick, 1985; pers. obs.), and may be an important predator of young jararacas during their dispersal in daytime or even at dusk. In his study on copperheads, *Agkistrodon contortrix,* Fitch (1960) found this viperid as the fourth most frequent prey of the red-tailed hawk, *B. jamaicensis.*

A captive young grison, *Grison* sp., readily attacked and devoured a 61 cm TL *B. jararaca* (Jackson, 1979). I observed a recently caught thick-tailed opossum, *Lutreolina crassicaudata,* preying on juvenile *B. jararaca* (29-32 cm TL) in

captivy. The opossum attacked and deftly bit the snake in the neck region, while holding it between its paws; the snake was immediately released after the bite, attacked and bitten again until it was limp, at which time it was devoured. Fitch (1960) found opossums, *Didelphis virginiana,* to prey on copperheads, and I observed a captive of another species *(D. albiventris)* preying on juvenile *B. jararaca.* These omnivorous, snake-venom tolerant mammals (Vellard, 1945; Perales et al., 1986) probably are effective predators of snakes.

The snake-eating snake *Clelia clelia* was recorded to prey on *B. jararaca* in captivity and was perhaps overpublicized as an important population controller of this and other pitvipers (e.g. Brazil, 1911; Fonseca, 1949; Abalos and Nader, 1968). Another species, *C. occipitolutea,* also preys on snakes (Vitt and Vangilder, 1983; pers. obs.), and I observed two captive individuals of this species preying on adult and juvenile *B. jararaca* (Fig. 12a). Both *C. clelia* and *C. occipitolutea* occur within the range of *B. jararaca,* are active at night (Beebe, 1946; Abalos and Nader, 1968; pers. obs.), and thus may occasionally prey on this pitviper.

Due to their large size and conspicuous warning movements (see below), I think adult *B. jararaca* have few, if any, predators with the probable exception of the laughing falcon and perhaps also large individuals of *Clelia.* On the other hand, although unobtrusive, juvenile *B. jararaca* probably are subject to being eaten by several occasional predators of small snakes, such as birds, mammals, other snakes, and perhaps even large anurans (see Amaral, 1934). However, actual field records of predation on snakes, especially on Neotropical pitvipers, are scarce (Greene, 1988) and much more data are needed.

Endo- and Ectoparasites

Several internal parasites have been recorded for *B. jararaca.* The nematode *Kalicephalus inermis* was found in 316 individuals in a sample of 646 snakes, whereas *K. costatus* was found in 17 individuals from the same sample; 15 snakes had both species (Fernandes and Artigas, 1978). These nematodes were also recovered from *Crotalus terrificus,* five additional species of *Bothrops,* one boid and six colubrid snakes. The pentastomid *Porocephalus* sp. was found in the lungs of *B. jararaca* and three other species of snakes, two viperids and one boid (Rego, 1982). The protozoan *Hepatozoon plimmeri* was identified from blood samples of *B. jararaca* and *B. moojeni* by Pessoa et al. (1975). Mites and ticks occasionally are found on snakes but I have found no ticks on *B. jararaca* in nature. Individuals of the related *B. insularis* occasionally bear several large ixodid ticks (G. Puorto, pers. comm.). The degree to which these various endo- and ectoparasites affect *B. jararaca* or other snake hosts remains unknown.

Injuries

Tail injuries were found in eight of 113 (7.0%) *B. jararaca* I examined at the Santa Genebra reserve (minor injuries such as scratches and small scars on the body were not recorded). The injuries on tail were all healed and comprised several degrees of absence of the tail tip (Fig. 12b). These losses may result from damage inflicted by predators
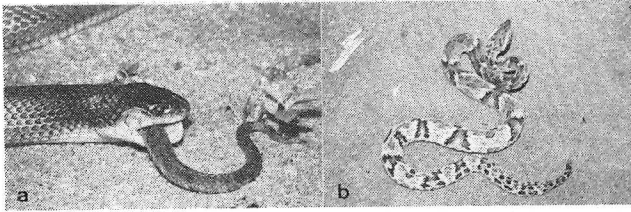
Fig. 12. Predator and injury: (a) the colubrid, *Clelia occipitolutea* (ca 100 cm SVL) at the end of swallowing an adult *B. jararaca* (ca 85 cm SVL), in captivity (photo courtesy of M. Sazima); (b) young female *B. jararaca* (ca 45 cm SVL) with missing tail tip.

(Arnold, 1988 presented this and other explanations for tail injuries in lizards), or some pathological condition (Neill, 1960). One adult female (111 cm TL) presented a slightly crooked mandible (healed fracture?), but otherwise seemed healthy. Greene and Hardy (1989) recorded the natural death of an adult *B. asper*, probably due to starvation, associated with skeletal injury (fractured mandible).

DEFENSIVE TACTICS

Antipredator mechanisms are better known for snakes than for any other reptile group (Greene, 1988), and this may be due to the hazards some snakes pose to human health. Yet the basic features of the defensive tactics of Neotropical pitvipers remain essentially unstudied, especially under field conditions (Greene, 1988). I am aware of a few anecdoctal reports of defensive behavior of *Bothrops asper* (March, 1928a; Greene, 1988), *Bothriechis schlegelii* (Greene, 1988), and *Crotalus durissus* (March, 1928b).

In a previous report on the behavioral biology of *Bothrops jararaca* (Sazima, 1989a), I surveyed the main components of its antipredator repertoire, following the procedure outlined by Duvall et al. (1985). Here I review the topic and comment on these behaviors and their context using the defensive categories of Greene (1988) and Duvall et al. (1985).

Procrypsis

The color pattern of several viperids, including species of *Bothrops*, may be regarded as procryptic or concealing (Greene, 1988; Pough, 1988a). Basking or resting individuals of *B. jararaca* sometimes blend so well with their immediate surroundings that even an observer warned about their presence will hardly perceive their contours (Fig. 13). Several kinds of indirect evidence support the suggestion that such color patterns in snakes have a defensive role (reviews in Greene, 1988; Pough, 1988a). The cryptic effect is further enhanced by the snake remaining immobile or, if previously moving, freezing upon being approached (Sazima, 1989a). Freezing was the first and most frequent reaction of moving jararacas when approached, a result similar to that found by Duvall et al. (1985) in their extensive study of the prairie rattlesnake, *Crotalus viridis*.

Locomotor Escape

Flight response after initial freezing was the most frequent reaction of moving *B. jararaca*, as well as of those individuals previously immobile (e.g. basking), when closely approached (Sazima, 1989a). These escape reactions were faster when compared to the speed at which the snakes were moving before being threatened, and often involved a change in the locomotion mode (e.g. from rectilinear to lateral undulatory, or from this latter to one similar to sidewinding; see Fig. 14, and Jayne, 1986). When relatively slow, locomotor escape often was accompanied by tail vibration, a warning behavior possibly derived from conflicting tendencies to attack and escape (Greene, 1988).

In *B. jararaca*, a locomotor mode similar to sidewinding (apparently combined with lateral undulation) was performed by young or slender individuals found away from cover and fleeing over open areas with smooth surfaces, such as sandy trails (Fig. 14c; see also Sazima, 1989a). As sidewinding is the swiftest locomotor mode a snake may use under such conditions (Klauber, 1972; Jayne, 1986), I think jararacas may be able to assess their chances of escape according to the circumstances of the predator's attack (Duvall et al., 1985 indicated this ability for *C. viridis*).


Fig. 13. Procrypsis in *B. jararaca*, illustrated by a gravid female (ca 110 cm TL) basking on vegetation (after Sazima, 1989a).

Bluffs and Threats

Since bluffs differ from threats in terms of consequences if ignored by an attacker (Greene, 1988), I am inclined to regard all defensive displays of *B. jararaca* as genuine threats. An attack upon an alert and displaying jararaca is likely to result in serious illness or even death for the attacker, unless the latter is able to avoid the snake's strikes or overcome their effect.

When cornered or otherwise restrained from fleeing, *B. jararaca* either displayed coiled or cocked postures (Figs. 14 and 15). These two postures seem to differ mainly by their being displayed while stationary (coiled), or retreating (cocked). In both postures the following categories of the phenotypic survey of Greene (1988) are found: dorsoventral body compression, body inflation, tail vibration, head and neck elevation, S-coil, and frontal display. Coiling often gradually changed to cocking (Figs. 14d-f, 15) as the snake began to move away from the attacker. When cocked the jararaca employed the posterior part of its body to retreat, backwards, while keeping its head directly trained on the attacker.
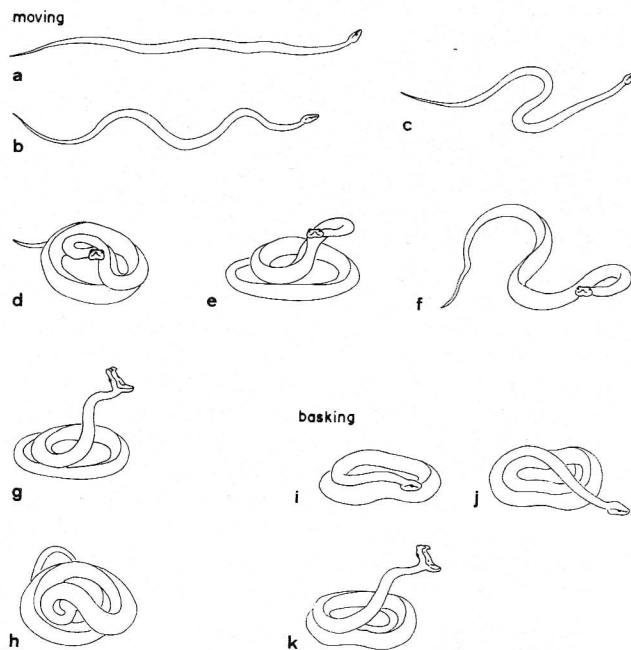
Fig. 14. Defensive tactics of *B. jararaca* include freezing when previously moving (a, b); locomotor escape with changes from a slow mode (almost rectilinear - a) to a swift one (lateral undulation - b, or a kind of sidewinding - c); threat with use of coiled (d) or cocked (e) postures, and retreat concomitant to warning tail vibration (f); offensive defense with strikes delivered from a warning posture (g) or without any evident previous warning (k); removal of cues by hiding the head (h). Basking, gravid females (i-k) habitually resort first to procrypsis (i) then either to unobtrusive locomotor escape (j) or, rarely, to offensive defense (k).

While in coiled or cocked postures, *B. jararaca* often delivered strikes when closely approached. As some strikes clearly would not reach the attacker, and some of them apparently were delivered with a closed or half-open mouth, I regard these as threat or warning displays (false strikes cf. Greene, 1988).

Offensive Defense

The defensive strike (Fig. 17a) was the most escalated form of defense I observed in *B. jararaca* (but see "Removal of cues"). This strike was delivered from either the coiled or cocked postures (Sazima, 1989a), and from other postures as well, provided the snake had its neck retracted into a sigmoid curve even if slight. The defensive strike of *B. jararaca* seems similar to that reported by Kardong (1986b) for *Crotalus viridis*.

Removal of Cues

In two adult males of *B. jararaca* I observed head-hiding (Fig. 17b) following a strike. Only once did a snake strike from head-hiding posture in which, together with the rarity of head hiding, *B. jararaca* seems to differ from *C. viridis;* this latter species adopted head hiding in approximately the same levels as striking, and it was not uncommon for a rattlesnake to strike from a head-hiding posture (Duvall et al., 1985).
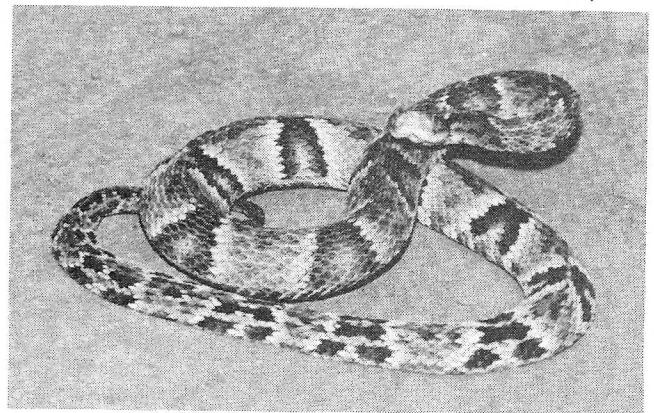
Fig. 15. Defensive display by an adult male *B. jararaca* (91 cm TL), as it changes gradually from a coiled posture to a cocked one preceding retreat (after Sazima, 1989a.)

Defense in Basking Snakes and Variable Behavior

The defensive behavior differed between moving and basking *B. jararaca* (Fig. 14). Basking snakes (gravid females) mostly used unobtrusive lateral undulation when fleeing, rarely resorted to threats, and sometimes struck without previous warning. These differences between moving and basking snakes may be due to proximity of cover and the reproductive condition of basking individuals (Fitch, 1960; Neill, 1964; Duvall et al., 1985), and perhaps to body temperature (as found in gravid *C. viridis,* see Goode and Duvall, 1989). The few gravid *B. jararaca* females which struck defensively did so consistently on successive encounters; typically, the snake first delivered one or two strikes and then escaped towards nearby cover. One gravid female behaved this way during the 1987 season and also two years later when found at the same site, gravid again. Those females which did not strike but used locomotor escape as defense instead, also did it consistently. Thus defensive tactics in *B. jararaca* seem to vary among individuals under apparently similar circumstances (see also Duvall et al., 1985; Greene, 1988; Goode and Duvall, 1989; Herzog and Schwartz, 1990, for comments on variation of defensive tactics). This variation possibly influences some of the epidemiological factors in snakebite cases due to *B. jararaca* (Sazima, 1989a).

MIMICRY OF *B. JARARACA* BY COLUBRID SNAKES

Resemblance between certain colubrids and viperids may be regarded as mimicry, the vipers acting as dangerous models and the colubrids being their mimics (reviews in Pough, 1988a, b). This presumed viper mimicry is a controversial issue, since some traits may be due to common snake ancestry, whereas others may be due to convergence on a common cryptic pattern (Sweet, 1985; Pough, 1988a, b) or a feeding device (e.g. wide gape in frog-eating snakes). Nevertheless, several presumptive mimics of pitvipers of the genus *Bothrops* have been suggested (see Pough, 1988a, b), and some of them are particularly convincing. Species in the colubrid genera *Dipsas, Lystrophis, Thamnodynastes, Tomodon, Waglerophis* (Fig. 16), and *Xenodon,* are among
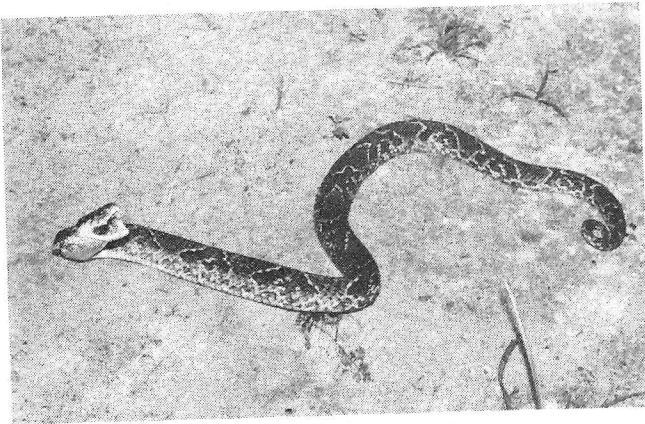
Fig. 16. Defensive display (mouth agape, cocked head, dorsoventral flattening of the body), performed by an adult female of the colubrid *Waglerophis merremii* (70 cm SVL; ZUEC 551) as it retreats. Note superficial resemblance of this presumed mimic, in dorsal pattern and defensive posture, to *B. jararaca*, its putative dangerous model.

Fig. 17. Two most escalated defensive tactics of *B. jararaca*: (a) defensive strike delivered by a young male (ca 65 cm TL) towards a boot (after Sazima, 1989a); (b) head-hiding performed by a young male (58 cm SVL) after delivering several strikes.

these putative mimics (Pough, 1988a; Yanosky and Chani, 1988; Campbell and Lamar, 1989; Sazima, 1989c). I would add species of *Tropidodryas*, and perhaps *Sibynomorphus* to the list of *Bothrops* "mimics", due not only to their superficial resemblance to *B. jararaca* (Fig. 18) but also to some of their defensive movements (see below).

Some Selected Mimics

Dipsas indica is a nocturnal, semi-arboreal snake that often forages on the ground for slugs and snails (Sazima, 1989c). The color pattern varies over this snake's range (Peters, 1960), and individuals from populations known as *D. indica bucephala* are yellowish to grayish brown, with darker trapezoidal blotches. These populations are found over most of the range of *B. jararaca* in southeastern Brazil (see maps in Peters, 1960; Campbell and Lamar, 1989). When found moving slowly on the ground, an individual of *D. indica* may easily be mistaken for a young or slender *B. jararaca*. This resemblance is enhanced when the disturbed snake coils, expands its body, cocks and triangulates its head (Fig. 18d), and thrashes the forebody as if delivering false strikes. *Dipsas albifrons* from the Atlantic Forest mimics even better the color pattern and defensive movements of *B. jararaca* (pers. obs.). Due to its specialized feeding habits and morphology (Peters, 1960; Sazima, 1989c), *Dipsas* probably is unable to pose an effective harm to a potential predator. In this respect, *Dipsas* seems unique among the suggested mimics of *Bothrops* pitvipers, and may approach the classical case of viper mimicry described for the African egg-eating snake, *Dasypeltis* (Gans, 1961).

Tropidodryas serra and *T. striaticeps* are diurnal and semi-arboreal snakes, which prey on lizards, frogs, birds, and rodents (Müller, 1970; Thomas and Dixon, 1977; pers. obs.). Both species occur in forested habitats and their distributions largely overlap that of *B. jararaca* in southeastern Brazil (see maps in Thomas and Dixon, 1977; Campbell and Lamar, 1989). The color pattern varies from greenish gray to yellowish brown with darker oblong and angular blotches. The tail tip is whi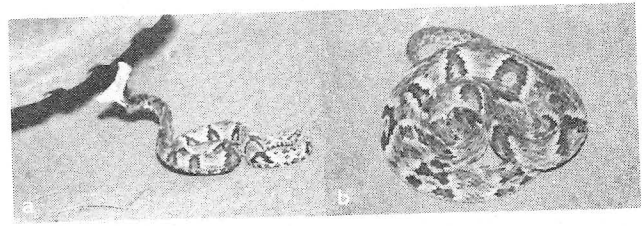tish to yellowish in juveniles of both species. The general appearance of *Tropidodryas* is reminiscent of juvenile or slender individuals of *B. jararaca*, notably when the snake is disturbed (Fig. 18b). The defensive movements of *Tropidodryas* include frontal display, tail vibration, body coiling, striking posture (S-coil), false strike, strike, and bite, this latter mostly in *T. serra* (defensive categories after Greene, 1988). The conspicuous tail tip of juvenile *Tropidodryas* possibly is employed in caudal luring of lizard and frog prey.

Other presumptive mimics of *Bothrops*, particularly *B. jararaca*, may include *Sibynomorphus neuwiedi*, *Thamnodynastes* sp., and *Xenodon neuwiedii* (Figs. 18c, e, and f). Defensive displays of the former, a nocturnal and semi-arboreal snail-eating snake (Laporta-Ferreira et al., 1986), approach those described here for *Dipsas*. The nocturnal, semi-arboreal and frog-eating *Thamnodynastes* sp. flattens its body, triangulates and tilts its head (Fig. 18e), delivers false strikes, and even strikes and bites when disturbed. The diurnal and terrestrial, anuran-eating *Xenodon* has a particularly convincing resemblance to a pitviper, with its wide body and ability to triangulate its head (Fig. 18c; see also Pough, 1988a). Both *X. neuwiedii* and the toad-eating *Waglerophis merremii* may cock the head, gape the mouth widely, and deliver false strikes, a display which enhances their resemblance to an aroused pitviper (Fig. 16).

Although some of the mentioned snakes possibly are able to discourage some of their potential predators regardless of the alleged mimetic deception, their chances of survival may increase if the predator mistakes them for a dangerous snake. As aptly pointed out by Pough (1988b), even a generalized or slight resemblance to a potentially lethal species may confer substantial protection to a snake mimic.

SUMMARY AND FURTHER RESEARCH

Bothrops jararaca is a forest inhabiting snake able to live in degraded habitats. It is mostly nocturnal, although some diurnal activity occurs. This viperid is active over most of the year, with little or no activity in the driest and coldest months (June to August in SE Brazil). Gravid females tend to keep within definite areas where they bask and shelter. Basking is done in partly or wholly shaded sites, rarely in direct sunlight; nocturnal use of warm surfaces also occurs.

Female *B. jararaca* tend to be larger and bulkier than males. This snake probably attains adult size by its third or fourth year and possibly reproduces the following season. Births occur during the rainy season, and a given female
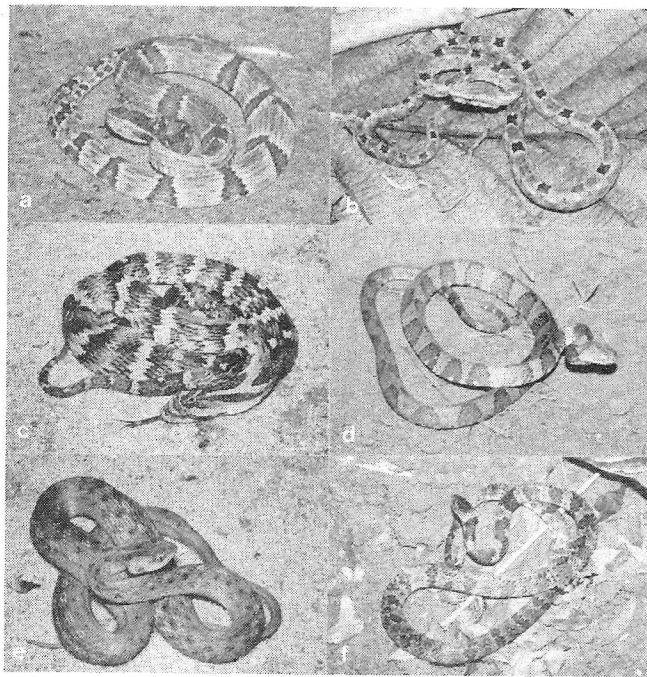
Fig. 18. Presumed mimetic snake assemblage in southeastern Brazil, with a viperid model and five colubrid mimics: (a) juvenile female *Bothrops jararaca* (ca 40 cm TL) in coiled defensive posture; note expanded body and pale (whitish) tail tip; (b) juvenile female *Tropidodryas serra* (55 cm TL; ZUEC 637) in cocked posture; note large, triangular-shaped head and whitish tail tip; (c) adult male *Xenodon neuwiedii* (67 cm TL; ZUEC 800) in coiled defensive posture; note triangulated head and dorsoventrally flattened body; (d) adult *Dipsas indica* (ca 70 cm TL) in cocked posture; note triangulated head and expanded body; (e) adult female *Thamnodynastes* sp. (66 cm TL; ZUEC 738) in cocked posture; note triangulated head and dorsoventrally flattened body; (f) adult male *Sibynomorphus neuwiedi* (69 cm TL; ZUEC 511) in cocked posture; note triangulated head. The colubrid *Waglerophis merremii* (Fig. 16) presumably also belongs here.

probably reproduces in alternate years. Typical litter size apparently is 8-14 young. Presumed natural hybrids are known between *B. jararaca* and three other species of *Bothrops (B. cotiara, B. jararacussu,* and *B. neuwiedi).*

Bothrops jararaca preys mainly on small vertebrates and has an ontogenetic shift in diet: juveniles feed mostly on frogs whereas rodents are the main food of adults. Feeding behavior on rodents is characterized by strike, release, and trailing, whereas frogs are struck and held until swallowed. This snake seems to hunt mostly by ambush and occasionally by active searching. Caudal luring is used by juvenile snakes; occasional scavenging may occur.

Adults of *B. jararaca* appear to have few predators, but juveniles may be vulnerable to several predators such as hawks, opossums, and ophiophagous snakes. Antipredator tactics escalate from procrypsis and locomotor escape to threats and offensive defense, as the threat escalates. Some sympatric colubrid snakes bear superficial resemblance both in appearance and defensive movements to *B. jararaca,* and possibly form a mimetic assemblage, with this viperid acting as the dangerous model.

It is apparent from the above outline that *B. jararaca* has traits in common with some other medium to large-sized crotaline snakes (see e.g. Fitch, 1960 on *Agkistrodon contortrix;* Duvall et al., 1985 on *Crotalus viridis;* Greene and Santana, 1983 and Greene, 1986 on *Lachesis muta* and *Bothrops asper;* Solórzano and Cerdas, 1989 on *B. asper).* Indeed, some trends in the feeding and reproductive biology of viperids are apparent and may include feeding strategies and mass of prey, and litter size and frequency of reproduction (e.g. Chiszar et al., 1982; Pough and Groves, 1983; Mushinski, 1987; Seigel and Ford, 1987; Dunham et al., 1988a).

Each year large numbers of live snakes are received in some Brazilian institutions engaged in antivenom production, such as the Instituto Butantan in the State of São Paulo (Fonseca, 1949; see also "Abundance" in this study) or the Instituto Vital Brazil in the State of Rio de Janeiro (Melgarejo-Giménez, 1986). These snakes provide an excellent, even if rarely appreciated, opportunity for studies on several aspects of the natural history of *B. jararaca* and other species of *Bothrops* (but see Fernandes et al., 1986, 1987; Puorto et al., 1990). We still know little about population attributes and most of reproductive biology of *B. jararaca.* Some of these subjects seem simple to resolve with access to large samples with reliable locality data. For instance, a more-or-less complete outline of life history may emerge from a small set of variables (Dunham et al., 1988a, b), and some of these are obtainable even from specimens preserved in collections (e.g. Shine, 1989). In view of the wide distribution of *B. jararaca,* some aspects of its natural history probably vary geographically (see examples in Shine, 1987, and Solórzano and Cerdas, 1989).

Species of *Bothrops* in southeastern Brazil apparently form distinct taxonomic assemblages (e.g. Janeiro-Cinquini et al., 1987; Campbell and Lamar, 1989; Fernandes and Pesantes, 1989), and it seems instructive to compare some forest dwellers such as *B. pradoi* or *B. fonsecai* to open habitat species such as *B. neuwiedi* or *B. moojeni* (this latter snake is perhaps mostly a gallery forest dweller). Such studies may examine the divergences and similarities among species in relation to their ecology and their presumed relationships (see approaches in Henderson et al., 1987; Shine, 1989; Greene, this volume).

Medium and long-term field studies are obviously needed but these generally are difficult and costly (e.g. Brown et al., 1982; Reinert et al., 1984; Duvall et al., 1985). My studies on *B. jararaca* at the Santa Genebra reserve, albeit limited by the observational and other simple methods I use (Sazima, 1989a, b; see also Fitch, 1960), disclosed some basic facts. However, without the introduction of more sophisticated methods (e.g. radiotelemetry, see Reinert, this volume), important subjects such as activity schedules, habitat use, thermoregulation, and foraging schedules will remain largely unknown or speculative. Some of the topics that I have discussed in this paper seem reasonably covered given the present knowledge of the biology of Brazilian or even Neotropical pitvipers. Other topics, however, I regard as initial guesses or working hypotheses at best, and I have included them to give a clearer picture of what is and what definitely is not known about the natural history of *B. jararaca.* I hope that this survey will stimulate further studies on this common and important snake, as well as on other Brazilian and Neotropical pitvipers (see Greene, this volume).

Lastly, I want to touch upon a crucial problem which emerges from the study of most Neotropical organisms: the proper identification, or more precisely, the proper allocation of a specific name to the population studied. The taxonomic status of species of *Bothrops* is far from satisfactory (e.g. Vanzolini, 1981, 1986; Campbell and Lamar, 1989), and I have doubts on the status of any very variable "species" such as *B. jararaca* (see Hoge et al., 1978; Castro and Rocha, 1987; Campbell and Lamar, 1989). I think that a thorough study on the variation of this pitviper is as necessary as the study of its natural history.

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