

## Natural history of the terciopelo *Bothrops asper* (Serpentes: Viperidae) in Costa Rica

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### ARTICLE INFO

#### Article history:

Received 25 February 2009

Received in revised form 17 June 2009

Accepted 18 June 2009

Available online 27 June 2009

#### Keywords:

Lancehead pitviper

Viperidae

*Bothrops*

Home range

Ontogenetic dietary change

La Selva

### ABSTRACT

The terciopelo *Bothrops asper* is the only lancehead species widely distributed in the humid lowlands of Middle America and northwestern South America. Its large body size, relative abundance and cryptic habits contribute to the high incidence of snakebites induced by this species throughout its distribution. The terciopelo plays an important role in ecosystems, both as prey and as a generalist predator. Diet comprises a great variety of prey items, including some species that are considered nuisances. *B. asper*, as other lancehead species, exhibits a notable ontogenetic shift in diet, consuming ectotherms (mainly frogs and lizards) when young, and increasingly incorporating birds, rodents, and other small mammals with maturity. Adult terciopelos also consume large anurans, especially when endothermic prey availability is low.

Using radiotelemetry we determined home range and movement patterns from 28 individual *B. asper* at La Selva Biological Station, Costa Rica. Overall home range estimates are relatively small compared with other pitvipers, averaging between 3.71 ha and 5.95 ha; home range size did not differ between males and females. Movement patterns are largely aseasonal and consist of short (<10 m) movements between daytime shelter and nocturnal ambush sites within a given area, interspersed with longer distance (>50 m) movements to new foraging areas. Habitat use is related to prey availability and therefore to foraging strategy. Our data support a strong preference for areas near swamps by both sexes. Reproduction in *B. asper* is highly seasonal, and – apparently – biannual. Reproductive cycles in Costa Rica are tightly related to rainfall patterns. Therefore, the timing of breeding differs between populations in the Caribbean and Pacific lowlands. *Bothrops asper* is adapted to areas with low levels of disturbance along the agricultural frontier, and consequently it is not rare to find it in or near human dwellings. However, despite popular belief, no evidence supports a purported increase in population density of this species in Costa Rica. Despite human persecution and substantial modification of habitat, *B. asper* is a species with a conservation status of least concern, and probably will likely persist well into the future. Thus, it is important to learn how to coexist with this species, and to improve mechanisms for the prevention and treatment of accidental snakebite and its consequences.

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### 1. Introduction

The genus *Bothrops* comprises over 37 species commonly referred to as lanceheads (Campbell and Lamar, 1989, 2004) which are chiefly distributed in South America,

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although two species (*Bothrops punctatus* and *Bothrops asper*) reach Central America. Owing to their relative abundance, large body size (some species can attain over 200 cm in total length), cryptic coloration, and ability to inhabit human-disturbed environments, the genus includes species responsible for most of the snakebite incidents in the New World.

In the last two decades, a number of studies have been conducted to understand the evolutionary relationships within the genus *Bothrops* (Wüster et al., 2002; Fenwick et al., 2009) and to evaluate the taxonomic status of currently recognized species (McDiarmid et al., 1999; Campbell and Lamar, 2004).

Parallel to these efforts, venom toxins have been the subject of intensive research, both at the biochemical and immunological level (Gutiérrez, 2002; Gutiérrez et al., 2005). As a result, much is known on the venom components of most lancehead species, as well as on the biological effects of these components and their potential medical uses (Zingali et al., 1993). Considering this growing body of work, it is ironic that the natural history of most *Bothrops* species remains poorly known, even for those considered abundant and of medical importance.

Natural history is concerned with the lifestyles of organisms, and incorporates spatial use, diet, reproduction, social structure, defense mechanisms, maintenance behavior, and interactions with other conspecific or heterospecific organisms (Greene, 1993). Thus information regarding natural history is critical for understanding biodiversity and evolution, and is the basis upon which biological research and conservation strategies should be built (Greene, 1986, 2005). In the case of highly venomous snakes, information about life history can also provide insights into strategies for minimizing incidence of human envenomings.

This gap in knowledge regarding the natural history of *Bothrops* is probably explained by the overall decline of natural history studies which permeates modern herpetological research (see Greene, 2005; McCallum and McCallum, 2006; for a contrasting view see Arnold, 2003). Ecological studies involving lanceheads are also complicated by their reputation as dangerous animals; further difficulties arise from their cryptic and chiefly nocturnal habits which make them hard to observe in the field. Several species are also found in environments that are unwelcoming to human observers (e.g. swamps), and as top predators, many exhibit low population densities, making them even more intractable as study organisms.

Fortunately, there are a few species of lancehead for which some aspects of natural history have been documented, including *B. moojeni* (Leloup, 1984; Nogueira et al., 2003), *B. atrox* (Henderson et al., 1976; Oliveira and Martins, 2003), and *B. jararaca* (Sazima, 1987, 1992). Studies conducted in these and other species have improved our understanding of lancehead biology, and reveal considerable variation in aspects of their natural history (see Martins et al., 2002).

Here, we present an account of the natural history of one of the most spectacular and intimidating lanceheads, the Central American lancehead (herein referred to as “terciopelo”) *Bothrops asper*. According to Scott (1983) *B. asper* is

“much more inclined to bite than other large vipers, which tend to retreat when approached”. Its reputation as an irritable and “aggressive” snake has been commented by other prominent researchers such as Picado (1931), and Bolaños (1984), and this snake has been called “ultimate pitviper” by Hardy (1994) owing to its willingness to defend itself, the large body size, and its involvement in more than 50% of all snakebite accidents in the lowlands of Central America, Mexico, and northwestern South America.

Being a relatively abundant species, it is paradoxical that gathering information on the lifestyle of *B. asper* is difficult: The terciopelo is usually killed on sight by humans alleging precautionary reasons, even in many national parks and biological stations. Scientific collections may be misleading, consisting of only the most impressive or large specimens, and often only the head or skin have been collected as vouchers. Consequently, further analyses into aspects such as allometry, reproductive status, diet, and presence of parasites are often limited. The need of keeping live specimens for venom extraction by medical and antivenom production programs has provided freshly collected specimens, which have been of key importance in gathering such information.

## 2. Materials and methods

### 2.1. Database

This review includes our field observations, many of which have not been published previously, and data from more than 1000 preserved or live specimens of *B. asper* obtained over two decades of research in Costa Rica and neighboring countries. We complete our observations with published and unpublished material from colleagues working in other areas where *B. asper* occurs. Additional data on reproductive biology came from direct observations in captive breeding programs in our home institutions or in other live collections in Costa Rica.

Two sites where we have conducted particularly intensive work on *Bothrops asper* ecology warrant mention: (a) Bajo Pérez de Acosta (BPA, located in Costa Rica's Central Pacific versant, San José Province, 84°19'1.70W, 9°43'21.67"N), and (b) La Selva Biological Station (LSBS, a lowland site located in Puerto Viejo de Sarapiquí, Heredia Province, 84°00'12.959 W, 10°25'52.51"N). BPA is located at mid-elevation (534 m a.s.l.), and the landscape is dominated by small farms devoted to agriculture and cattle production, with small patches of secondary growth forest. LSBS consists of a 1700 ha lowland (30–70 m a.s.l.) reserve that includes primary and secondary forest, as well as open swamp areas. We include material from additional localities that is referred to in the text.

### 2.2. Predatory ecology

We examined the stomach and large intestine contents of over 110 preserved or recently killed specimens deposited at Instituto Clodomiro Picado (Universidad de Costa Rica).

Although diet may vary between localities and seasons, the overall pattern of prey taken by *B. asper* in the country was inferred by combining data from individuals of various

localities within the same versant (Caribbean or Pacific). Whenever possible, prey items were identified to the Order level for arthropods, and to the genus/species level in case of vertebrates. Mammals were identified from hair and bone remnants by comparing them with samples from suspected prey species deposited at the Museo de Zoología, Universidad de Costa Rica, or kindly identified by Robert M. Timm (University of Kansas). Prey orientation and identity, number of items, and body mass (measured to the nearest 0.1 g) were recorded.

### 2.3. Spatial ecology

Habitat use, movements, and home range estimations of the terciopelo have been studied by two of us in LSBS (see Wasko and Sasa, 2009). A total of 99 adult individuals (37 males, 59 females, 3 unknown) were captured in major habitat types (swamps, primary, and secondary forest), and a radio-transmitter was implanted in the body cavity of 28 of them, following the procedures of Hardy and Greene (1999). Snakes were released at the point of capture and then located daily, relating their position to LSBS's known coordinate system, or to previously marked locations.

Home range, movement, and macrohabitat cover (primary forest, secondary forest, swamp, developed areas) were determined for each snake using ArcView 3.2 (Hooge and Eichenlaub, 2000), and current GIS maps of LSBS based on vegetation structure and history of usage. Home range was estimated using minimum convex polygon (MCP) and 95% kernel density (KD, Worton, 1989). Only snakes with more than 100 relocations were included in the analysis (Wasko and Sasa, 2009).

We determined whether snakes demonstrated active selection for structural microhabitat by comparing sites actually used by snakes to 500 randomly selected unused points, chosen from within the area enclosed by all individuals' home ranges (Wasko and Sasa, unpublished).

## 3. Results and discussion

### 3.1. Diagnostic features

Specimens currently assigned to *Bothrops asper* have a long history of taxonomic change (see McDiarmid et al.,

1999), which is not surprising given the broad distribution of this species, resemblance to other lanceheads, and the history of herpetological exploration in the region.

The currently accepted species name was proposed by Garman in 1884 (published as 1883) who described the species as *Trigocephalus asper*, from the locality of Obispo, Darién, Panama. Later, Cope (1876, 1887) recognized the species as a synonym of *Bothrops atrox*, and during the next six decades, most researchers followed his proposal (see Amaral, 1924, 1929; Picado, 1931; Axtell and Wasserman, 1953; Álvarez del Toro 1960; Hirth 1964; Schätti and Kramer, 1993). Taylor (1954) and Smith and Taylor (1945) recognized *B. asper* as a subspecies of *B. atrox* from South America, and therefore the trinomial *Bothrops atrox asper* was adopted by some researchers of venom toxins and their effects (Jiménez-Porras, 1964). The binomial *Bothrops asper* was adopted after Hoge (1966), Peters and Orejas-Miranda (1970), Burger (1971), and Bolaños (1984), and is currently the accepted nomenclature (Campbell and Lamar, 1989, 2004; McDiarmid et al., 1999).

The species name *Bothrops asper* is a reference to the distinct heat-sensing pit in the loreal region and the rough aspect of its skin owing to the coarse keeled dorsal scales (from the Greek *bothros*: pit or eye; and the Latin *asper*: rough). The species has a variety of common names that differ according to language, region, and snake size and color pattern (see Campbell and Lamar, 2004).

Overall, *B. asper* is a large (maximum length reported 250 cm, maximum length in Costa Rica up to 223 cm) but moderately slender snake that exhibits great variation in external meristic characters (see Saldarriaga et al., 2009). There is a strong sexual dimorphism, and females are significantly larger, have a higher number of dorsal scale rows, and fewer subcaudal scales than males. Dorsal coloration is brown, olive, or gray to dark gray, whereas the venter is often cream-colored and may be entirely unmarked to darkly spotted. A narrow (1–2 scales wide) dark postorbital stripe extends from behind the eye to the angle of the mouth (Fig. 1a). Dorsal pattern consists of a series (14–28) of triangular dark blotches, with their apices toward the vertebral line, along each side of the body. Blotch and line shape differ substantially, and at least six distinct patterns can be recognized among Middle American specimens (Sasa, 2002). Dorsal scales are



**Fig. 1.** *Bothrops asper* from Bajo Pérez de Acosta, Costa Rica. (A) Lateral aspects of the head of a female (140 cm TL). Note narrow postorbital dark stripe that characterizes this species. (B) Typical S-coiled posture for “aggressive” defense in a large female *B. asper*. This is an escalated defensive display often performed only when the snake is cornered. (C) Male neonate *B. asper*. Note the yellow tip of the tail and heavy pigmentation between supralabial scales.

strongly keeled, usually disposed in 25 or 27 rows (depending on the sex), rarely 29 rows. Both scutellation and color pattern characters found in *B. asper* overlap with other members of the genus, in particular with species included in the *B. atrox asper* complex (Campbell and Lamar, 1989, 2004).

### 3.2. Growth and longevity

*Bothrops asper* is a relatively fast-growing snake in captivity, especially when food is offered frequently. This species may attain sexual maturity at around 1 m in length (males 99.5 cm, females 111.3 cm TL, according to Solórzano and Cerdas, 1989), or in a little over 3 years. We have not quantified growth rates for this species, but in our observations there seems to be a gender effect on growth, with females attaining larger dimensions sooner. Interestingly, no significant differences in mass are observed between male and female neonates (see Section 3.9) and the rate at which terciopelos gain mass is similar between sexes, once corrected for SVL (ANCOVA  $F_{1,39} = 0.56$ ,  $P = 0.81$ ).

As with some other vipers, *B. asper* may be relatively long-lived, but its average lifespan in the wild remains unknown. Recaptures of this species are infrequent, precluding a good estimation of survivorship rate. However, as maximum lifespan in captivity is often associated with longevity in the wild, we have some idea on the matter. Bowler (1975) reported the maximum lifespan of a *B. asper* a little over 20 years. This snake, of unknown sex, was presumably collected in Chiapas, and was deposited in the Instituto de Historia Natural (Chiapas, Mexico). Similarly, a 1.73 cm SVL female from Petén, Guatemala, was kept in our live collection for over 21 years. Some specimens from Costa Rica have remained alive in captivity from 15 to 17 years. Thus, it is likely that maximum lifespan for this species is around two decades.

### 3.3. Distribution and habitat

*Bothrops asper* is continuously distributed from the Caribbean versant of Tamaulipas (Mexico), throughout much of the Caribbean lowlands (Flores-Villela et al., 1987) including the Península de Yucatán (Lee, 1996; Campbell, 1998) and Central America (Wilson and Myers, 1985; Savage 2002), northeastern Colombia, Trinidad, and Venezuela. On the Pacific versant, a disjunct population occurs in western Chiapas and Guatemala (Álvarez del Toro, 1960; Campbell and Vannini, 1989). The species crosses over to the Pacific at moderate elevations of the Cordillera de Guanacaste in northwestern Costa Rica (Solórzano, 2004), and is widespread from the central Pacific lowlands of this country southwards along the Pacific versant of the Colombian and Ecuadorian Andes to extreme northern Peru (Peters and Orejas-Miranda, 1970; Freire-Lascano and Kuch, 1994). Insular populations of *B. asper* include Isla Violines (Costa Rica), Gorgona (Colombia), and Trinidad.

The terciopelo prefers wet environments, and is present in most life zones (*sensu* Holdridge, 1967) located at low or middle elevations (0 to ~600 m), excluding those with strong seasonal dry periods. Occasionally, *B. asper* reaches

environments at higher elevations, such as the premontane forest in Costa Rica (i.e. Alto Telire, Solórzano, 2004), the cloud forest of Guatemala and Mexico (Cuesta-Terrón, 1930), or the lower montane wet forest in Caribbean Colombia and Ecuador (U. Kuch, personal communication) but in those regions the species is not as abundant.

In dry or deciduous forests, the species is mainly restricted to evergreen and riparian vegetation, along permanent rivers which may serve as refuge during dry periods (Freire-Lascano and Kuch, 1994). This is true in northwestern Costa Rica, where the species can be found along riparian systems in areas otherwise covered by dry forest. Moreover, Víquez (1935) and Taylor et al. (1974) reported the presence of *B. asper* from the inner part of the Península de Nicoya, in northwestern Costa Rica. This region was once covered by tropical dry forest, although some other vegetation associations also occur at higher inland elevations. Several specimens allegedly from that region were brought to the Instituto Clodomiro Picado in the early 1970s. While no further specimens have arrived in recent years from that region, the presence of *B. asper* in such an environment cannot be ruled out. Up until the 1970s there was a heavy forest cover in the Nicoya region but this underwent strong deforestation during the next decade. Thus, macrohabitat – and probably microclimatic conditions as well – were fairly different from dry patterns currently observed.

### 3.4. Feeding biology

#### 3.4.1. Diet

Diet of *B. asper* is likely to reflect opportunism, as the species exhibits great plasticity in its use of prey resources. The terciopelo is euryphagous and consumes a variety of prey types (Table 1), the most important being rodents, birds, and anurans. Other items, including centipedes, lizards, snakes, and fishes, constitute an infrequent, yet important, part of the diet, especially for juveniles.

Boada et al. (2005) dissected 21 specimens from the Pacific coast of Ecuador. Overall, 67% had prey remains, only one of them undigested, in the stomach. From the individuals with gut contents in the sample, 42.8% consumed rodents, 64.3% arthropods, 21.4% anurans, 7.1% lizards, and 7.1% birds. Eight of the 14 snakes with contents had more than one prey type in their guts.

We analyzed gut contents of a sample of 56 adult or semi-adult terciopelos (SVL range 54.5–138.2 cm) from Bajo Pérez de Acosta (BPA). Snakes were collected during two periods covering rainy (July to November, 18 individuals) and dry (December to April, 38 individuals) seasons. During the rainy season, 44% of the individuals had remains of prey items in their digestive track. From these, 12.5% had recently fed, as evidenced by the presence of prey remains in the stomach rather than intestines. During the dry season, 63% of the snakes had prey remains in their digestive tracts, 46% of them showing evidence of recent meals. The proportion of snakes with stomach contents at each season did not differ ( $\chi^2 = 1.49$ ,  $P = 0.22$ ).

Overall, 57% of the snakes from BPA have prey remains in their digestive tracts, 21.4% of them holding a recent meal. All prey items were consumed head first. Rodents

**Table 1**

Identified prey items consumed by *Bothrops asper* along its range. BPA (Bajo Pérez de Acosta) and LSBS (La Selva Biological Station).

Taxa	Locality	Reference
<b>ANURANS</b>		
Bufonidae		
<i>Rhinella marinus</i>	Muisne (Ecuador), Costa Rica	Boada et al. (2005); Sasa, unpublished
Craugastoridae		
<i>Craugastor fitzingeri</i>	Costa Rica	Sasa, unpublished
Leptodactylidae		
<i>Leptodactylus savagei</i>	BPA (Costa Rica)	This paper
<i>L. boliviensis</i>	Corcovado, Costa Rica	Sasa, unpublished
Ranidae		
<i>Lithobates forneri</i>	BPA (Costa Rica)	This paper
<i>L. vaillanti</i>	LSBS (Costa Rica)	This paper
<i>L. warzewitzchi</i>	LSBS (Costa Rica)	Sasa, unpublished
Strabomantidae		
<i>Pristimantis achatinus</i>	Muisne (Ecuador)	Boada et al. (2005)
Hylidae		
<i>Smilisca phaeota</i>		Sasa, unpublished
<i>S. sordida</i>		Sasa, unpublished
<b>BIRDS</b>		
Thraupidae		
<i>Volantinia jacarina</i>	BPA (Costa Rica)	This paper
Unidentified passerines	BPA (Costa Rica), Guatemala	Barbour and Loveridge (1929)
Unidentified	Guatemala	Barbour and Loveridge (1929)
Troglodytidae		
<i>Thryothorus nigricapillus</i>	Muisne (Ecuador)	Boada et al. (2005)
<b>MAMMALS</b>		
Non-rodents		
Didelphidae		
<i>Caluromys derbianus</i>	Costa Rica	Hirth (1964)
<i>Didelphis marsupialis</i>	Caribbean Costa Rica, Trinidad	Mole (1924); Murphy (1997)
<i>Philander opossum</i>	Caribbean Costa Rica, Guatemala, Belize	Sasa, unpublished; Campbell (1998)
Leporidae		
<i>Sylvilagus brasiliensis</i>	LSBS (Costa Rica)	Greene and Hardy (1989)
Rodents		
Heteromyidae		
<i>Heteromys desmarestianus</i>	Costa Rica, Guatemala	This paper; Campbell (1998)
Echimyidae		
<i>Proechimys semispinosus</i>	BPA, LSBS (Costa Rica)	This paper; Greene (1997)
Muridae		
<i>Melanomys caliginosus</i>	Caribbean	This paper
<i>Mus musculus</i>	Caribbean Costa Rica	This paper
<i>Oligoryzomys fulvescens</i>	BPA (Costa Rica)	This paper
<i>Oryzomys sp.</i>		
<i>Rattus rattus</i>	BPA (Costa Rica), Costa Rica, Los Tuxtlas (Mexico)	Buttenhoff and Vogt (1995)
<i>Sigmodon hirsutus</i>	Caribbean Costa Rica	This paper
<i>Sigmodon peruanus</i>	Ecuador	Kuch et al. (2004)
<b>REPTILES</b>		
Lizards		
Iguanidae		
<i>Ctenosaura similis</i>	BPA (Costa Rica)	This paper
Polychrotidae		
<i>Anolis sp.</i>	Guatemala	Campbell (1998)
Sphaerodactylidae		
<i>Gonatodes fuscus</i>		Nicéforo-María (1930)

**Table 1 (continued)**

Taxa	Locality	Reference
Teiidae		
<i>Ameiva festiva</i>	Caribbean Costa Rica	Sasa, unpublished
Xantusiidae		
<i>Lepidophyma reticulatum</i>	BPA (Costa Rica)	This paper
Snakes		
Colubridae		
<i>Erythrolamprus bizona</i>	Costa Rica	Solórzano (2004)
<i>Ninia atrata</i>	Trinidad	Murphy (1997)
<i>Ninia sebae</i>	LSBS (Costa Rica)	Sasa, unpublished
Viperidae		
<i>Bothrops asper</i>	Costa Rica	Tryon (1985a); Buttenhoff and Vogt (1995)
<b>ARTHROPODS</b>		
Orthopterans		
<i>Scolopendra angulata</i>	Isla Gorgona (Colombia)	Parker (1926)
Other centipeds		
Crayfish	Muisne (Ecuador)	Boada et al. (2005)
	Trinidad	Emsley (1977)

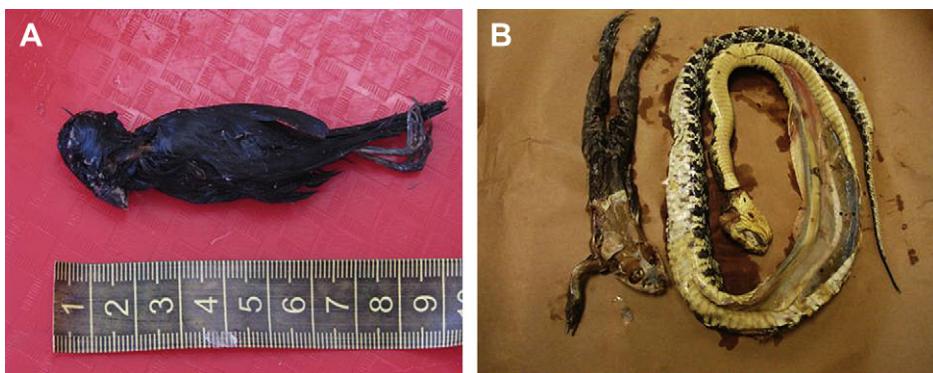
were by far the most important prey item taken (69% of the individuals in the sample), followed by birds (10.3%, Fig. 2a), and lizards (10.3%). Interestingly, anurans were present in 6.9% of the adult snakes with contents, and include the large-bodied species (Fig. 2b). Remains of arthropods (orthopterans) were present in 3.4% of the samples, but it is not known whether they constitute secondary prey items eaten by already-digested frogs.

In our BPA sample, the percentage of males and females found with gut contents was similar, although the proportional composition of various types consumed by each sex differed ( $\chi^2 = 11.34$ , df = 5, P = 0.022). These differences result from the effects of non-rodent categories, since all birds and most lizards were taken by males. As male *B. asper* are significantly smaller than females, observed differences in prey consumption by gender might reflect the effects of body size in prey selection or, alternatively, result from food-resource partitioning between sexes. None of these hypotheses have been evaluated yet.

Gut contents from individuals at other localities in Costa Rica reveal similar patterns. In a sample (n=37) from the Caribbean lowlands, 42% of the snakes had prey remains in their digestive tract, and 32% of them had recently fed. Identified prey species are listed in Table 1.

Snakes are not considered common prey items for *B. asper*, but several reports in the literature and our own observations (Table 1) indicate that perhaps ophiophagy may be more common than previously thought. Tryon (1985a) and Buttenhoff and Vogt (1995) reported cannibalism by juveniles, a feature that has been observed frequently in our own collection.

Rodents observed as stomach contents of *B. asper* (Table 1) are abundant species found in semi-urban environments or in forest edges, and secondary growth. Similarly, birds consumed are usually abundant species that nest or feed on the ground. Thus, *B. asper* does not seem to disproportionately select for any particular prey species in the areas where it occurs.



**Fig. 2.** Birds and anurans constitute part of the diet of terciopelos in adulthood. (A) A blue-black grassquit *Volatinia jacarina* found in the stomach of a 89.6 cm (TL) *B. asper* male from Bajo Perez, Acosta, Costa Rica. This grassquit is a common bird in secondary growths where it is usually found foraging or nesting in or near the ground. (B) A large smoky-jungle frog *Leptodactylus savagei* (202.99 g) found in the stomach of a 133.4 cm (TL) female that weighted 635.0 g.

### 3.4.2. Scavenging

In snakes, reports of scavenging behavior are scarce, and traditionally the herpetological literature has downplayed the importance and prevalence of such activity. Interestingly, while it is general knowledge that most snakes accept dead prey in captivity, the ingestion of carrion under natural conditions has been difficult to accept for most snake researchers (DeVault and Krochmal, 2002). As a result, relatively few species are known to use this tactic to supplement their diets. DeVault and Krochmal (2002) reviewed published instances of scavenging and conclude that around 35 snake species worldwide occasionally use that strategy, a good proportion of them being vipers. Necrophagy has been observed in *Bothrops jararaca* by Sazima and Strüssmann (1990) who suggest that occasional scavenging might be widespread among other snakes. In the case of *B. asper*, an adult female was observed in the field feeding on a spiny rat which had been dead for at least 18 h (see Section 3.4.5). Direct observations at LSBS also show that this snake is an occasional scavenger (C. Montero, personal communication). Scavenging in *B. asper*, and probably in other snake species, may be more common than previously thought, especially in those species that use chemical cues for prey detection. Necrophagy not only has the advantage of opportunistically providing a supplemental source of food, but also may be an intentional feeding strategy, as in some habitats carrion might be predictably found (e.g. on roads).

### 3.4.3. Drinking

Like other lancehead species, the terciopelo often drink from water that has accumulated on its coils during rainfall (Greene, 1997; Andrade and Abe, 2000), although they also take water from droplets in forest leaf litter and in water reservoirs such as creeks and puddles. In captivity, *B. asper* is often reluctant to accept water from a bowl and is prone to desiccation, and in the wild the species seems to avoid areas that experience low levels of relative humidity.

### 3.4.4. Ontogenetic diet shift

A remarkable ontogenetic shift occurs in venom composition (see Alape-Girón et al., 2008; Gutiérrez

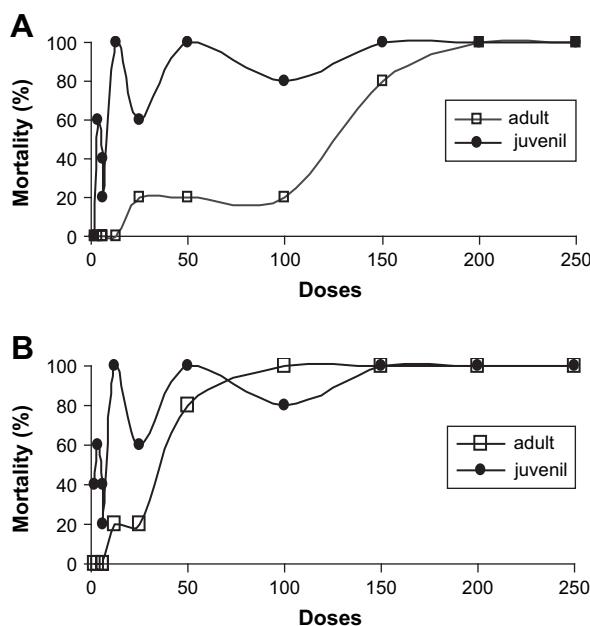
et al., 2009). This change is often related to diet modification, as *B. asper* is known to shift from an ectothermic-based diet (mainly lizards and frogs, perhaps some arthropods) to a diet chiefly based in homeothermic prey (mainly mammals, mostly rodents: Picado, 1931; Solórzano, 2004). Similar diet shifts are reported in related species of *Bothrops* (see review in Martins et al., 2002), and are widespread in other snake groups (Holycross et al., 2002).

In *B. asper*, venom is highly lethal for mice, although it seems that toxicity decreases with ontogeny ( $LD_{50}$  adults 3.82  $\mu\text{g/g}$  (3.65–4.00),  $LD_{50}$  newborns 2.06  $\mu\text{g/g}$  (1.89–2.04) for specimens from the Pacific lowlands). However, toxicity to frogs (and presumably to other ectotherms) is significantly lower in this species. Using the frog *Smilisca sordida* (Anura: Hylidae) as a model for ectothermic prey, one of us (MS, unpublished data) has estimated  $LD_{50}$  in 31.72  $\mu\text{g/g}$  (16.49–47.32) for the venom of adults and 6.69  $\mu\text{g/g}$  (1.97–29.7) in those of newborns and young terciopelos. As occurs in mice, it seems that *B. asper* venom toxicity toward ectotherms also decreases with ontogeny, and the venom of juvenile *B. asper* is more toxic and kills more quickly than that of adults (Fig. 3).

Low toxicity in frogs has also been noticed in the venom of other pitvipers (*Agkistrodon contortrix*, *A. piscivorus* Heatwole et al., 1999; rattlesnakes genus *Sistrurus*, Gibbs and Mackessy, 2009; and the lancehead *Bothrops moojeni*, Andrade et al., 1996) and has been interpreted as counter-adaptation of frogs to resist the venom of their predators. Conversely, it is possible that higher toxicity to mammalian prey (Andrade and Abe, 1999) is a consequence of the evolution of a functional characteristic of pitviper venom toward that prey type (Gibbs and Mackessy, 2009). Differences in venom toxicity among prey types in *B. asper* might also explain the different strategies employed after the bite (see below).

### 3.4.5. Predatory behavior

*Bothrops asper* employs different tactics to deal with prey of differing size, strength, defensive behavior, and general threat level. Adult terciopelos mostly forage at night: in more than 3524 encounters at LSBS, 1246



**Fig. 3.** Lethal effect of adult (open squares) and juvenile (solid circles) *B. asper* venom in the frog *Smilisca sordida*. Each dose ( $\mu\text{g/g}$ ) was tested in a group of 5 individuals, injecting 200  $\mu\text{l}$  of venom solution in the body cavity of the frogs. (A) 2 h after injection. (B) 48 h after injection. Venom of juvenile *B. asper* kills more quickly and is more lethal to frogs than that of adults.

observations correspond to snakes in ambushing position (i.e. the body tightly coiled and the head raised at a 45° angle) at night, and only 73 to those exhibiting such behavior during the day. The snake remains immobile in a previously selected site, and usually remains in this position throughout most of the night, or until they are able to strike at a potential prey animal.

In the case of juvenile *B. asper*, ambushing is also the favorite posture at night, although we have also witnessed young terciopelos chasing frogs across the forest floor. In the rainforest of Costa Rica, it is not uncommon to observe young terciopelos feeding on *Craugastor fitzingeri* and *Lithobates vaillanti* also during the day, especially in the early morning or late afternoon. These observations indicate that some differences in foraging tactics exist between juveniles and adults, and that ambushing may not be the sole foraging strategy employed by this species.

Frogs and lizards pose little danger to a hungry terciopelo. Thus, they are held once bitten, and as soon their movements cease, are immediately ingested. The procedures to subdue birds or arthropods are not known, but presumably they are also held in the snake's jaws until immobilized. Birds are considered difficult prey to immobilize, and the venom of bird specialized-lanceheads (i.e. *B. insularis*) often shows higher toxicity to avians (Cogo et al., 1993).

On the other hand, rodents and other small mammals might deliver a powerful bite to a relatively small or inexperienced snake, and thus this prey is potentially dangerous. *B. asper* strikes and releases rodents and other small mammals (although in supplemental feeding experiments

conducted in the field, one of us (DKW) observed snakes striking and holding rodents in 5 of 70 feeding attempts). After the bite, the snake waits a few minutes and increases tongue flicking, and then locate the envenomed prey by following its chemosensory trail (possibly sensing its own venom track). Tracking envenomed prey items is not always an easy feat for a snake, and in the case of *B. asper* – which consumes relatively large mammals – it can be particularly challenging. For example, while conducting a field course at LSBS, one of us (MS) observed a large female terciopelo (SVL 168 cm) feeding on a large spiny rat *Proechimys semi-spinosus*. The event took place at the edge of a swamp, among the roots of a *Pentaclethra macroloba* tree around 11:30 am, which is an unusual time for an adult terciopelo to feed. The rat's corpse was found to have maggots (probably Calliphoridae) averaging 0.8 cm in size. Feeding was interrupted and both predator and prey were taken to the lab for further examination. Upon further observation, the rat showed signs of necrosis at the bite site, identified from two clear holes on the right flank. In order to reconstruct the predation event, a dead white rat (*Rattus rattus*) was positioned at the exact same location in the forest 24 h later, and it acquired similar-sized maggots only after approximately 18 h. Thus, it is likely that the terciopelo bit the spiny rat during the early hours of the night, the rat jumped away before dying, making it difficult for the snake to follow its chemical trail within the wet swamp. It took more than half a day for the snake to locate its prey. Alternatively, the snake may have been feeding on a decaying carcass on the forest floor, but this scenario is less likely given the evidence of snakebite on the rat.

#### 3.4.6. Caudal luring

Neonate *B. asper* are born with yellow or cream-colored tail tips, a characteristic that has been related to caudal luring behavior observed in other vipers (for instance: *Agkistrodon* Carpenter and Gillingham, 1990; *Bothrops jararaca*, *B. jararacussu* Janeiro-Cinquini et al., 1991; Sazima, 1991; *B. moojeni* Andrade et al., 1996). However, a closer evaluation reveals that this feature is sexually dimorphic, as yellow tail tips are a property only of males while females bear pink tail color (Burger and Smith, 1950). Whether caudal luring behavior differs between male and female terciopelos is unknown, but Tryon (1985a) reported a case of caudal luring in a *B. asper*. The snake positioned itself in a tight coil with the distal 5–10 mm of tail exposed from beneath the coils. The tail was usually situated close to the head, and was undulated slowly from side to side. However this behavior might be infrequent, as we have seen thousands of *B. asper* neonates and have not been able to observe caudal luring.

#### 3.4.7. Predator-prey relationship

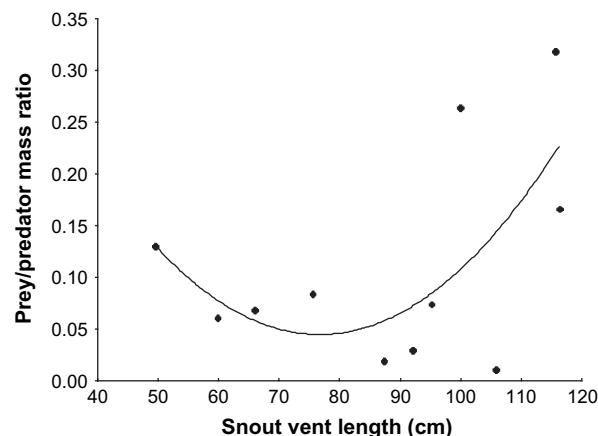
The ability of vipers to ingest bulky or heavy prey items has been largely recognized. In lanceheads, prey of high mass ratio (prey mass divided by snake mass) are often consumed (Greene, 1992) and the general opinion is that venom components allow the snake not only to subdue large prey, but also help in their digestion, preventing prey items from beginning to decompose between ingestion and digestion.

Despite some observations on extremely large relative mass ratio (Greene, 1992), allometric constraints and prey availability may shape prey consumption in these snakes. Martins et al. (2002) suggest that owing to the considerable disparity in size and stoutness exhibited by snakes within *Bothrops*, there is considerable variation in the relationships between prey size and snake size. Overall, these authors report low to high mass ratios (0.002–0.889) in well-sampled species from Brazil.

Although extensive samples are not available for *B. asper*, it seems that this species follows the typical mass ratio pattern observed in related lanceheads. Greene (1992) reports a moderate ratio of 0.65 in a specimen from Costa Rica, whereas Kuch et al. (2004) found a prey/predator ratio of 0.75 in a subadult terciopelo from Pacific Ecuador. In our samples from Costa Rican adults, prey/predator mass ratios range between 0.029 and 0.317 (Fig. 4), although we observed one small male with an obvious food bulge (probably a large frog) that weighed around 70 g, and after digestion weighed under 35 g. We have also observed neonates in captivity that regularly ate frogs at or close to their own body mass.

Because mammals are bulkier and have a higher relative mass than ectotherms, it is often thought that the relative mass ratio consumed by lanceheads increases as the proportion of mammals consumed increases in the diet (Martins et al., 2002). If so, a change in mass ratio should be expected in species that experience ontogenetic diet variation.

Nevertheless, in the related *B. atrox* and *B. moojeni*, this expectation is not supported and actually the mass ratio seems to decrease in adulthood (Martins et al., 2002; Nogueira et al., 2003). In *B. asper*, the situation is not totally clear given the small sample size of fully recovered prey items. Although it seems that there is a tendency to increase mass ratio in adult individuals, juveniles also take relatively large prey items (Fig. 4). Furthermore, large snakes also accept prey with relatively low body mass, a pattern that supports the opportunistic nature of this snake's predatory habits.



**Fig. 4.** Relative prey mass ratio consumed by *B. asper* from Central Pacific Costa Rica. Data presented for 14 cases in which stomach contents were indigested.

### 3.5. Spatial biology

#### 3.5.1. Daily activity

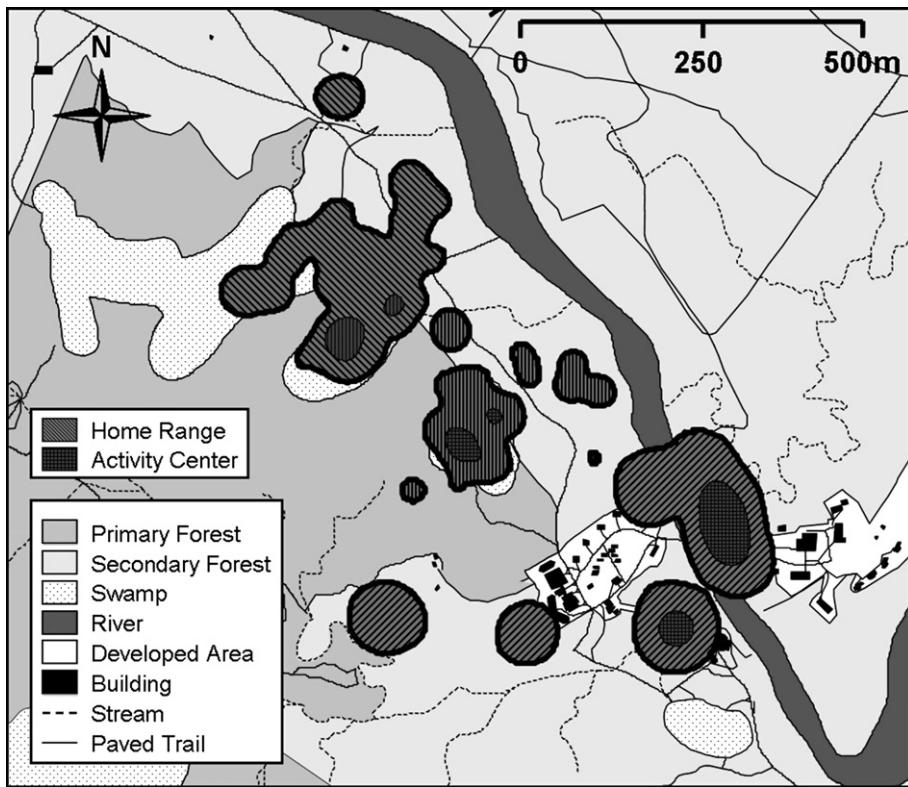
During the day, terciopelos usually remain completely inactive whether in exposed or sheltered areas, lying motionless with the body loosely coiled. At dusk, snakes emerge from their refuges and assume the ambush posture that is characteristic of many sit-and-wait foraging pit-vipers (Greene, 1992). Our observations at LSBS suggest that snakes used one to four ambush sites over the course of a night, separated by 5–10 m between sites (Wasko and Sasa, 2009) and coincide with Greene's (1986) view that large individuals move only a few meters during the night. Any longer distance movements usually occurred in a single session at the beginning or end of that evening's activity cycle, rather than interspersed with ambushing efforts.

In some cases, the species is found as it basks in the sun on banks of forest streams (Emsley, 1977), and we found them more-or-less regularly in similar situations along rivers in the southern Chocó of Colombia. Basking is documented among other *Bothrops* species (Sazima, 1992) but was rarely seen during an intensive 2-year survey at LSBS, where it was observed on only 11 occasions and mostly involving the same individual. Basking may be used more often by juveniles or gravid females, neither of which was monitored. However, postprandial individuals tended to remain in shelter for up to several days following feeding, rather than seeking higher temperatures as do many snakes (Blouin-Demers and Weatherhead, 2001). Basking and other thermophilic behavior may be more prevalent among *B. asper* populations in more thermally challenging environments.

Henderson and Hoevers (1977) describe the activity pattern of *B. asper* in Belize, stating that the species is more active during the dry season. In Costa Rica, popular knowledge holds that during this season, snakes actively search for wetter spots in creeks and streams. In contrast, Campbell (1998) suggested that the terciopelo is more commonly observed during the rainy season, coinciding with birth of neonates. In support of that view, Henderson et al. (1978) indicated that frequency of encountering tropical snakes increases with increased precipitation. As many agricultural activities are conducted during the rainy season, it is also possible that during this period the species may seem more conspicuous.

#### 3.5.2. Movement and space usage

*B. asper* are highly sedentary, with most movements at LSBS consisting of short (<10 m) distances between daytime refuges and nocturnal ambush sites, with the same or nearby refuges often used for days to weeks at a time. This pattern was interspersed with occasional longer-distance movements (>50 m) to a new foraging area. Although they infrequently do so, terciopelos are capable of considerable movements, to a maximum observed displacement of more than 1200 m over two nights, including crossing a wide river (Fig. 5). Neither movement frequency nor distance varied seasonally at LSBS, but may do so in regions with more pronounced annual cycles of temperature or rainfall.



**Fig. 5.** Partial study site map of LSBS, showing the 95% kernel density home ranges for four adult *B. asper*. These individuals were selected for illustrative purposes; home ranges overlap extensively with those of other snakes.

With a mean size of 3.7 ha, as estimated by kernel methods, home ranges of *B. asper* are small compared to those of similarly sized temperate pitvipers such as rattlesnakes (various *Crotalus* sp.; Macartney, 1985; Reinert and Zappalorti, 1988; Secor, 1994). Home ranges are not used uniformly, but have one or more “hot spots” of activity to which snakes return repeatedly; at LSBS these were most often near swamps (Fig. 5). Snakes seem to move between these foraging areas irregularly, similar to the traplining behavior of nectivorous animals (Janzen, 1971a; Stiles, 1975).

Home ranges and movement patterns did not differ between male and female *B. asper* (Fig. 6), although males were sometimes seen to actively follow females during March and April, the peak of the mating season along the Caribbean versant (see below).

### 3.5.3. Macrohabitat usage

*B. asper* uses a variety of habitats throughout its distribution. At LSBS, telemetered snakes were located in or near swamps during 57.4% of all observations (Fig. 5), even though swamps cover only 17.0% of the study site (Wasko and Sasa, unpublished). The remainder of observations occurred in primary and secondary forests, with no apparent preference among forest types. Other areas included selectively logged forests and abandoned agroforestry sites, plantations, and pastures.

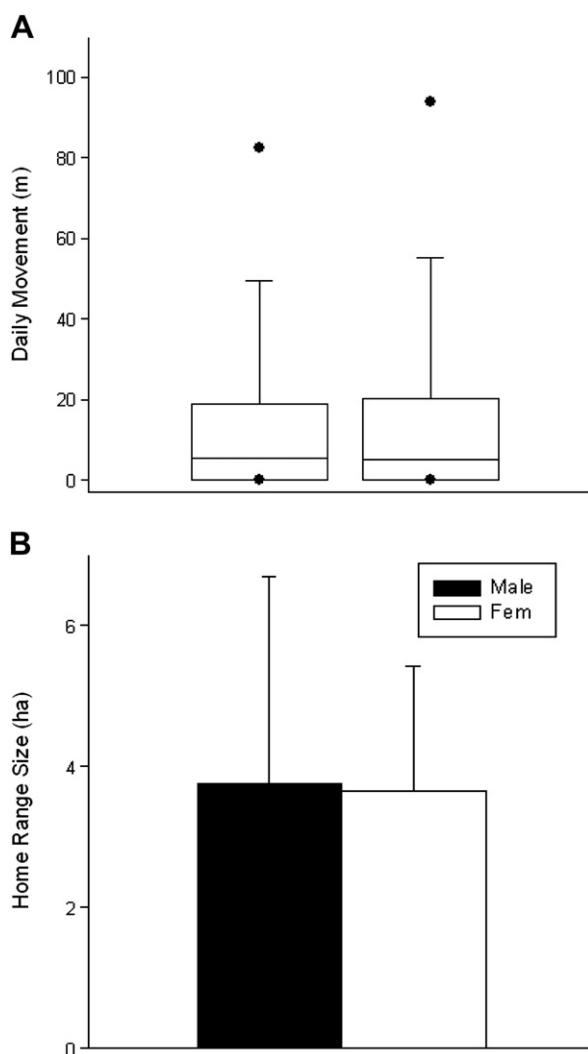
At LSBS, areas immediately surrounding laboratory and residential facilities are cleared of most canopy and all

understory vegetation, and terciopelos only rarely entered these areas (0.2% of observations, vs. 7.1% land coverage). This suggests that snakes may be somewhat averse to areas featuring greatly reduced canopy closure and ground structural cover, rather than to human activity itself. The fact that many agricultural practices develop dense ground vegetation or may retain existing canopy (as in shade coffee plantations or agroforestry), and along with rural residences are often established in close proximity to existing forest habitat, may in part explain the high incidence of snakebite under such circumstances (Rojas et al., 1997; Sasa and Vázquez, 2003).

### 3.5.4. Microhabitat usage

*B. asper* is highly terrestrial; however, adults sometimes are found on tree roots or fallen logs, usually less than 1 m high but occasionally at greater heights. Greater arboreality is presumed for juveniles, and we have observed subadult individuals resting in branches 1.3 m above the ground, and some shed skin, evidence of recent molting, at elevations of 2.1 m. Moreover, few reports (Mole and Ulrich, 1894; Greene, 1997), confirm that adults can climb to well over 2 m. In the Chocó region of Colombia and adjacent Ecuador, we have observed *B. asper* coiled on logs and roots during the morning hours after heavy rains the previous night.

Terciopelos are capable swimmers, and at LSBS individuals crossed a 60 m wide river on several occasions but spent little time in water other than actual crossings. Even when in swamp habitats, *B. asper* were more often



**Fig. 6.** (A) Movements of males ( $n = 920$  observations) and females ( $n = 2106$  observations) *B. asper* at LSBS. Lines are median values (4.8 m male, 5.1 m female), boxes are 25th and 75th percentiles, and whiskers are 90th and 10th percentiles. Closed circles are outliers. (B) Mean ( $\pm$ SD) home range size per sex (males,  $3.74 \pm 2.94$  ha; females,  $3.64 \pm 1.77$  ha). No differences were observed between males and females in activity pattern or home range area.

observed on dry land 1–2 m from the bank even when hunting at night. Conversely we have regularly observed *B. atrox* at water's edge or swimming in Amazonian Peru.

Structural microhabitat usage is largely dependent upon activity and time of day. During daylight resting hours, *B. asper* may remain exposed on the open forest floor, but more often lie adjacent to structures such as logs or large trees, within clusters of dense vegetation, or take shelter below a log or the root system of a tree. At night, snakes typically emerge from such refuges and assume more exposed ambush positions. Ambush sites were most often in open leaf litter a short distance (0.5–1 m) from structural cover. Our data suggest that *B. asper* actively select particular sites for both diurnal retreat and nocturnal foraging sites.

It is notable that *B. asper* is often reported in field guides and other popular media as preferring to shelter in the buttresses of large trees, and to ambush at the edge of trails; in reality we found this to be the case on less than 1% of occasions at LSBS. Such depictions likely reflect the circumstances in which snakes have been encountered by human observers, or possibly unrealistically colorful depictions of the rainforest rather than snakes' actual activity.

### 3.6. Population data

#### 3.6.1. Abundance

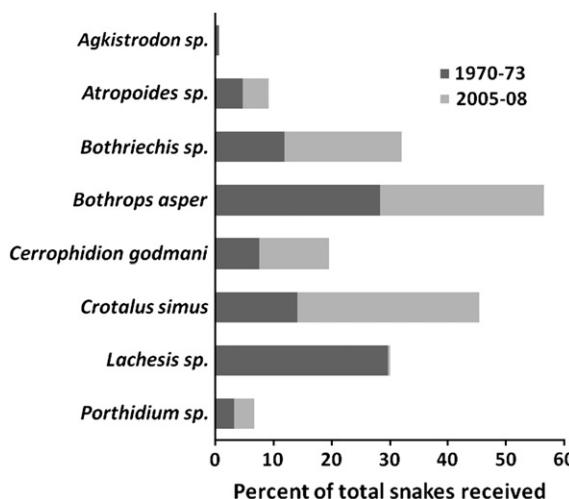
With few exceptions, our knowledge of the population status of Neotropical snakes is fragmentary, and most accounts of snake populations are, at best, estimations of the relative abundance (proportion of individuals of a species under consideration in relation to the overall number of snakes found). While not a solid demographic parameter, relative abundance allows for comparisons over space and time of the number of individuals of observed species.

In the case of *B. asper*, several accounts support the notion that it is one of the most abundant snakes, at least in some localities. Dunn (1949, cited in Campbell and Lamar, 2004) recovered close to 820 specimens of *B. asper* from Panamá over a period of 12 years. In his collection, the terciopelo was the fourth most common species. Furthermore, *B. asper* stands as one of the most abundant species received at Instituto Clodomiro Picado in almost 40 years: from 1003 pitvipers received during the period 1970–1973, 28.3% (284 individuals) were terciopelos (Taylor et al., 1974), whereas in the last 4 years (2005 to present), *B. asper* constituted 28.1% of the 511 pit vipers received (Fig. 7).

On the central Pacific of Costa Rica, one of us (MS) has been sampling areas of 6- to 12-year-old vegetation used to grow "frijol tapado" (covered beans; their seeds germinate under the cut vegetation). This type of agriculture is common in small farms throughout the country, and over 3000 ha are devoted each year to it (Berstch, 2004). In these areas, estimated (mean  $\pm$  SD) density is  $0.48 \pm 0.28$  individuals/ha, mostly adult and subadult snakes. No bias has been observed in the sex ratio of the overall sample. Moreover, snake abundance is often estimated as the number of snakes observed per unit of search effort (the number of person-hours (p-h) expended in the search). Thus, mean abundance estimated for *B. asper* in central Pacific is 0.03 snakes/p-h. This figure is slightly lower than the estimations reported by Nogueira et al. (2003) for *B. moojeni* in riparian habitats of the Brazilian Cerrado. Overall, our data suggest that the species has relatively low densities, and that great heterogeneity exists among density estimates.

### 3.7. Mortality

Little is known about the rate and consequences of mortality of *B. asper* in natural conditions. However, as with other snakes, it is likely that encounters with predators, starvation, and the effects of parasitism are among the main causes of death for this species. Casual encounters



**Fig. 7.** Percentage of vipers (from total) received at Instituto Clodomiro Picado. Periods: 1970–1973 (dark bars), and 2005–2008 (light bars).

with large or aggressive mammals could also result in severe injuries or even death in this species. Boinski (2005) reports on an interesting case in which a large *B. asper* was attacked and severely injured by three white-faced monkeys (*Cebus capucinus*) that used a branch as a tool to hit it.

Considering the high fecundity rate of the species (see below), and the relatively low densities of adults in most populations, survivorship of young terciopelos might be lower than that of adults. In adulthood, it is not clear whether there are differences in mortality between sexes, although it is tempting to speculate that because of the distinct body size differences, males might be more vulnerable to predators than females. In a sample of 77 snakes collected from a single locality (BPA), 48 correspond to females whereas only 29 are males, frequencies that are not expected by chance ( $\chi^2 = 4.57$ ,  $P < 0.05$ ). While it is true that this could result from other factors besides differences in mortality (i.e. divergence in habitat usage or the tendency of males to roam), our studies on the spatial biology of this species do not support this view.

### 3.7.1. Starvation

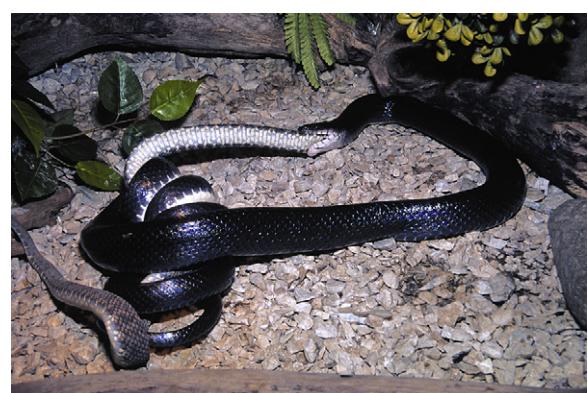
Greene and Hardy (1989) reported the case of an adult female found dead at LSBS. Further examination of this specimen led the authors to conclude that the snake was injured in the mandible, preventing it from properly ingesting prey and leading to starvation. Working at the same site, we have found other cases of recently deceased terciopelos. A 62.6 cm SVL male was found on 2 July 2008 near a trail, without any sign of injury. The snake presented two nematodes (*Rhabdias sp.*) in the lung, but as no obvious damage was noticed, they were disregarded as the cause of death. Likewise, during our tracking study at LSBS four individuals marked with radio-transponders died, presumably from starvation. In these cases, we observed the snakes' progressive deterioration, and post mortem revision confirms a malnourished state, dehydration, and the complete absence of stored fat in the body.

Feeding rates of *B. asper* depend on the population dynamics of prey, which fluctuate in space and time. Consequently, access to sufficient meals for maintenance might be limited during years of low prey population density, threatening snake survival. One of us (DKW) unsuccessfully attempted to estimate rodent densities at LSBS during 2005: no rodents were captured in over 9000 trap-nights, an extremely low capture rate for a site otherwise known for its extensive rodent community (Fleming, 1974; Rivas-Pava and Colton, 1999).

### 3.7.2. Predators

Given its large body size and the high volume of potent venom that it can potentially inject, *B. asper* is a formidable adversary for even powerful and strong predators. Thus, it is difficult to envision many predators that could effectively prey upon adults of this dangerous snake with any regularity. Among the few predators that are known to actively search, subdue, and eat adult terciopelos, the best known example is the mussurana (or zopilota, as it is known in Costa Rica), *Clelia clelia*. This large (up to 2.6 m TL) rear-fanged colubrid snake uses venom and powerful constriction to subdue other large snakes, among them *B. asper* (Fig. 8). The mussurana's blood plasma possesses toxin inhibitors that are capable of neutralizing some of the major components of *B. asper* venom (Cerdas and Lomonte, 1982), a feature that is present at birth (Lomonte et al., 1990). Another large ophiophagous snake that is sympatric with *B. asper* and might be able to subdue it is the cribo, *Drymarchon melanurus*, although we are not aware of observations confirming this.

Perhaps the most important predators for adult terciopelos are raptors. Within the falcons, the laughing falcon *Herpetotheres cachinnans* deserves special mention as a snake killer, as it is capable of subduing even large female *B. asper*. This is a large (up to 600 g) falcon known to prey extensively on snakes, lizards, and other vertebrates (Stiles and Skutch, 1989). We have observed a large *H. cachinnans* confronting and killing a large female (over 1.5 m TL) *B. asper* along a roadside. Other birds of prey that might eat adult terciopelos are: swallow-tailed kites *Elanoides forficatus*, and the crane hawks *Geranospiza caerulescens*.



**Fig. 8.** The mussurana *Clelia clelia* constricting and eating a large male *B. asper*. Photo courtesy of Alejandro Solórzano.

Predators are more numerous for juvenile and neonate terciopelos; their small size makes them easier – although still dangerous – prey items. Raptors again are probably the most important predators (roadside hawks, *Buteo magnirostris* among others), although we have witnessed a large hen *Gallus gallus* killing and swallowing a neonate *B. asper*.

Mammal predators known to feed on small to moderate sized terciopelos include hog-nosed skunks *Conepatus mesoleucus* (Bogert, 1954), coatis *Nasua nasua* and *N. narica*, and raccoons *Procyon lotor*. To our knowledge, the popular belief that peccaries (*Tayassu pecari*, *T. tajacu*) can feed on this pitviper has not yet been confirmed. However, *T. tajacu* in the Amazon Basin preys upon both *B. atrox* and *Lachesis muta* (personal observation). The mustelids *Eira barbara* and *Galictis vittatus* would also be likely predators of young terciopelos. Observations on predation by invertebrates include the spider *Phoneutria* sp. (Araneae: Ctenidae) and an unusual predation by a large unidentified terrestrial crab. Tarantulas (Theraphosidae) are important invertebrate predators of small vertebrates, including newborn and juvenile lanceheads (Fig. 9).

### 3.7.3. Parasites

Mortality owing to parasites is difficult to evaluate, and most information available about parasites comes from studies of snakes in captivity. Protozoans reported in *B. asper* include hemogregarines *Hepatozoon* sp. (Apicomplexa: Hepatozoidae), with a prevalence of 35% in a sample from Costa Rica (Moreno and Bolaños, 1977). Other protozoans reported are amoebas (or amoeba-like organisms) in stomach mucosa and intestines, sometimes associated with gastroenteritis. Moreover, on some occasions infections have been associated with hepatitis: The snake's liver changes in size and color, and several micro-hemorrhages can be noticed in it (Quesada-Morúa, 2005). In some circumstances, amoebiasis has led to secondary infections by bacteria.

Quesada-Morúa (2005) reports on health problems from parasite origin in a sample of *B. asper* kept in captivity,



**Fig. 9.** Tarantulas (Theraphosidae) and ground-dwelling spiders (Ctenidae) are important predators of young lanceheads, including *B. asper*. Here, a 53 cm *B. atrox* being eaten by a *Theraphosa apophysis* female (~27 cm leg span) from Ayacucho, Venezuela. According to Rick West, who witnesses the event, "the spider had it by the head/neck region on the first grab, and it took 18 h to totally consume the *B. atrox*, with the exception of bone, scales and about 8 cm of the tail section". Photo courtesy of Richard West.

and the following account is based in his findings. Nematodes resembling *Filaria* were observed in the blood vessel of one individual, *Kalicephalus inermes* (Nematoda: Diaphanocephalidae) was encountered in the esophagus and stomach (Fig. 10a) and *Rhabdias vellardi* (Nematoda: Rhabdiasidae) were found in the bronchio-alveolar lumen of several terciopelos. Other reported parasites in this sample include *Ochetosoma* sp. (Trematoda: Ochetosomatidae), often found in the oral cavity and esophagus (Fig. 10b), an unidentified species of flatworm (Cestoda: Proteocephalidae) in the intestine, and several acanthocephalan (Acanthocephala: Oligacanthorhynchidae) in the coelomic cavity.

In captivity, the most important causes of death for *B. asper* are bacterial infections. Among the most common is pneumonia associated with *Pseudomonas* sp. that often causes abnormal alveolar infection and filling with fluids.

External parasites include ticks of the genus *Amblyoma* (Acari: Ixodidae), in particular *A. savanae* and *A. dissimile*. There is strong evidence that at least this last species is a vector of hemogregarines in *B. asper* and other Neotropical snake species (Moreno and Bolaños, 1977).

### 3.8. Defensive tactics

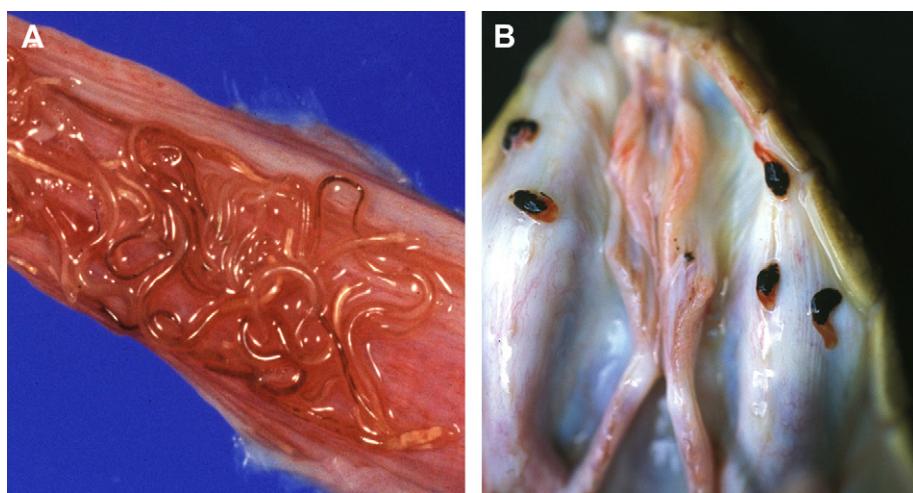
#### 3.8.1. Defensive strategy

*B. asper* is considered an alert and ready-to-react snake, an impression that derives from the formidable defensive posture attained under some circumstances. Nevertheless, this species relies primarily on its cryptic coloration and passive behavior to escape notice by predators. Thus, as in other vipers, crypsis might be the most important mechanism for defense (Greene, 1988).

Within the genus *Bothrops*, dark cryptic colors and the contrasting disruptive blotches provide an excellent resemblance to the immediate surroundings, especially leaf litter. Coupled with immobility, terciopelos are almost invisible in the forest even for experienced observers, and certainly for many of their predators. In *B. asper*, concealing behavior sometimes involves active manipulation of the environment: on several occasions, we have observed a large terciopelo use a dry palm or a *Cecropia* leaf as protection on the forest floor, first lifting one edge of the palm, then coiling and introducing the coils deeper inside the leaf until all the body is under it. This behavior shows that the snakes are able to use elements of the environment for their own benefit.

Another common defensive behavior is to flee when approached; typically this is employed at night when the snake is more alert. This reaction is often conducted at high speed and often involves changes in direction and in locomotion mode. As observed by Sazima (1992) in *B. jararaca*, *B. asper* also uses tail vibration during locomotor escape.

When cornered or surprised, the snake may adopt a defensive display that consists of a series of threats and bluffs. During the display, *B. asper* typically unravels the coils and adopts a cocked posture, although threats and strikes can also be conducted from this coiled posture. The snake then elevates the head and neck, makes an S-coil along the anterior part of the body and confronts the



**Fig. 10.** Common parasites of *Bothrops asper*. (A) Infection of *Kalicephalus inermes* (Nematoda: Diaphanocephalidae) in the esophagus. (B) Trematoda in the mouth of a terciopelo. Both photographs courtesy of Juan Alberto Morales.

adversary with a frontal display (Fig. 1b). This behavior is accompanied by body inflation and, very often, by tail vibration against the substrate, which produces an intense threatening sound.

If the intruder continues the approach, the snake often responds with a series of strikes. Some of them can be considered warning strikes as they are usually slow and often projected when the intruder is out of reach. However, there are also defensive strikes aimed to inject venom. These defensive strikes in *B. asper* seem similar to those reported for *B. jararaca* (Sazima, 1992), and start when the neck of the snake is retracted into an S-posture and the mouth is slightly opened.

Although these postures are often an escalated form of defense that usually involves snakes restrained from escaping, on rare occasions it is possible to encounter individuals that, with no warning, make an impressive display that involves strikes (see Wasko and Losos, in press for a description of one such encounter, and Lamar, 2001, for the opposite reaction).

In our experience, geographic variation in defensive mechanisms is exhibited among populations of this species, although certainly there is evident variation at the individual level. In some species, individual variation can be translated into geographic variation if a selective pressure acts differentially across an environmental gradient (Greene, 1988). For instance, we have observed differential behavior in *Lachesis muta* in portions of the Amazon Basin still frequented by the white-lipped peccary *Tayassu tajacu*, a known predator. Where the predator is absent the snakes tend to be more reluctant to strike. It is important to stress, however, that *B. asper* is an unpredictable snake. We have observed individuals remaining motionless, even when closely approached or stepped on. We have also seen individuals strike and spray venom seemingly without provocation and we have seen specimens flee recklessly. Much of the information about geographic variation in defensive tactics is anecdotal and difficult to interpret in light of circumstances and stimuli.

### 3.8.2. Venom yield

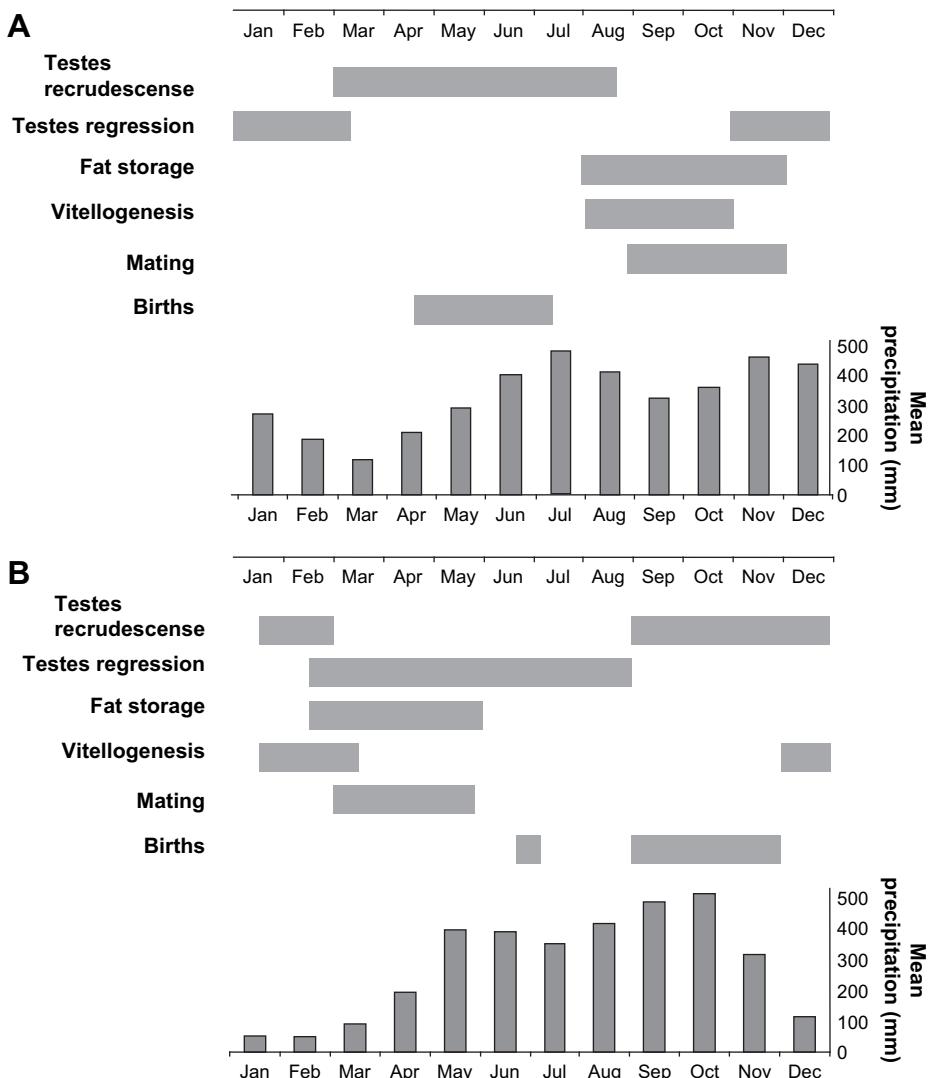
Venom production in *B. asper* is high, and laboratory yields are likely correlated with the volume of venom injected during snakebite. Individual extractions from some individuals at Instituto Clodomiro Picado reached the astonishing amount of ~10 ml (D. Chacón, personal communication) although in our experience even large females seldom yield more than 3 ml. A sample of over 98 extractions of adult and subadult terciopelos averaged  $0.65 \pm 0.37$  ml of venom, for a mean of 180 mg of dry venom (A. Gómez, personal communication). Dry venom in this sample conformed to the mean of 187.5 mg reported by Bolaños (1984). Picado (1931) reported a large individual (size unknown) from Costa Rica that produced 1135 mg of dry venom and a total of 863 mg some 25 days later. This is one of the highest yields ever reported for a lancehead.

### 3.9. Reproduction

#### 3.9.1. Reproductive phenology

*B. asper* is considered one of the most prolific species of venomous snake in the Americas (Tryon, 1985b; Campbell and Lamar, 2004). Owing to the extent of its geographic range, populations of this species exhibit considerable variation in the reproductive cycle. These are attributed to differences in the climatic conditions that trigger differential hormonal responses in time at any particular locality. Solórzano and Cerdas (1989) reconstructed the reproductive cycle and provided related information for this species in Costa Rica, contrasting Pacific and Caribbean populations. Their study, based on observations from more than 647 adult specimens, is the most comprehensive account of the reproductive biology of this species, and herein we summarize their findings.

On the Caribbean versant of Costa Rica, vitellogenesis develops from December to February, in the transition from the rainy to the dry season. Testicular recrudescence of males extends almost parallel to vitellogenesis, from September to February (Fig. 11a). Mating starts during the driest month of



**Fig. 11.** Reproductive phenology of *B. asper* in Costa Rican lowlands. Modified from Solórzano and Cerdas (1989). (A) Caribbean versant, (B) Pacific versant.

the year (March) and continues throughout the next few months until early June. Gravid females can be observed from May to November, and hatching occurs generally from September to November. During this period, there is little relief in the intensity of the rainy season along the versant, which potentially is an important period that allows juveniles to find better climatic conditions where prey availability is probably higher. Testicular cycles regress from March to August, in the transition of dry to rainy periods.

The pattern in Pacific populations is different in timing, but the events are similarly associated with the pluvial regime and pattern of the region. In the Pacific lowlands of Costa Rica, climate is strongly seasonal, with a clearly defined dry season that starts in late December and extends until mid May (Fig. 11b). According to Solórzano and Cerdas (1989), in this region female terciopelos undergo vitellogenesis from August to October during the wetter months of the year. Testicular recrudescence starts in March through August in the transition between the dry season

and the beginning of the rainy season. Thus, it seems that there is less overlap in the timing of gonad development in males and females on this versant. Testicular cycles regress from November to February, in the transition from rainy to dry season. Mating in Pacific populations is observed during the wetter months of the year, from September to November, whereas hatching season goes from April to June, in the transition from dry to rainy season, presumably coinciding with an increase in prey availability. Testicular cycles in this population decrease from November to February, early in the dry season.

Based on these cycles, it is possible for individual females to produce litters every year if conditions are favorable. This possibility is supported by the annual production of offspring from females in captivity in several breeding facilities in the country (Goldmann, personal communication). However, food availability and the costs associated with reproduction might prevent annual reproduction of individual females in the wild. Long sperm

storage (up to several years) has been noticed in *B. asper* females captive at Instituto Clodomiro Picado (D. Chacón, personal communication), and the period between mating and births can be considerably long. For instance, a 112 cm (SVL) female from Sarapiquí that copulated on March 26 2008 (A. Solórzano, personal communication) give birth to 14 offspring 327 days after (F. Bonilla, personal communication). Therefore, *B. asper* reproductive phenology might be similar to that of other lanceheads living at higher latitudes. In *B. moojeni*, fertilization is apparently delayed and there is long-term sperm storage (Nogueira et al., 2003). Likewise, Almeida-Santos and Salomão (2002) studied 13 *Bothrops* species and indicated that dissociation can occur between time of mating and time of fecundation. Thus the period between parturition and the onset of vitellogenesis is relatively short, resulting in a shortage of body fat accumulation to initiate follicular maturation. In addition, females of these species show evidence of sperm storage for long periods, leading the authors to conclude that biennial reproduction might be the norm with these species. We suspect that this is also the case in wild populations of *B. asper*.

### 3.9.2. Courtship behavior

In many vipers, male–male interactions precede mating, usually in the form of male combat. Snakes within the genus *Bothrops* are no exception (Almeida-Santos and Salomão, 2002) and male combat has been observed even in species marked by a strong female-biased dimorphism: *B. atrox* (Cardoso et al., 1993), and *B. moojeni* (Leloup 1975). In the case of *B. asper*, however, we have not observed any indication of male antagonistic behaviors, although it is not unusual to find females with several males during the mating season.

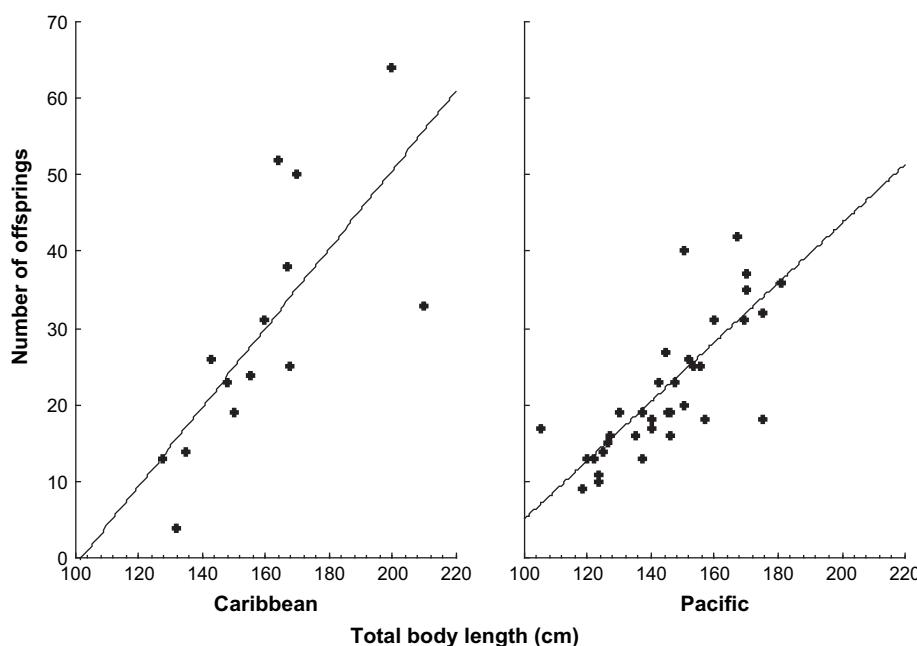
Courtship behavior has been partially observed in the field and in captivity and includes a series of movements of the male, chasing a receptive female slowly and often bobbing his head at her side. Once the female stops movements and assumes an extended posture, the intensity of caresses increases and the male slowly positions himself on the larger female's dorsum. Although we have not witnessed copulation, it is likely that it occurs in this position.

### 3.9.3. Reproductive potential

As in other pitvipers, fertility in *B. asper* is related to female body size (Fig. 12). Solórzano and Cerdas (1989) report litter sizes that ranged from 5 to 86 neonates, and suggested that substantial differences in mean ( $\pm SD$ ) litter size were observed between Pacific ( $18.6 \pm 8.6$ ) and Caribbean ( $41.1 \pm 5.2$ ) populations. These differences, however, are not sustained in another sample from 58 litters produced in captivity at Instituto Clodomiro Picado (Mann–Whitney  $U = 231.0$ ,  $P = 0.405$ , Fig. 12).

Sexual dimorphism is noticeable at birth, where males are more pigmented (Fig. 1c) and smaller than females from each versant. Mean weight at birth ranged between 6.82 g and 18.28 g, but no sexual differences are observed within litters in the mean body mass (Wilcoxon matched pair test  $Z = 1.32$ ,  $P = 0.186$ ). However, Caribbean neonates are larger and more massive (mean  $12.12 \pm 3.01$  g) than their Pacific counterparts (mean  $9.77 \pm 1.21$  g;  $F_{1,25} = 8.31$ ,  $P = 0.007$ ). These results coincide with the findings of Solórzano and Cerdas (1989). Reproductive data from other sources along *B. asper*'s distribution are sparse, but in general are congruent with the pattern previously described (Campbell and Lamar, 2004).

Observed mortality in *B. asper* born in captivity is usually low, ranging between 0 and 21%, and only 18% of



**Fig. 12.** Relation between litter size and female body length in *Bothrops asper* from the Caribbean ( $r = 0.737$ ,  $P = 0.0026$ ,  $n = 17$ ) and Pacific ( $r = 0.768$ ,  $P < 0.0001$ ,  $n = 41$ ) lowlands of Costa Rica. No differences in the rate of change of litter size were observed between regions ( $P > 0.05$ ).

the litters show evidence of mortality at birth. This low rate might in part contribute to the species' relative abundance in some locations.

### 3.10. Relation with humans

#### 3.10.1. Snakebite capacity

In any country where *B. asper* occurs, it is listed as the most deadly and dangerous snake, a result of being the species responsible for the majority of human envenomations in the region. [Bolaños \(1984\)](#) suggested that about 46% of 477 snakebites that occurred in Costa Rica in 1979 could be attributed to *B. asper*. In the other hand, from 5550 snakebite cases occurring between 1990 and 2000 in Costa Rica, [Sasa and Vázquez \(2003\)](#) indicate that nearly 80% can be attributed to this species, based in its distribution and the origin of bites. Similar incidence is reported in some regions of Ecuador, where up to 82% of snakebites are credited to terciopelos ([Freire-Lascano and Kuch, 1994](#)).

The high frequency of snakebites attributed to this species is not unexpected: *B. asper* is one of the largest venomous snakes in the Neotropics, and definitely one that produces a great volume of venom (see Section 3.8.2). Furthermore, the head of a full grown female terciopelo can reach well over 9 cm and, like other vipers, it can open its jaws up to 180°. Thus, virtually any anatomical surface on a person is vulnerable of being bitten. Moreover, the fangs can develop to well over 2 cm in length, long enough to penetrate clothing and even soft leather before perforating skin to deliver venom.

Another reason for the high frequency of accidents is the relative abundance of terciopelos, which makes them one of the most frequently encountered snakes in some areas. The high reproductive capacity might contribute in part to such success. Also, *B. asper* is capable of living near human dwellings, and it is not uncommon to find individuals near or even inside houses in rural areas, which might result in snakebites. Recent clearings in forested areas permits sunlight to strike the ground, giving rise to herbaceous plants and the succession of insects and insect predators that follow. These areas are rich in potential prey and thus may be frequented by *B. asper*.

A third reason might relate to defensive tactics. The snake is often resting during the day, and remains immobile when an intruder approaches. For the unlucky individual who fails to detect the snake until it has been touched, stepped upon, or otherwise disturbed, a bite may quickly result.

#### 3.10.2. Bothrops asper in culture and folklore

Being the most important snake from a public health standpoint, it is not surprising that *B. asper* has played a significant role in regional folklore, culture, and mythology ([Solórzano, 2003](#)). The terciopelo is well respected by local societies throughout its distribution, and it constitutes an important part of their traditional beliefs and artistic expressions. Diego de Landa, writing in 1566 (Relación de las Cosas de Yucatán) wrote about the dreaded *taxinchan* (*B. asper*) and the fear it inspired among the Mayan Indians. [Morelet \(1871\)](#) citing Herrera about Chiapas, mentions "great brown vipers resembling decayed wood," and further

states that the bite of one killed a horse. [Lee \(1996\)](#) summarizes the role of *B. asper* in Mayan civilization from ancient times to the present. Cabecar and Bribri indigenous groups from Costa Rica feared Shulàkama, the guardian of the snakes, that protects this species ([Jara-Murillo and García-Segura, 2003](#)); and the species has inspired numerous Central American writers (e.g. Carlos Luis Fallas 1909–1966, Emilio Quintana 1908–1971) in their descriptions of the natural world and their denouncement of the social injustice and difficulties faced by agricultural workers during the expansion of banana production in the region.

In recent times, one widespread myth is that of a rapid, dramatic increase in the terciopelo population in Costa Rica, an idea that started in the Central Pacific and rapidly spread to other regions of the country. Some unscrupulous journalists in local newspapers and television media, and even an international nature-film producer (despite solid advice to the contrary), have exploited this myth, raising further concern in various sectors of the population. Despite the fact that no demographic study on *B. asper* has been conducted in the country, such increment is not sustained by our field observations. Not only we have failed to detect an increase in densities, but there is also no evidence that snakebite incidence has increased through time ([Sasa and Vázquez, 2003](#)), which is predicted by the alleged increase. It is possible; however, that the relative abundance of *B. asper* (in relation to other members of the snake community) has increased in some disturbed areas of the country (see below), or that shifting human populations have resulted in increased contact.

#### 3.10.3. Conservation and the future of Bothrops asper

Several species of *Bothrops* are experiencing a severe decline (as listed in [Greene and Campbell, 1992](#)), mostly owing to human impact. However, it is clear that some species have expanded their range in recent times, a phenomenon that results from some degree of human disturbance of the habitat that favors such species. In Middle America, *B. asper* populations seem to be doing relatively well even in some impacted environments (shadow coffee plantations, banana and cacao fields) and is particularly abundant in *tacota*les (abandoned agriculture fields at early forest-succession stages). However, it is clear that other snake species cannot survive well under those conditions; therefore the relative position of *B. asper* in samples from those localities can be high, sometimes being the most common snake encountered. This may explain in part the alleged increment of *B. asper* populations in the country.

Despite this adaptability, the terciopelo cannot cope with drastic changes in the environment, and in some areas it is becoming less frequently encountered. The substitution of traditional crops for mechanized agriculture (for example in pineapple production), the overuse of pesticides, and the decline of amphibians and other prey species ([Whitfield et al., 2007](#)) might be important factors for some local populations of predators, including *B. asper*. In addition to habitat destruction, *B. asper* is considered a plague and is usually killed on sight, actions that have support even among government agencies.

Still, given its formidable capacity to adapt to new environments, it is unlikely that *B. asper* will be extirpated

from all localities within its range, at least not in the near future. Thus, it is imperative that humans learn how to deal with this species, improving prevention of the snakebite and its treatment. A first logical step is to advance our understanding of its lifestyle and habits.

Beyond its aesthetic value, *B. asper* plays an important role in the complex trophic web in the Neotropics, both as predator and prey. The broad diet previously described is a good indication of the potential contribution of this lancehead in controlling populations of various types of prey, from ectotherms to endotherms. Moreover, *B. asper* may have indirect effects on prey species, affecting their habits and behavior. It has been recognized that a number of rodent species respond to the presence of predators (including snakes) or their cues, by reducing foraging, altering microhabitat use, and decreasing home ranges and activity (Dickman, 1992; Bouskila, 1995; Randall and King, 2001; Orrock et al., 2004; Hayes et al., 2006; Rundus et al., 2007). As rodents are among the most important seed predators in tropical forests (Janzen, 1971b), antipredator responses may have indirect consequences in seed predation and dispersal rates and, therefore, be of relevance in shaping forest dynamics at the local scale.

On the other hand, *B. asper* venom constitutes an exceptional source of biologically active components (Gutiérrez, 2002), some of which might have important pharmacological applications in biomedicine.

Although the usual arguments for species preservation – the need to conserve all life forms; the possibility that useful properties have yet to be discovered; the largely unknown but presumably important role of each organism in the ecology of its surroundings; our role as custodians of the natural world – all sound trite owing to repetition; the fact is, *Bothrops asper* merits respect and protection for these and many more reasons. For those who have suffered accidents with terciopelos, the notion of preservation as opposed to eradication is unlikely to resonate. But biological common sense tells us that a species as dominant and successful as *B. asper*, were it to be removed or severely decimated, would doubtless cause unknown but likely severe changes in the natural landscape.

It seems far more prudent to increase the access and quality of education, to actively work with communities to reduce trash piles and other sources of potential snakebite accidents, and to follow the model of Costa Rica in producing and distributing antivenom, and promoting competent medical assistance throughout the country for the adequate treatment of these envenomations.

For those of us who work closely with terciopelos, there will always be a strong attraction coupled with respect for this most formidable of New World venomous snake – The Ultimate Pitviper.

## Acknowledgments

We wish to sincerely thank Alejandro Solórzano for years of collaboration in the field, and for sharing some of his unpublished data. Harry W. Greene and David Hardy started studies on the ecology of *B. asper* at La Selva, and their efforts in part inspired this work. Danilo Chacón, Fabian Bonilla, and Aaron Gómez have been very helpful in

securing natural history data from a large collection of terciopelos at the Instituto Clodomiro Picado. Ulrich Kuch, Jonathan A. Campbell, Quetzal Dwyer, Marcel Goldmann, Christopher Montero, and Louis Porras provided additional information to complete our understanding of the natural history of the terciopelo. Robert Timm identified mammal prey, and Raul Ramirez help obtaining them, Christian Voigt and Detlev Kelm generously loaned radiotelemetry receivers when our own malfunctioned. Alejandro Solórzano, Rick West and Juan Alberto Morales kindly allow us to use their unpublished photographs. We also thank Cecilia Diaz-Oreiro, Jose María Gutiérrez and an anonymous reviewer who provided important suggestions to improve this manuscript. Data presented here was partially funded by the University of Miami's Tropical Biology Fellowship, American Society of Ichthyologists and Herpetologists' Gaige Award, and American Society of Naturalists to DKW, and by a grant from Vicerrectoría de Investigación, UCR 741-A5-050 to MS.

## Conflicts of interest

All authors declare that there are no conflicts of interest.

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