Herpetologica, 58(3), 2002, 303–312

A NEW INSULAR SPECIES OF PITVIPER FROM BRAZIL, WITH COMMENTS ON EVOLUTIONARY BIOLOGY AND CONSERVATION OF THE *BOTHROPS JARARACA* GROUP (SERPENTES, VIPERIDAE)

OTAVIO A. V. MARQUES[1], MARCIO MARTINS[2,4], AND IVAN SAZIMA[3]

[1]*Laboratório de Herpetologia, Instituto Butantan, 05535-900 São Paulo SP, Brazil*
[2]*Departamento de Ecologia, Instituto de Biociências, C. P. 11461, Universidade de São Paulo, 05422-970 São Paulo SP, Brazil*
[3]*Departamento de Zoologia and Museu de História Natural, C. P. 6109, Universidade Estadual de Campinas, 13083-970 Campinas SP, Brazil*

ABSTRACT: We describe a new pitviper species, *Bothrops alcatraz*, of the *Bothrops jararaca* group, from Alcatrazes Island, off the coast of São Paulo, southeastern Brazil. It differs from the mainland coastal populations of *B. jararaca* in southeastern Brazil mostly by its darker coloration; smaller size; lower number of ventrals, subcaudals, and infralabials; number and shape of anterior cephalic scales; shape of hemipenis spines; intense coagulant activity of venom; and three specific venom proteins. From *Bothrops insularis*, another island species from southeastern Brazil, the new species differs mainly by its color pattern, smaller size, lower number of subcaudals in males, and absence of hemiclitoris in females. *Bothrops alcatraz* presents some features that may be viewed as paedomorphic within the *B. jararaca* group, such as small adult size, proportionally large eyes, intense coagulant venom activity, and diet composed of centipedes and lizards. We postulate that the dwarfism and characteristics of venom in *B. alcatraz* may be related to its diet (similar to that of juveniles of the mainland *B. jararaca*). *Bothrops alcatraz* and *B. insularis* may have originated through the isolation of populations of a *B. jararaca*-like ancestor on the Alcatrazes and Queimada Grande islands, respectively. The new species is regarded as critically endangered due to its very small area of occurrence and the declining quality of its habitat.

Key words: *Bothrops alcatraz*; Crotalinae; Evolution; Island endemics; Natural history; Southeastern Brazil

THE SYSTEMATICS of snakes of the genus *Bothrops* is notoriously difficult (Campbell and Lamar, 1989; Hoge and Romano-Hoge, 1981; Werman, 1992), although several species groups have been recognized recently (Cadle, 1992; Gutberlet, 1998;

[4] CORRESPONDENCE: e-mail, jararaca@ib.usp.br

Salomão et al., 1997, 1999; Werman, 1992). The genus is probably paraphyletic (see Gutberlet, 1998; Parkinson, 1999), and comprises about 40 species including those previously allocated in *Bothriopsis* (Gutberlet, 1998; Parkinson, 1999; Salomão et al., 1997, 1999; Vidal et al., 1999).

Members of two groups of *Bothrops* occur on coastal islands on southeastern Brazil. Snakes related to *Bothrops jararaca* (Wied), including *Bothrops insularis* (Amaral), are known from several islands of various sizes and distances from the coast (up to about 35 km), ranging from Franceses Island off Espírito Santo (latitude about 21° 00′ S) south to Santa Catarina Island (latitude about 27° 30′ S), whereas *Bothrops jararacussu* (Lacerda) is more restricted in its distribution and occurs mainly on larger islands close to the coast of São Paulo (<1 km from the mainland; Amaral, 1921*a*; Duarte et al., 1995; Luederwaldt and Fonseca, 1923; personal observation). Island populations of snakes are good subjects for evolutionary studies, especially when compared to their generally widespread mainland relatives (e.g., Forsman, 1991; Schwaner, 1985). These populations also deserve special attention for conservation as they generally occur exclusively in very restricted areas (e.g., 43 ha in the case of *B. insularis,* Duarte et al., 1995).

The *B. jararaca* group comprises two species (Salomão et al., 1999), the widespread *B. jararaca,* probably a complex of several species (Salomão et al., 1997), and the insular endemic *B. insularis.* The latter species is restricted to Queimada Grande Island, off the coast of São Paulo, southeastern Brazil (Campbell and Lamar, 1989). Herein, we describe a second insular pitviper species from Brazil, first collected in 1914 and previously referred to the widespread species *B. jararaca* (e.g., Luederwaldt and Fonseca, 1923).

Materials and Methods

We examined 24 specimens of the new insular species and 39 specimens of *B. jararaca* from adjacent continental populations of coastal São Paulo (Appendix I) in the collection of Instituto Butantan (IB) and Museu de História Natural da Universidade Estadual de Campinas (ZUEC). For each snake, we measured the snout–vent length (SVL) and tail length (TL) to the nearest 1 mm with a flexible rule. Head length (HL; from snout to extreme posterior part of mandible) and eye diameter (ED) were measured with a caliper to the nearest 0.1 mm; to compare HL and ED between species, we divided HL by the "trunk" length (TR = SVL − HL) and ED by HL. Mass (to the nearest 1 g) was obtained with spring scales after draining the excess preservative liquid through ventral incisions; to compare mass between species, we divided mass by total length (TTL). Description and scale counts follow Campbell (1985). We considered the first ventral as being the first scale wider than long. Additionally, we counted the anterior cephalic scales (i.e., the total number of cephalic scales, including the intersupraoculars) to the tip of the snout. Hemipenial ornamentation names follow Dowling and Savage (1960). Color names follow Kornerup and Wanscher (1961). Data for *B. insularis* in Table 1 are from Amaral (1921*a*). Data on microhabitat use, feeding, and reproduction were obtained during fieldwork and by examining preserved specimens in museum collections.

The population of pitvipers inhabiting Alcatrazes Island is well differentiated from both populations of snakes occurring in Queimada Grande Island (*B. insularis*) and on adjacent mainland (*B. jararaca*). After carefully analyzing the morphological and ecological attributes of the Alcatrazes pitviper, we concluded that the Alcatrazes Island population represents a distinctive species that may be known as:

Bothrops ***alcatraz*** sp. nov.

Holotype.—IB 62545 (Fig. 1), male from Alcatrazes Island (24° 06′ S, 45° 42′ W), São Sebastião, São Paulo State, Brazil, 15 December 1999, collected by O. A. V. Marques, M. Martins, M. E. Oliveira, D. N. Pereira and A. Martensen.

Paratypes.—Eighteen specimens, all from the type locality: MZUSP 1453, October 1920, collected by H. Luederwaldt; ZUEC 2224, male, 22 March 2000, col-

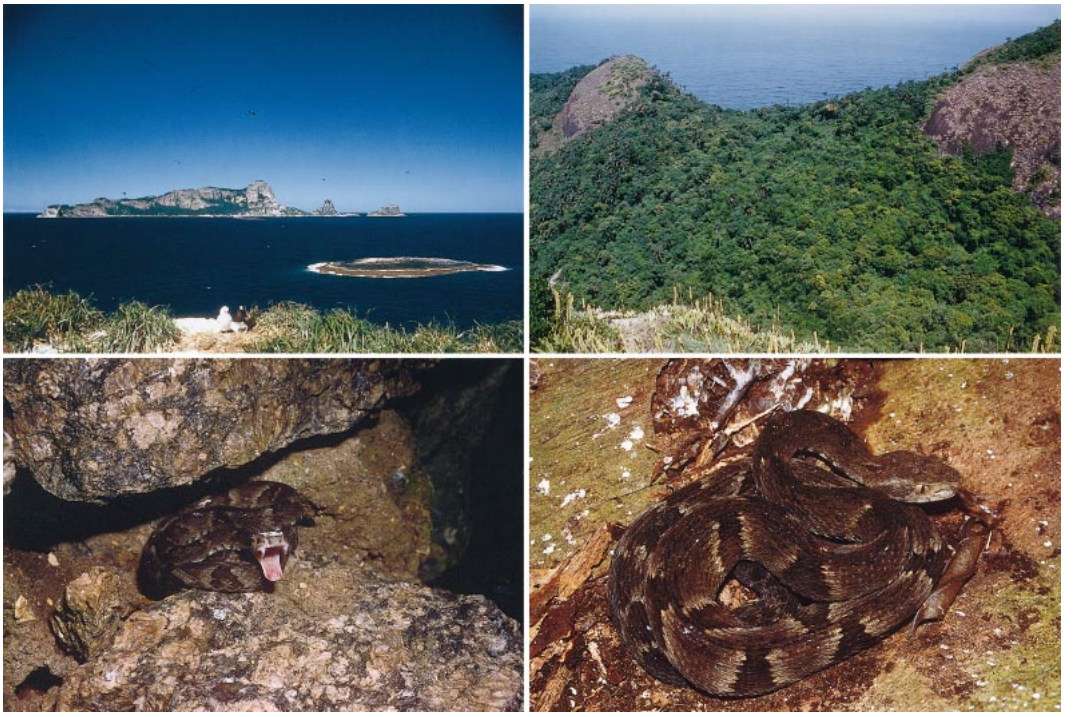

FIG. 1.—*Bothrops alcatraz* type locality and two specimens in situ. Alcatrazes Island photographed from a nearby islet with two brown boobies in foreground (upper left); the Atlantic forest on Alcatrazes Island (upper right); holotype (IB 62545), showing gaping behavior and seabird droppings on the head (lower left); male (IB 62290) showing body proportions, dorsal pattern, and seabird droppings scattered on the adjacent ground (lower right). Photos of the island by F. P. de Campos.

lected by M. Martins, R. Sawaya, M. E. Oliveira, D. N. Pereira, A. Martensen and O. A. V. Marques; ZUEC 2225, female, 24 March 2000, collected by O. A. V. Marques; IB 584 male, IB 585 female, IB 586 female, IB 587 female, and IB 588 female, June 1914, collected by A. A. Gomes; IB 13032, female, February 1950, collected by Instituto Butantan expedition; IB 13135 female, 1950, collected by Instituto Butantan expedition; IB 16211 and IB 16212 both females, 7 January 1955, collected by F. Witaker; IB 55579 male, 14 December 1992, collected by W. Langeani; IB 55580, female, April 1992, collected by M. Buononato; IB 55791 male, 16 April 1994, collected by A. Eterovic; IB 57105, male, 2 December 1996, collected by S. Sant'anna; IB 57107, female, 17 June 1994, collected by Instituto Butantan expedition; IB 62238, female, 15 December 1999, collected by O. A. V. Marques, M. Martins, M. E. Oliveira, D. N. Pereira, and A. Martensen.

Referred specimens.—Six specimens from the type locality: IB 13031 male, IB 13126 male, and IB 13183 female, February 1950, Instituto Butantan expedition coll.; IB 55578 male, December 1992, W. Langeani coll.; IB 55581 male, 24 January 1992, W. Langeani coll.; IB 56133 female, 1994, Instituto Butantan expedition coll.

Diagnosis.—The new species is superficially similar to *B. jararaca* from coastal São Paulo, from which it may be distinguished by the following combination of characters (*B. jararaca* in parentheses): smaller adult size, mean male TTL 425.6 ± 32.5, range 365–462 mm (versus 801.6 ± 107.6 mm, range 378–924 mm); mean female TTL 455.7 ± 41.4, range 365–505 mm (versus 969.0 ± 107.1, range 337–1080 mm); shorter tail, TL/SVL 0.161 ± 0.007 (0.168 ± 0.009) in males, 0.138 ±

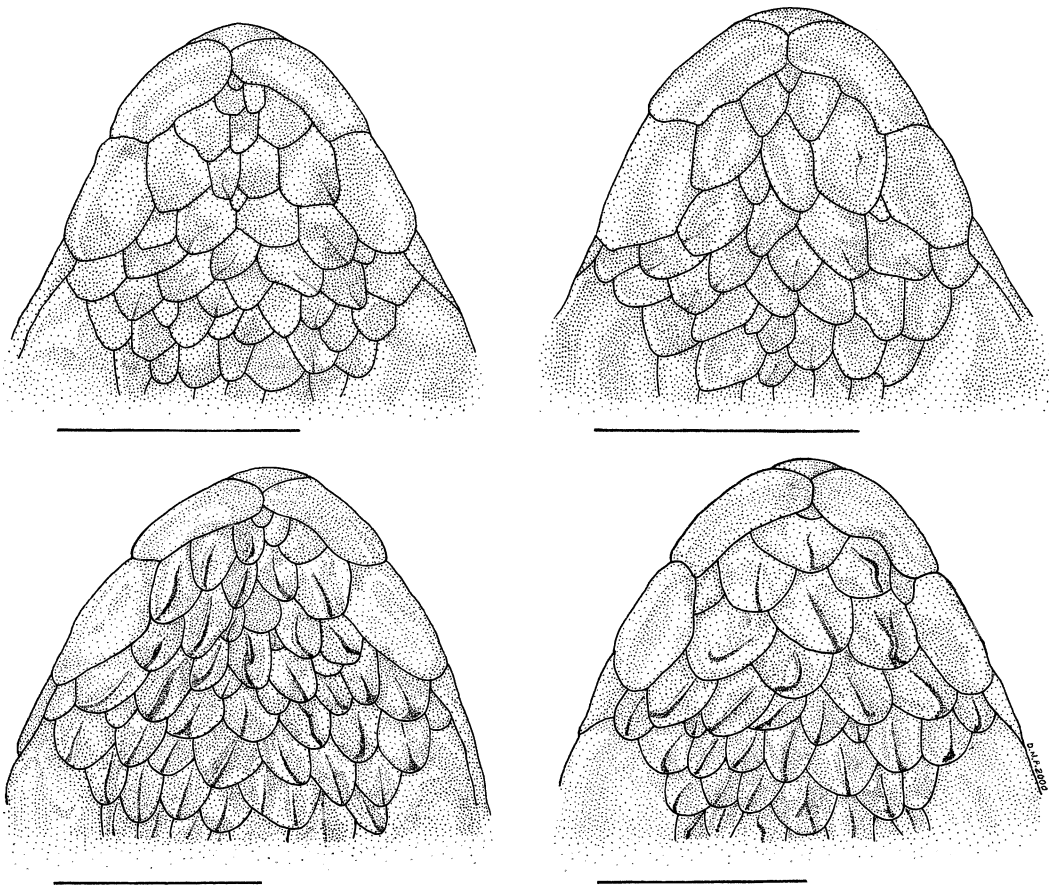

FIG. 2.—Heads of *Bothrops alcatraz* (paratypes IB 587 and IB 585, upper) and *Bothrops jararaca* (IB 57903 and IB 58130, lower) in dorsal view showing variation in scalation. Line = 5 mm.

0.011 (0.144 ± 0.012) in females; longer head, HL/TR 0.0053 ± 0.0003 (0.0041 ± 0.0002) in males, 0.0055 ± 0.0003 (0.0045 ± 0.0010) in females; larger eyes, ED/HL 0.157 ± 0.010 (0.149 ± 0.010) in males, 0.154 ± 0.009 (0.126 ± 0.022) in females; 32–50, 37.5 ± 4.2, anterior cephalic scales generally rounded and with no or feeble keels (32–64, 47.0 ± 8.2, generally elongate and distinctly keeled, Fig. 2); lower number of infralabials usually 10/10 (usually 11/11); lower number of ventrals, 173–186 (197–218); lower number of subcaudal scales in males 47–58 (62–72) and in females 45–52 (53–68) (Table 1), and hemipenis spines relatively slender (stouter in *B. jararaca*) (Fig. 3). Additional characters that distinguish *B. alcatraz* from *B. jararaca* are the presence in the former of three venom proteins with molecular weights of 20, 40, and 60 kD, which do not occur in *B. jararaca*, and the intense coagulant activity of venom of adult *B. alcatraz* (M. F. D. Furtado, personal communication), a character that occurs only in juvenile *B. jararaca* (Furtado et al., 1991). From *B. insularis*, the new species is easily distinguished by color pattern and smaller size (Campbell and Lamar, 1989: Figs. 214 and 215), and lower number of subcaudals in males (47–54 versus 55–65, respectively). An additional diagnostic character of *B. insularis* is presence of the hemiclitoris (cf. Ziegler and Böhme, 1997) in females. Furthermore, *Bothrops alcatraz* is known only from Alcatrazes Island, whereas *B. insularis* is known only from Queimada Grande Island, and *B. jararaca*

TABLE 1.—Comparison of selected characters of *Bothrops alcatraz*, coastal specimens of *B. jararaca*, and *B. insularis*. Measurements in mm, number of individuals in parentheses.

	B. alcatraz	*B. jararaca**	*B. insularis***
Snout–vent length males	365–462 (10)	378–996 (15)	393–788 (94)
Snout–vent length females	365–505 (14)	320–1080 (24)	332–882 (106)
Ventrals males	173–182 (10)	200–211 (15)	171–188 (94)
Ventrals females	175–186 (14)	197–218 (19)	176–195 (106)
Subcaudals males	47–54 (10)	62–72 (15)	55–65 (94)
Subcaudals females	45–52 (14)	53–68 (19)	48–59 (106)
Mid-body scale rows	22–26 (24)	21–27 (34)	23–25 (200)
Intersupraoculars	6–8 (24)	7–10 (34)	7–9 (203)
Anterior cephalics	31–48 (24)	31–64 (34)	—
Infralabials	10/10 (19); 10/11 (4); 9/10 (1)	10/10 (6); 10/11 (5); 9/11 (1); 11/11 (15); 11/12 (4); 12/12 (2); 12/10 (1)	—
Hemipenial spines	stout	slender	—
Postorbital stripe	present	present	absent or faint

* From coastal São Paulo.
** Data from Amaral (1921*a*).

is a widespread species in southeastern Brazil, both on the mainland and on some larger islands close to the coast (Campbell and Lamar 1989, personal observation).

Etymology.—The specific epithet is a noun in apposition and refers to the local name of the frigate bird, *Fregata magnificens* (Pelecaniformes), whose colonies on the Alcatrazes Island give name to the type locality of the new species. We suggest the common name "Alcatrazes lancehead" for the new species.

Description of holotype.—An adult male (Fig. 1) preserved in ethanol with both hemipenes everted; SVL 448 mm; TL 72 mm, comprising 16.1% of total length; HL 22.6 mm; maximum head width 15.1 mm; mass 53 g (preserved); rostral scute 3.6 mm wide and 3.8 mm high; nasals divided anterior and posterior to nostril; loreal single; 3/3 prefoveals; 1/1 subfoveals; 1/1 post-foveals; prelacunal contacting the second supralabial on the right side of the head, fused with it on the left side; 1/1 suboculars; 2/2 preoculars; 2/2 postoculars; 9/8 supralabials; 10/10 infralabials, first pair in contact posteriorly; mental longer than broad, contacting the first three infralabials on each side; five gulars between chin shields and first ventral; six rows of gulars separating first ventral from infralabials; three anterior internasals; 2/2 canthals; 5 posterior intercanthals; 6 intersupraoculars; 34 cephalic scales with no or feeble keels from mid level of the intersupraoculars to the tip of snout (Fig. 2); 25-25-19 dorsals; 177 ventrals; anal scute single; 57 subcaudals (proximal 54 divided and distal three undivided); five small scales on each side of the cloaca; tail spine three times as long as adjacent subcaudals, dorsal scales covering anterior half of tail spine.

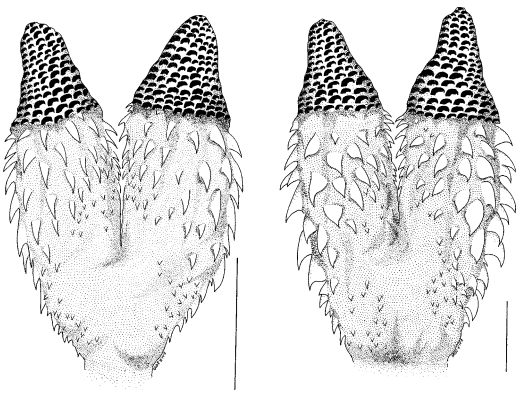

FIG. 3.—Asulcate side of right hemipenes of *Bothrops alcatraz* (paratype ZUEC 2225, left) an *Bothrops jararaca* (IB 62478, right) showing ornamentation. Line = 5 mm.

Dorsal scales 2.5 times as long as wide anteriorly, becoming wider posteriorly, about 1.5 times as long as wide on tail; all dorsal scales strongly keeled; paraventral row of scales smooth to very weakly keeled

on posterior part of body, parasubcaudals noticeably keeled; paraventrals about twice as wide as adjacent dorsal scales; posterior cephalic scales strongly keeled and longer than wide; anterior cephalic scales rounded, smooth to weakly keeled; temporal scales keeled; internasals, canthals, and supraoculars smooth; scale row dorsal to supralabials weakly keeled.

Everted hemipenis subcylindrical, bilobed, extending to seventh subcaudal scale; bifurcation of sulcus spermaticus at level of first subcaudal; sulcus extending to tip of each lobe; bifurcation of lobes at level of second subcaudal scale; small to large ossified spines assymetrically distributed on hemipenis extending from level of first subcaudal; largest spines about the same length as adjacent subcaudal scales; lobes covered with high retiform ridges forming papillate calyces (Fig. 3).

Dorsum of head (in preservative) brownish gray with diffuse dark olive-brown markings. A prominent dark olive-brown postorbital stripe extending from behind the eye to below the angle of the jaw, encroaching upon the posterior three supralabials on the right side of head and the posterior two scales on the left side; this stripe bordered dorsally by a diffuse pale brown zone. Canthal region and supralabials uniform gray. Iris grayish yellow with darker flecking. Body brown gray with a series of 14 large, pale gray-edged, dark olive-brown trapezoidal markings on each side, with their apices on the vertebral line; trapezoidal markings arranged opposite each other, or partly or completely juxtaposed; the pale borders of dark markings diffuse (Fig. 1). Tail dark brown dorsally. Venter pale yellowish gray with irregular brown blotching to flecking becoming more concentrated on tail.

Distribution.—Known only from Alcatrazes Island (1.35 km^2), the largest of four small islands of Alcatrazes Archipelago (Fig. 1), approximately 35 km from the coast of São Paulo (Vanzolini, 1973), southeastern Brazil, with an elevational range of 3–266 m above sea level.

Natural history.—We found the new species active both on the ground ($n = 6$) and on low vegetation ($n = 5$) within the Atlantic forest covering Alcatrazes Island (semi-arboreal habits are characteristic within the *B. jararaca* group: see Martins et al., 2002); the holotype was found on the rocks of the wall of an old building (Fig. 1). Two individuals were resting by day, one within a decomposing palm trunk and the other under a fallen palm leaf. Of 12 prey found in the guts of *B. alcatraz,* nine were otostigmine centipedes (*Otostigmus* sp.) and three were lizards (two introduced gekkonid lizards, *Hemidactylus mabouia,* and one scincid, *Mabuya macrorhyncha*). Centipedes and *H. mabouia* are common on the low portions of tree and palm trunks, as well as on the walls of old buildings. Most specimens of *B. alcatraz* were found under seabird (*Sula leucogaster* and *Fregata magnificens*) roosts on the canopy of the low forest, where large amounts of guano accumulate on the leaf litter (individuals of *B. alcatraz* are often found with bird droppings splashed over their body, Fig. 1). Cockroaches and centipedes (which probably prey on the former) are abundant on and around the guano. This is the only species of *Bothrops* known to feed mostly, if not exclusively, on ectothermic prey (Martins et al., 2001). This prey type and the venom properties of *B. alcatraz* probably are related, as a relationship was found between the diet and venom composition for some *Bothrops* species and/or ontogenetic phases (Andrade and Abe, 1999; Andrade et al., 1996; Furtado et al., 1991; M.F.D. Furtado, personal communication). Curiously, despite preying on lizards, neither juveniles ($n = 3$) nor adults have whitish or otherwise conspicuous tail tips, a feature present in all species of *Bothrops* known to prey on lizards or frogs, which are lured by the snake's tail movements (Martins et al., 2001).

Other snake species recorded on Alcatrazes Island are two colubrids, *Dipsas albifrons* and *Siphlophis pulcher,* and an elapid, *Micrurus corallinus,* which also occur in the mainland Atlantic forest of southeastern Brazil (Peters and Orejas-Miranda, 1970). Species of *Dipsas* are arboreal but may forage on the ground and prey on slugs and snails. *Siphlophis pulch-*

er is arboreal and may also forage on the ground preying on lizards (including *M. macrorhyncha* and *H. mabouia*). *Micrurus corallinus* is fossorial and feeds on amphisbaenians and other elongate reptile prey (Marques and Sazima, 1997; Sazima, 1989; Sazima and Argôlo, 1994; personal observation). Thus, only *S. pulcher* overlaps with *B. alcatraz* in food requirements.

The smallest mature male (with opaque efferent ducts and enlarged testes) of *B. alcatraz* was 365 mm SVL and the smallest mature female (with oviductal embryos) was 477 mm SVL; males and females of *B. jararaca* attain sexual maturity at about 650 and 750 mm SVL, respectively (Janeiro-Cinquini et al., 1993; Sazima, 1992). Thus, individuals of *Bothrops alcatraz* attain sexual maturity at a much smaller size than individuals of *B. jararaca.* A female of *B. alcatraz* collected in December contained one oviductal embryo and one atresic vitellogenic follicle. The embryo was fully-developed (SVL 130 mm, TL 27 mm). Another female collected in January contained two atresic vitellogenic follicles, apparently not ovulated. These data indicate that the period of juvenile recruitment in *B. alcatraz* may be similar to those of most species of *Bothrops,* in which parturition occurs generally between January and May (Almeida-Santos and Salomão, 2001; personal observation). Fecundity in *B. alcatraz* may be low due to its small body size, a trend recorded for several snake species (e.g., Shine, 1994). Another island species, *B. insularis,* also shows a low fecundity (litters of 2–10 and a high frequency of atresic eggs: Hoge et al., 1959).

Discussion

Available data on the natural history of the three species of the *B. jararaca* group (see Sazima, 1992; Martins et al., 2001) suggest to us the following scenarios for diversification within this group. Two populations of a *B. jararaca*-like ancestor became isolated in the past (see below) on Queimada Grande and Alcatrazes islands. Small mammals, the main prey of adult *B. jararaca* (and of most *Bothrops*; Martins et al., 2001), do not presently occur on these islands and there is no evidence that they previously occurred there. Thus, from a semiarboreal, dietary generalist ancestor (Martins et al., 2001), two distinct evolutionary routes seem to have been taken by these two insular species. As a result of the absence of small mammals on the islands, adult *B. insularis* relied heavily on migrant passerine birds (approximately 85% of their current diet; Martins et al., 2001), became more arboreal (Martins et al., 2001), and evolved a venom that kills birds more effectively (Amaral, 1921*b*; Cogo et al., 1993). On the other hand, adults of *B. alcatraz* retained two characters of juveniles, a diet based on ectotherms (present study) and venom composition (M.F.D. Furtado, personal communication). The isolation of populations of the *B. jararaca*-like ancestor on coastal islands of southeastern Brazil may have occurred during one or more of the several oscillations of sea level during the Pleistocene (Martin et al., 1986), the last of these occurring about 11,000 yr ago (Rodrigues, 1990).

The main prey of the two insular species (birds and centipedes) occur in the diet of almost all generalist species of *Bothrops,* including *B. jararaca,* although in much lower frequencies (Martins et al., 2001), and were likely already present in the diet of their *B. jararaca*-like ancestor. Thus, feeding mostly on ectothermic prey by *B. alcatraz* and on birds by *B. insularis* may be considered as exaptations. A comprehensive study of the phylogeny and habits of the *jararaca* group, including other island populations along the coast of southeastern and southern Brazil, would provide useful tools for evaluating the hypotheses above.

In general, resources on islands are in short supply, especially on small islands, and this may explain why mammals seldom colonize these isolated habitats (McNab, 1994). On the other hand, ectotherms require lower levels of resource use and several reptiles are successful island colonizers (e.g., Case, 1983; Hasegawa and Morigushi, 1989). Well known examples of successful island colonizers among pitvipers include four species of *Bothrops* in the Caribbean and in south-

eastern Brazil (Campbell and Lamar, 1989; Duarte et al., 1995; our study), *Agkistrodon piscivorus* in coastal Florida (Wharton, 1969), and several species of rattlesnakes (e.g., Case, 1983) in the New World, as well as *Ovophis okinavensis* (Morigushi, 1989) and *Gloydius sheddaoensis* (Jian-Li, 1995) in Asia. The generalist habits of most pitvipers (Greene, 1992; Martins et al., 2001) may have greatly facilitated the colonization of islands by species of *Bothrops* and other pitvipers.

Although body size among species of island snakes is highly variable (e.g., Case, 1983; Schwaner, 1985), crotalines are generally smaller on islands (Case, 1983). Variation in body size in insular snakes may be a consequence of prey size and availability, as well as other factors such as presence or absence of predators and competitors (Case, 1983; Hasegawa and Morigushi, 1989; Kohno and Ota, 1991). Both insular species of the *B. jararaca* group are smaller than their mainland relative and have specialized diets. Competitors and predators are apparently absent or rare on both islands (see above). Thus, dwarfism in *B. alcatraz* (the smallest species in the *B. jararaca* group) may be related to the small size of its prey (centipedes and small lizards). On the other hand, *B. insularis* feeds mostly on relatively large prey (birds), and thus smaller size in this latter species may be related mostly to arboreal habits, as there seems to be an upper body size limit (around 1 m) for arboreality in *Bothrops* (Lillywhite and Smits, 1992).

The Alcatrazes lancehead is restricted to a small island off southeastern Brazil, where it is relatively common, although not as common as *B. insularis* on Queimada Grande Island (personal observation). A cliff portion of the Alcatrazes Island (Saco do Funil) has been used for target practice by cannons of the Brazilian Navy (F. P. de Campos, personal communication; personal observation). Should the practice continue, it would impose a threat for the Alcatrazes lancehead and other island endemics. Based on the information above, *B. alcatraz* is now included in the category Critically Endangered, criteria B1 (area of occupancy <10 km^2 and known from a single locality) and B2c (continuing decline observed in quality of habitat) of the IUCN Red List of Threatened Species (IUCN, 2000, www.redlist.org). *Bothrops insularis* of Queimada Grande Island is placed in the same category based on the same criteria (IUCN, 2000; see also Duarte et al., 1995), and the same may apply to several other island populations of *Bothrops* along the coast of southeastern Brazil, for which the taxonomic allocation remains uncertain. On the other hand, the coastal populations of *B. jararaca* are not under special threat at present, as most of the coastal Atlantic forest remnants in southeastern Brazil are included in protected areas (Kronka et al., 1993). Furthermore, *B. jararaca* is able to survive in disturbed habitats provided that some forest cover remains (Sazima, 1992).

RESUMO

Uma espécie nova de viperídeo, *Bothrops alcatraz,* pertencente ao grupo *jararaca,* é descrita da Ilha de Alcatrazes, situada na costa de São Paulo no sudeste do Brasil. Esta espécie difere das populações continentais da costa do sudeste do Brasil pela coloração mais escura, menor tamanho, menor número de escamas ventrais, subcaudais e infra-labiais, número e forma das placas cefálicas anteriores e formato dos espinhos do hemipênis, além da intensa atividade coagulante e da presença de três proteínas específicas do veneno. A espécie nova difere de *Bothrops insularis,* outra espécie insular de jararaca do sudeste do Brasil, pelo padrão de coloração, menor tamanho, menor número de subcaudais em machos e ausência de hemiclitoris em fêmeas. Algumas características de *B. alcatraz,* como o tamanho pequeno do adulto, os olhos proporcionalmente grandes, a intensa atividade coagulante do veneno e a dieta composta por centopéias e lagartos, podem ser interpretadas como pedomórficas dentro do grupo *jararaca.* Sugerimos aqui que o pequeno tamanho e as características do veneno de *B. alcatraz* estejam relacionados à sua dieta (semelhante à dos juvenis de *B. jararaca* do continente), o que pode ser resposta à difer-

ente disponibilidade de tipos de presas na Ilha de Alcatrazes (especialmente a ausência de pequenos mamíferos). *Bothrops alcatraz* e *B. insularis* podem ter se originado através do isolamento de populações ancestrais semelhantes a *B. jararaca* nas ilhas de Alcatrazes e Queimada Grande, respectivamente. A espécie nova é considerada como criticamente ameaçada devido a sua pequena área de ocorrência e o declínio da qualidade de habitat.

Acknowledgments.—We thank J. A. Campbell, J. R. Mendelson III, and an anonymous referee for helpful comments on the manuscript; H. Ferrarezzi and F. L. Franco for useful comments throughout the study; the Brazilian Navy for allowing access to Alcatrazes Island; M. E. Calleffo, A. Martensen, M. E. Oliveira, D. N. Pereira, R. Sawaya, and the marines for help in fieldwork; J. Cavalheiro, H. Ferrarezzi, V. J. Germano, and J. L. Oliveira for help in laboratory work; F. P. de Campos and Projeto Alcatrazes for help during field trips; M. F. D. Furtado for information on venom of island species; W. Duleba and H. W. Greene for help with literature; F. P. de Campos for photographs of Alcatrazes Island; D. N. Pereira for expertly finishing our line drawings. This study is part of the project Natural History and Evolution of *Bothrops* supported by FAPESP (1995/09642-5). Providential fellowships were provided by the CNPq to O. A. V. Marques and I. Sazima.

Literature Cited

Almeida-Santos, S. M., and M. G. Salomão. 2001. Reproductive strategies in tropical pitvipers, genus *Bothrops* (Serpentes: Viperidae: Crotalinae). In press. *In* G. Schuett, M. Höggren, and H. W. Greene (Eds.), Biology of the Vipers. Eagle Mountain Publishing, Eagle Mountain, Utah, U.S.A.

Amaral, A. 1921*a*. Contribuição para o conhecimento dos ophidios do Brasil. Parte I. Quatro novas espécies de serpentes brasileiras. Anexos das Memórias do Instituto Butantan 1:1–37.

———. 1921*b*. Contribuição para o conhecimento dos ophidios do Brasil. A. Parte II. Biologia da nova espécie. Anexos das Memórias do Instituto Butantan 1:39–44.

Andrade, D. V., and A. S. Abe. 1999. Relationships of venom ontogeny and diet in *Bothrops*. Herpetologica 55:200–204.

Andrade, D. V., A. S. Abe, and M. C. dos Santos. 1996. Is the venom related to diet and tail color during *Bothrops moojeni* ontogeny? Journal of Herpetology 30:285–288.

Cadle, J. E. 1992. Phylogenetic relationships among vipers: immunological evidence. Pp. 41–48. *In* J. A. Campbell and E. D. Brodie (Eds.), Biology of the Pitvipers. Selva, Tyler, Texas, U.S.A.

Campbell, J. A. 1985. A new species of highland pitviper of the genus *Bothrops* from southern Mexico. Journal of Herpetology 19:48–54.

Campbell, J. A., and W. W. Lamar. 1989. The Venomous Reptiles of Latin America. Cornell University Press, Ithaca, New York, U.S.A.

Case, T. J. 1983. The reptiles: ecology. Pp. 159–209. *In* T. J. Case and M. L. Cody (Eds.), Island Biogeography in the Sea of Cortéz. University of California Press, Berkeley, California, U.S.A.

Cogo, J. C., J. P. Prado-Franceschi, M. A. Cruz-Hofling, A. P. Corrado, and M. A. Rodrigues-Simioni. 1993. Effect of *Bothrops insularis* venom on the mouse and chick nerve-muscle preparation. Toxicon 31:1237–1247.

Dowling, H. G., and J. M. Savage. 1960. A guide to the snake hemipenis: a survey of basic structure and systematic characteristics. Zoologica (New York) 45:17–28.

Duarte, M. R., G. Puorto, and F. L. Franco. 1995. A biological survey of the pitviper *Bothrops insularis* Amaral (Serpentes, Viperidae): an endemic and threatened offshore island snake of southeastern Brazil. Studies on Neotropical Fauna and Environment 30:1–13.

Forsman, A. 1991. Adaptative variation in head size in *Vipera berus* L. populations. Biological Journal of the Linnean Society 43:281–296.

Furtado, M. F. D., M. Maruyama, A. S. Kamiguti, and L. C. Antonio. 1991. Comparative study of nine *Bothrops* snake venoms from adult female snakes and their offspring. Toxicon 29:219–226.

Greene, H. W. 1992. The ecological and behavioral context of pitviper evolution. Pp. 107–117. *In* J. A. Campbell and E. D. Brodie (Eds.), Biology of Pitvipers. Selva, Tyler, Texas, U.S.A.

Gutberlet, R. L. 1998. Phylogenetic Relationships of New World Pitvipers (Squamata: Crotalinae) as Inferred from Gross Anatomy, Epidermal Microstructure, and Mithochondrial DNA. Ph.D. Dissertation, University of Texas at Arlington, Arlington, Texas, U.S.A.

Hasegawa M., and H. Morigushi. 1989. Geographic variation in food habits, body size and life history traits of the snakes on the Izu islands. Pp. 414–432. *In* M. Matsui, T. Hikida, and R. C. Goris (Eds.), Current Herpetology in East Asia: Proceedings of the second Japan-China Herpetological Symposium, Kyoto, July 1988. Herpetological Society of Japan, Kyoto, Japan.

Hoge, A. R., H. E. Belluomini, G. Schreiber, and A. M. Penha. 1959. Sexual abnormalities in *Bothrops insularis* (Amaral, 1921). Memórias do Instituto Butantan 29:17–88.

Hoge, A. R., and S.A.R.W.L.D. Romano-Hoge. 1981 (dated 1978/79). Sinopse das serpentes peçonhentas do Brasil. Memórias do Instituto Butantan 42/43:373–496.

Janeiro-Cinquini, T. R. F., F. F. Leinz, and E. C. Farias. 1993. Ovarian cycle of the *Bothrops jararaca*. Memórias do Instituto Butantan 55:33–36.

Jian-Li, L. 1995. China Snake Island. Liaoning Science and Technology Press, Liaoning, China.

Kohno, H., and H. Ota. 1991. Reptiles in seabird colony: herpetofauna of Nakanokamishima Island of the Yaeyama group, Ryukyu archipelago. Islands Studies in Okinawa 9:73–89.

Kornerup, A., and J. H. Wanscher. 1961. Tas-

chenlexikon der farben. Musterschmidt Verlag, Zürich, Switzerland.

KRONKA, F. J. N., C. K. MATSUKUMA, M. A. NALON, I. H. DEL CALI, M. ROSSI, I. F. A. MATOS, M. S. SHIN-IKE, AND A. A. S. PONTINHAS. 1993. Inventário florestal do Estado de São Paulo. São Paulo, SMA/CINP/IF, São Paulo, Brazil.

LILLYWHITE, H. B., AND A. W. SMITS. 1992. The cardiovascular adaptations of viperid snakes. Pp. 143–153. *In* J. A. Campbell and E. D. Brodie (Eds.), Biology of the Pitvipers. Selva, Tyler, Texas.

LUEDERWALDT, H., AND J. P. FONSECA. 1923. A Ilha de Alcatrazes. Revista do Museu Paulista 13:441–512.

MARQUES, O. A. V., AND I. SAZIMA. 1997. Diet and feeding behavior of the coral snake, *Micrurus corallinus,* from the Atlantic forest in Brazil. Herpetological Natural History 5:88–91.

MARTIN, L., N. A. MÖRNER, J. M. FLEXOR, AND K. SUGUIO. 1986. Fundamentos e reconstrução de antigos níveis marinhos do Quartenário. Boletim do Instituto de Geociências, Publicação Especial 4:1–161.

MARTINS, M., O. A. V. MARQUES, AND I. SAZIMA. 2001. Ecological and phylogenetic correlates of feeding habits in Neotropical pitvipers of the genus *Bothrops.* In press. *In* G. Schuett, M. Höggren, and H. W. Greene (Eds.), Biology of the Vipers. Eagle Mountain Publishing, Eagle Mountain, Utah, U.S.A.

MCNAB, B. K. 1994. Resource use and the survival of land and freshwater vertebrates on oceanic islands. American Naturalist 144:643–660.

MORIGUSHI, H. 1989. Preliminary observation on *Trimeresurus okinavensis* in the field. Pp. 393–400. *In* M. Matsui, T. Hikida, and R. C. Goris (Eds.), Current Herpetology in East Asia: Proceedings of the Second Japan-China Herpetological Symposium, Kyoto, July 1988. Herpetological Society of Japan, Kyoto, Japan.

PARKINSON, C. L. 1999. Molecular systematics and biogeographical history of pitvipers as determined by mitochondrial ribosomal DNA sequences. Copeia 1999:576–586.

PETERS, J. A., AND B. OREJAS-MIRANDA. 1970. Catalogue of Neotropical Squamata. Part I. Snakes. United States National Museum Bulletin 297:1–347.

RODRIGUES, M. T. 1990. Os lagartos da floresta Atlântica distribuição atual e pretérita e suas implicações para estudos futuros. Pp. 404–410. *In* II Simpósio sobre ecossistemas da costa sul brasileira. estrutura, manejo e função. Academia de Ciências do Estado de São Paulo, São Paulo, Brazil.

SALOMÃO, M. G., W. WÜSTER, R. S. THORPE, AND BBBSP (Butantan-British *Bothrops* Systematics Project). 1997. DNA evolution of South American pit vipers of the genus *Bothrops.* Pp. 89–98. *In* R. S. Thorpe, W. Wüster, and A. Malhotra (Eds.), Venomous Snakes: Ecology, Evolution and Snakebite. Claredon Press, Oxford, U.K.

SALOMÃO, M. G., W. WÜSTER, R. S. THORPE, AND BBBSP (Butantan-British *Bothrops* Systematics Project). 1999. MtDNA phylogeny of Neotropical pitvipers of the genus *Bothrops* (Squamata: Serpentes: Viperidae). Kaupia: Darmstädter Beiträge zur Naturgeschichte 8:127–134.

SAZIMA, I. 1989. Feeding behavior of the snail-eating snake, *Dipsas indica.* Journal of Herpetology 23: 464–466.

———. 1992. Natural history of the jararaca pitviper, *Bothrops jararaca,* in southeastern Brazil. Pp. 199–216. *In* J. A. Campbell and E. D. Brodie (Eds.), Biology of Pitvipers. Selva, Tyler, Texas, U.S.A.

SAZIMA, I., AND A. J. ARGÔLO. 1994. *Siphlophis pulcher.* Prey. Herpetological Review 25:126.

SCHWANER, T. D. 1985. Population structure of black tiger snakes, *Notechis ater niger,* on offshore islands of south Australia. Pp. 35–46. *In* G. Grigg, R. Shine, and H. Ehmann (Eds.), Biology of Australian Frogs and Reptiles. Royal Zoological Society of New South Wales, Chipping Norton, New South Wales, Australia.

SHINE, R. 1994. Allometric patterns in the ecology of Australian snakes. Copeia 1994:851–867.

VANZOLINI, P. E. 1973. Distribution and differetiation of animals along the coast and in continental islands of the state of S. Paulo, Brasil. I. Introduction to the area and problems. Papéis Avulsos de Zoologia 26:281–294.

VIDAL, N., G. LECOINTRE, J. CHRISTOPHE, AND J. P. GASC. 1999. What can mitochrondrial gene sequences tell us about intergeneric relationships of pitvipers? Kaupia: Darmstädter Beiträge zur Naturgeschichte 8:107–112.

WERMAN, S. D. 1992. Phylogenetic relationships of Central and South American pitvipers of the genus *Bothrops* (*sensu lato*): Cladistic analyses of biochemical and anatomical characters. Pp. 21–40. *In* J. A. Campbell and E. D. Brodie (Eds.), Biology of the Pitvipers. Selva, Tyler, Texas, U.S.A.

WHARTON, C. H. 1969. The cottonmouth moccasin on Sea Horse Key, Florida. Bulletin of the Florida State Museum 14:227–272.

ZIEGLER, T., AND W. BÖHME. 1997. Genitalstrukturen und Paarungsbiologie bei squamaten Reptilien, speziell den Platynota, mit Bemerkungen zur Systematik. Mertensiella, Supplement zu Salamandra 8:6–207.

Accepted: 5 October 2001
Associate Editor: Joseph Mendelson III

APPENDIX I

Specimens Examined

Bothrops jararaca Ubatuba (ZUEC 01051, 01052, 01057, 01080, 01247, 01445, 01600, 01601, 01602); Peruibe, Estação Ecológica Juréia-Itatins (IB 57790, 57792, 57866, 57871, 57953, 58002, 58014, 58088); Iguape, Estação Ecológica Juréia-Itatins (IB 55196, 57805, 57808, 57811, 57840, 57856, 57888, 57896, 57897, 57903, 57904, 57908, 57927, 57940, 57941, 57989, 58001, 58035, 58108, 58130, 58134, 58145).