

Corallus caninus from Rio Formoso, Rondônia, Brazil. Photograph by Laurie J. Vitt.

The Emerald Puzzle: Geographic Variation in *Corallus caninus*

Robert W. Henderson

Section of Vertebrate Zoology, Milwaukee Public Museum, Milwaukee, WI 53233, USA (rh@mpm.edu)

Abstract.—The Emerald Treeboa (Corallus caninus) is one of the most famous and easily recognized snakes in the world. Despite this and its aesthetic appeal as an exhibit animal, surprisingly little is known about its biology. It has a wide geographic distribution in South America (the Guiana Shield and Amazonia), but is common nowhere. Emeralds are nocturnal and occur in mature rainforest where they prey on lizards, marsupials, and rodents. Corallus caninus has had a remarkably stable taxonomic history since being described nearly 250 years ago, but ongoing examination of geographic variation in morphological characters and analysis of DNA sequences strongly indicates that more than one species may be masquerading under the C. caninus umbrella.

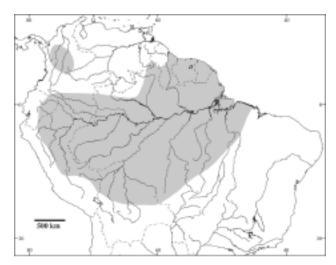
Key Words: Treeboas, Corallus caninus, South America, Amazonia, Guiana Shield

The Emerald Treeboa (Corallus caninus) is one of the species $oldsymbol{1}$ most readily recognized by snake enthusiasts worldwide, yet we know remarkably little about its natural history. It has an extensive distribution on the Neotropical mainland that encompasses most of the Guianas, a large portion of Venezuela, Amazonian Colombia, Ecuador, and Perú, northern Bolivia, and much of the Brazilian Amazon at elevations from sea level to about 1000 m. In addition, valid records of Corallus caninus exist for the departments of Antioquia and Córdoba in northwestern Colombia. Although largely arboreal, the Emerald Treeboa does occasionally descend to the ground. Like other members of the genus, it is nocturnal. Its diet is comprised mostly of rodents (e.g., Rice Rats, Oecomys sp.), but it also includes opossums and lizards. Despite many references to a diet of birds in the popular and technical literature, stomach content analysis has failed to support this notion. Observations in the field strongly suggest that C. caninus is an ambush predator that may perch close to ground level with its head angled downward to await a passing rodent. Next to nothing is known regarding population biology. A population density estimate of one treeboa per 2.7 km² (= 0.004/hectare) came from Departamento San Martín, Perú, but the investigator was dubious about the reliability of that figure. In contrast, I have calculated densities in excess of 50 Corallus grenadensis per hectare at one site on Grenada. However, most C. grenadensis in a local population prey on ubiquitous and phenomenally abundant *Anolis* lizards, whereas *C. caninus* prey almost exclusively on small mammals that occur at much lower densities.

Emeralds may reach a total length in excess of 2.0 m, with those from the Guiana Shield attaining larger size than those from Amazonia. The head of *Corallus caninus*, attached to a relatively slender neck, looks menacing, due, in part, to the heat-sensitive labial pits. In addition, these snakes are armed with long teeth on the anterior portions of the maxillae and

mandibles. These meat hook-like teeth prevent prey from accidentally falling irrecoverably to the ground below.

Emerald Treeboas are called "emerald" because of the exquisite green ground coloration on the dorsum. Coupled with the striking white markings typically occurring along the dorsal midline and in the form of the ventrolateral blotches found in some populations, their aesthetic appeal as exhibit animals in zoos and for herpetoculturists is easy to understand. Some of the latter are sufficiently enamored to specialize only in this species. Occasionally snakes from the Guiana Shield lack the typical middorsal white markings, yet are still eye-catching because of the vivid shades of green that may occur on a single individual. Still other individuals are heavily pigmented with black on the dorsum. Newborn treeboas are usually brick-red dorsally, and



Map illustrating the approximate range of the Emerald Treeboa (*Corallus caninus*).



Print of *Corallus caninus* capturing a domestic chicken (from an unknown source). Currently, we have no evidence of emeralds preying on birds (domestic or otherwise) by day or night.

the ontogenetic change to adult coloration is, I believe, part of the attraction of this species.

Taxonomic History

Corallus caninus has maintained a rather remarkable taxonomic stability since described by Linnaeus nearly 250 years ago. Although other "emerald" species were subsequently described (e.g., Boa aurantiaca Laurenti 1768, Chrysensis batesii Gray 1860), all were eventually relegated to the synonymy of Corallus caninus. One hundred and forty-five years have passed since Gray described Chrysensis batesii based on a juvenile specimen collected by pioneer Amazon naturalist, Henry Walter Bates, in the "Upper Amazon." Boulenger placed it into the synonymy of Corallus caninus in 1893. Since then, surprisingly little attention has been paid to the biological relationships of C. caninus,

despite its enigmatic juvenile coloration, its eye-catching adult coloration, and its popularity in zoos and among herpetoculturists.

Aside from a long-standing interest in *Corallus* biology, I was intrigued by the apparent lack of interest in and information about such a "famous" snake. I knew it was highly coveted by herpetoculturists, and that some pattern morphs commanded prices in the thousands of dollars. I also was aware that the species is exported in substantial numbers for the pet trade (e.g., during 1990–1996, 6830 *C. caninus* were exported from Guyana and Suriname) and may be vulnerable to local extirpations. Most boas are listed as CITES Appendix II (i.e., species which may be threatened with extinction or which may be affected by international trade; those not listed as Appendix II are Appendix I), and that includes Emerald Treeboas. Although

the species occurs over a wide geographic area, it is nowhere common, and occurs mostly in primary rainforest, which is disappearing at alarming rates.

I began borrowing preserved specimens of Emerald Treeboas about 15 years ago. Geographic variation was apparent, and I published some of my data over a decade ago. Subsequently, however, articles by herpetoculturists who specialized in breeding C. caninus caught my attention when they referred to "northern" or "shield" emeralds and "basin" emeralds. Although I had already observed and described some of the same geographic variation, I felt the species warranted more intensive scrutiny. I began anew my examination of preserved specimens of Corallus caninus, but only about 75 with reliable locality data were held in U.S. collections. Some countries within the range of *C. caninus* either were not represented by any specimens (e.g., French Guiana) in U.S. collections, or were poorly represented (e.g., Venezuela; one specimen). Also, treeboas from Brazil were, again, poorly represented in U.S. collections, and about 60% of the species' range falls in that country. I contacted collection curators in Brazil, Colombia, and Venezuela (Museo de Historia Natural La Salle), and also France (for French Guiana material), the Netherlands (for Suriname specimens), and Germany. Not surprisingly, more specimens were in Brazilian collections than elsewhere, and I received enthusiastic assistance from the Instituto Butantan, Museo de Zoologia at the Universidade de São Paulo, and the Museo Paraense Emílio Goeldi in Belém. Not all of the Brazilian specimens I wished to examine were available for loan, so I solicited the collaboration of Marinus Hoogmoed. A Dutch herpetologist, Dr. Hoogmoed has been studying South American frogs and reptiles for many years, and he now lives in Brazil. I was pleased when he agreed to collaborate and examine the many specimens housed at the Museo Paraense Emílio Goeldi.

Pieces of the Puzzle

After examining several dozen treeboas from across the wide range of the species, I clearly recognized that snakes from the Guiana Shield (the area north of the Rio Amazonas and east of the Rio Negro, *fide* Hoogmoed 1979) were distinct from those elsewhere in the range. Most obvious was the virtual lack of lateral blotches (mean of 1.5 ± 0.52 in 32 snakes), a low number of scales across the top of the muzzle (mean = 3.4 ± 0.24), and pale tissue (usually) in the mental groove. That was the easy part. South and west of the Guiana Shield, variation was more like a jigsaw puzzle.

To date, I have had the opportunity to examine about 125 Corallus caninus with accompanying locality data. Most snakes from eastern Brazil south of the Amazon (states of Pará and Maranhão) have conspicuous lateral blotches (mean of 16.4 ± 1.46), a white middorsal stripe connecting the bases of the white triangle-like markings that lie along the dorsum, more scales across the top of the muzzle (mean of 6.7 ± 0.34 in 16 snakes), and black interstitial tissue in the mental groove. In the state of Rondônia in western Brazil and in western Mato Grosso state, lateral blotches are absent or greatly reduced in number (mean of 5.8 ± 2.3 in 9 snakes), the middorsal stripe is absent, the number of scales across the top of the muzzle is reduced (mean of 4.9 ± 0.45), and the tissue in the mental groove is variable (white, gray, or black). In Amazonas state north of the Amazon and west of the Rio Negro (i.e., west of the Guiana Shield), the number of scales across the dorsal surface of the muzzle increases, lateral blotches are present, and the interstitial tissue



Engraving of Gray's Chrysensis batesii from the "Upper Amazon," based on a juvenile C. caninus (from the Proceedings of the Zoological Society, London 28:132–133).

A young Emerald Treeboa from kilometer 88 on the road between El Dorado and Santa Elena de Uairen, Bolivar, Venezuela. Note the absence of a middorsal stripe and lateral blotches. *Photograph by César Barrio, courtesy of Serpentario Los Llanos*.



Adult *Corallus caninus* from the vicinity of Ariquemes, Rondônia, Brazil, illustrating the absence of a middorsal stripe and lateral blotches. *Photograph by W. Carl Taylor*.

of the mental groove is black in adults (like dorsal ground color, this tissue undergoes an ontogenetic shift from yellowish to black). Surprisingly, I have no records from central Brazil (south of the Rio Amazonas) in the state of Amazonas.

Moving west into Ecuador, Perú (where the species occurs to 1000 m above sea level), and Bolivia, lateral blotches are a constant (although shapes are variable) and are more numerous than elsewhere across the range (mean of 23.4 ± 1.1 in 36 snakes). Likewise, the dorsal triangles are more numerous (mean



A juvenile *Corallus caninus* (SMF 80017) collected at ca. 1000 m above sea level at Pozuzo, Depto. Pasco, Perú. This is probably at or close to the upper altitudinal extreme for the species. *Photograph by Edgar Lehr*.



Emerald Treeboa from Santa Cecilia, Sucumbios, Ecuador, illustrating the middorsal stripe and lateral blotches common in *C. caninus* from some areas of Amazonia. *Photograph by William E. Duellman*.

of 32.8 ± 1.04 versus 25.9 elsewhere). A middorsal stripe may or may not be present. *Corallus caninus* from Ecuador and Perú also exhibit more scales across the muzzle than elsewhere (mean of 8.1 in 36 snakes).

Legitimate records of Emerald Treeboas at what appear to be localities isolated from the rest of the range occur north of the Colombian cordilleras Occidental and Central. Through the kind cooperation of Olga Castaño (Instituto de Ciencias Naturales, Universidad Nacional de Colombia) and Juan Manuel Daza-R. (Instituto de Biologia, Universidad de Antioquia), I have seen photographs and received scale and pattern data regarding these snakes. They lack middorsal stripes, but have lateral blotches typical of snakes from the upper Amazon. Likewise, the number of scales across the muzzle falls into the range for Colombian emeralds collected east of the Andes.

Assembling the Puzzle

Considering the breadth of the range of *Corallus caninus*, that the species displays geographic variation is not surprising. DNA



A road-killed *Corallus caninus* from Tierra Alta, Depto. Córdoba, Colombia (ICN 8398). *Photograph by Mikael Lundberg*.

sequences from critical areas across the range of *C. caninus* parallel the morphological data so far collected, and more than one species appears to be masquerading under the taxonomic umbrella of *C. caninus*. Many hypotheses (e.g., refugia, riverine barrier, marine incursion) have been addressed in order to explain speciation in Amazonia, and various authorities have noted that any Amazonian speciation model will be complex and, to some extent, species-specific. Collecting pieces of the "emerald puzzle" and their assembly is ongoing, with the analysis of morphological data hopefully providing additional insights into geographic variation and possible taxonomic partitioning of *C. caninus*.

Acknowledgements

I am grateful to Laurie Vitt for providing photographs of Emerald Treeboas and for sharing his observations from the field and lab. Juan Manuel Daza-R. called my attention to the Colombian record from Antioquia. Bill Lamar provided much useful information and offered photographs for my use. Nicolas Vidal was a pleasure to work with on the DNA material. Additional photos were provided by César Barrio, William Duellman, Edgar Lehr, Mikael Lundberg, Marcio Martins, and Carl Taylor. Rose Henderson scanned images from old sources, and Robert Powell provided the map. Joseph Polanco and Tony Nicoli shared information based on their experiences breeding emeralds in captivity. I especially thank the personnel from many institutions in several countries who have, so far, loaned specimens for my examination.



An Emerald Treeboa from Triunfo, slopes of Santa Rosa Tepui, Serrania del Supamo (100 km SSE of El Manteco), Estado Bolivar, Venezuela clearly showing the heat-sensitive labial pits that help give these snakes a menacing appearance. *Photograph by César Barrio.*

References

Boulenger, G. A. 1893. Catalogue of Snakes in the British Museum (Natural History). Vol. 1., Containing the Familes Typhlopidae, Glauconiidae, Boidae, Ilysiidae, Uropeltidae, Xenopeltidae, and Colubridae aglyphae, Part. Trustees of the British Museum, London.

Bush, M. B. 1994. Amazonian speciation: A necessarily complex model. *Journal of Biogeography* 21:5–17.

Chiras, S. 1998. Identification and husbandry of Amazon Basin Emerald Tree Boas (*Corallus caninus*). *Reptiles* 69(3):48–67 + 70–75.

Cracraft, J. and R. O. Prum. 1988. Patterns and process of diversification: Speciation and historical congruence in some Neotropical birds. *Evolution* 42:603–620.

Emmons, L. H. 1984. Geographic variation in densities and diversities of non-flying mammals in Amazonia. *Biotropica* 16:210–222.

Gray, J. E. 1860. Description of a new genus of Boidae discovered by Mr. Bates on the Upper Amazon. *Proceedings of the Zoological Society, London* 28:132–133.

Henderson, R. W. 1993. On the diets of some arboreal boids. *Herpetological Natural History* 1(1):91–96.

Henderson, R. W. 1993b. Corallus caninus. Catalogue of American Amphibians and Reptiles (574):1–3.

Henderson, R. W. 2002. Neotropical Treeboas: Natural History of the Corallus hortulanus Complex. Krieger Publishing Co., Malabar, Florida.

Hoogmoed, M. S. 1979. The herpetofauna of the Guianan region, pp. 241–279. In: W. E. Duellman (ed.), The South American Herpetofauna: Its Origin, Evolution, and Dispersal. University of Kansas Museum of Natural History Monograph (7), Lawrence, Kansas.

Kivit, R. and S. Wiseman. 2000. The Green Tree Python & Emerald Tree Boa: Their Captive Husbandry and Reproduction. Kirschner & Seufer Verlag, Keltern-Weiler, Germany.

Laurenti, J. N. 1768. Specimen Medicum, Exhibens Synopsin Reptilium Emendatum cum Experimentis circa Venena et Antidota Reptilium Austriacorum, quod Authoritate et Consensu. J. Thomæ Trattnern, Viennae.

Lehr, E. 2001. New records for amphibians and reptiles from departamentos Pasco and Ucayali, Peru. *Herpetological Review* 32:130–132.

Martins, M. and M. E. Oliveira. 1998. Natural history of snakes in forests of the Manaus Region, Central Amazonia, Brazil. Herpetological Natural History 6:78–150.

Renjifo, J. M. and M. Lundberg. 1999. Anfibios y Reptiles de Urrá. Skanska, Sweden

Schulte, R. 1988. Observaciones sobre la boa verde, *Corallus caninus*, en el Departamento San Martín-Perú. *Boletim de Lima* 55:21–26.

Vidal, N., R. W. Henderson, A.-S.Delmas, and S. B. Hedges. Submitted. Phylogeny of the Emerald Treeboa (*Corallus caninus*).