The Ecogeography of the Bushmaster, Lachesis muta, in Central America

JAMES L. VIAL and JESUS M. JIMENEZ-PORRAS
Department of Biology, University of Missouri at Kansas City 64110, and Biochemistry Department, University of Costa Rica, School of Medicine, San Jose, Costa Rica, C.A.

ABSTRACT: The ecological distribution of isthmian *Lachesis* is analyzed on the basis of its association with vegetation formations. The species is essentially restricted to tropical moist and wet forests in the coastal lowlands of Panama, Costa Rica and southeastern Nicaragua. Tropical dry forest areas have not significantly restricted populational interchange in the past, however, the cooler subtropics have been an effective limiting factor to latitudinal and altitudinal distribution. Present confinement of the bushmaster to the moist tropics is related to its historical origin in Central America, thermal requirements demanded by its large size and oviparous habit of reproduction.

INTRODUCTION

A paucity of captures and of sufficiently detailed locality records has accounted for the poorly known geographic limits and ecological distribution of the bushmaster. During the period 1961-64 we had the opportunity of acquiring several specimens of *Lachesis muta* from various localities within the Republic of Costa Rica, Central America, and to examine its distribution from hitherto unpublished records.

GENERAL DISTRIBUTION

The distributional range of *Lachesis* in South America has been generally defined as tropical Brazil, Bolivia, eastern Peru, Ecuador, the Guianas, the island of Trinidad, Venezuela and Colombia. The species is well known from certain areas in Panama, but has been considered extremely rare in Costa Rica. Although there are several references to the bushmaster occurring in Nicaragua (Ditmars, 1937; Cochran, 1943; Allen and Neill, 1959; Villa, 1962), no locality records from that country have been published. According to W. Leslie Burger (pers. comm.) the designation of "Nicaragua" for the specimen (USNM 14221) collected by J. F. Bransford is probably inaccurate; in fact the catalogue of the U. S. National Museum assigns the number to another species. Also, a substantial part of the Bransford collection is now known to be from Panama.

Much of the isthmian material in museum collections includes multiple records from limited areas, as can be seen from the localities listed in Table 1. However, our recent acquisitions in Costa Rica give evidence of a more extensive range and greater ecological valence for the species than has been previously recognized.

The bushmaster occupies the low-lying coastal belts in lower Central America; its distribution pattern being interrupted by mountain ranges and high plateaus. On the basis of actual capture records it

is presently reported from the El Darien lowlands, both Atlantic and Pacific versants in western Panama and Costa Rica, and as far north as the vicinity of Acoyapa, Chontales Province, Nicaragua (Villa, pers. comm.). With the exception of Villa (1962) inclusion of the latter country within the range of *Lachesis* has been based on dubious evidence, although the probability of its occurrence there has been a reasonable assumption.

ECOGEOGRAPHICAL CONSIDERATIONS

Almost invariably the bushmaster has been considered as a dweller of tropical rain forests (Ditmars 1937, and others). Undoubtedly the lack of any detailed information on much of the tropical environ-

TABLE 1.—Isthmian localities for *Lachesis*

Number		Locality
USNM	14221	Nicaragua
	32479	Costa Rica, Sipurio
KU	75767	Panama, Darien Province, Laguna
	102539	Costa Rica, Puntarenas Province, 4.5 km W Rincon de Osa
MCZ	27321	Panama, Chiriqui Province
	31538	Panama, Chagres River
	32444	Panama, Darien Province, Boca de Cupe
	32451	Panama, Alhajuela, Chagres River
	34196	Panama, Chagres River
	37084	Panama, Fork of Pihuila
	37085	Panama, Midbasin of Chagres
	37138	Panama, Darien Province, Yavisa
	37881	Panama, Boca de Pihuila
	37882	Panama, Madden Dam Rd.
	37883	Panama, Old San Juan
	43929	Panama, Chagres River
	43930	Panama, Chagres River
	43931	Panama, Chagres River
	50222	Panama
JVR	275	Nicaragua, Chontales Province, Between Acoyapa and Santo Tomas
USC-CR	2666	Costa Rica, Heredia Province, El Muelle de Sarapiqui
	2667	Costa Rica, Alajuela Province, San Carlos, "La Palmera"
	2668	Costa Rica, Limon Province, Siquirres (Km 53)
	2669	Costa Rica, Alajuela Province, Cedral de San Carlos
	2670	Costa Rica, Puntarenas Province, Villa Neilly
	2671	Costa Rica, Alajuela Province, Ciudad Quesada
	2672	Costa Rica, Alajuela Province, Hacienda Vieja de San Carlos
	2673	Costa Rica, Puntarenas Province, Buenos Aires
	8027	Costa Rica, Puntarenas Province, 7.5 mi SE Piedras Blancas (on Pan Am Hwy)

ment has contributed to this overgeneralization. The concept of rain forest (or hylea) vegetation, until recently ill-defined, has been treated as occupying a rather broad and continuous latitudinal region with its principal boundaries delimited by the 23½° tropic latitudes (Richards, 1957). However, Holdridge (1947, 1964), in his studies of the tropical vegetation formations, has established a basis for empirical determination of tropical "life zones." In the map (Fig. 1), major vegetational features associated with the distribution of *Lachesis* in Panama, Costa Rica and Nicaragua are delineated according to Holdridge (1959a, b; Holdridge and Budowski, 1962).

In lower and middle Central America the tropical humid vegetation includes the Tropical Moist Forest and Tropical Wet Forest. These two formations comprise a narrow, continuous belt along the Atlantic from El Darien in Panama to southeastern Nicaragua. The moist forest irregularly traverses the eastern Panamanian boundary. Much of the El Darien lowlands are represented by a transitional zone grading into a Tropical Dry Forest, which occupies a considerable part of the Pacific coastal area of central Panama and, to a lesser extent, the Chiriqui region. Tropical humid forests dominate the remaining Pacific lowlands to the vicinity of the Rio Tarcoles in west-central Costa Rica and are rather abruptly replaced by the Tropical Dry Forest. The latter vegetation forms an almost continuous

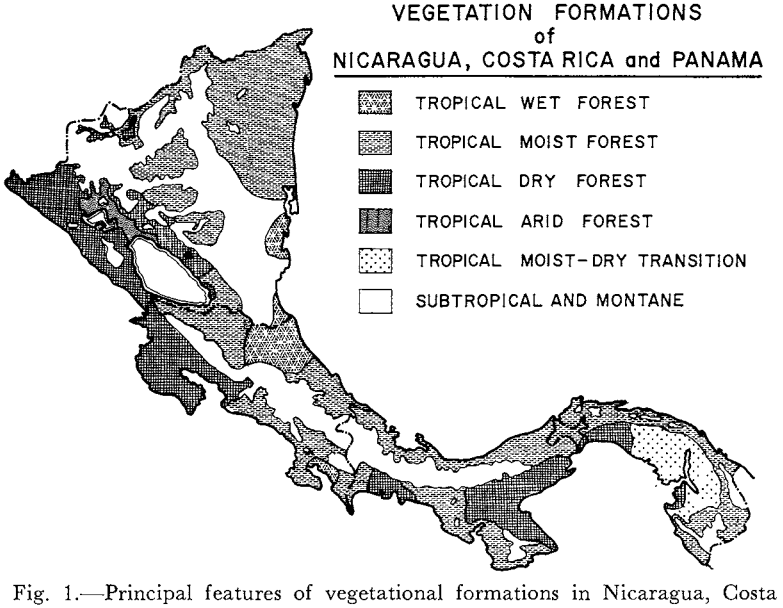

Fig. 1.—Principal features of vegetational formations in Nicaragua, Costa Rica and Panama related to the isthmian distribution of *Lachesis muta*, based on Holdridge's life zones. Solid circle indicates locality of the Acoyapa specimen.

strand along the coast of middle and upper Central America. Through the highlands of central Panama to northwestern Costa Rica, there extends a well-defined region of subtropical and montane vegetation, conspicuously separating Atlantic and Pacific lowland forests. Small, isolated pockets of subtropical vegetation occur within both coastal belts of the Tropical Moist Forest in Panama and Costa Rica. What appears to be of major relevance is the presence of a broad, irregular band of Subtropical Moist Forest extending from the Rio San Juan, northward through central Nicaragua, which completely intersects the humid forests of the Atlantic lowlands and the Tropical Dry Forest to the west.

The bushmaster is closely associated with the virginal distribution of tropical humid forests. Specific locality records at hand indicate that it inhabits the Tropical Moist and Tropical Wet Forests in Panama and Costa Rica and probably occurs with the latter formation in the extreme southeastern corner of Nicaragua. The El Darien localities are within the broad ecotone between Tropical Moist and Tropical Dry formations in Pacific eastern Panama.

It is unfortunate that the Chiriqui locality of the MCZ (27321) specimen is not exact enough to indicate its ecological association. However, Acoyapa, Nicaragua, where Villa's specimen was obtained, is situated in a Tropical Dry Forest area. It seems probable that the bushmaster has been capable of occupying this formation to a certain degree, most likely along riparian habitats in which moisture conditions are considerably in excess of those primarily determined by precipitation. This may explain why the Pacific dry forests of Veraguas and Chiriqui, in central and western Panama, respectively, have not effectively limited its distribution in the recent past. Certainly the strictly warm tropical *Lachesis* has not been capable of traversing the central highlands conspicuously dividing its range.

According to Brattstrom (1964), *Lachesis* demonstrates a remarkable homogeneity of morphological characters throughout its range. Such uniformity suggests that geographic isolation of populations is either not significant or has been of but short duration. In the former case continued interchange of the Pacific populations through the dry forest areas would be required; regarding the latter, it should be noted that intensive shifting agriculture and heavy cattle grazing have decimated much of the original vegetation. The dry forest areas are probably a more stringent barrier now than in the past.

Apparently subtropical temperatures have been an effective barrier to any recent northward expansion of the bushmaster's range. North of where the Subtropical Moist Forest intersects the Atlantic coast in southeastern Nicaragua, the tropical humid formations form an unbroken margin extending into Mexico. Although much of this region is remote and inaccessible, certain localities, such as Bluefields, Nicaragua (Tropical Wet Forest) and Lancetilla, Honduras (Tropical Moist Forest) have been extensively utilized for years as agricultural field stations. Nevertheless, no reliable reports of *Lachesis* have ap-

peared from these areas nor from British Honduras. The northernmost Acoyapa record is more likely a vagrant from the southern Tropical Moist Forest, rather than representing any population in the subtropical forests to the east.

It is appropriate to summarize here some of the physical features of those formations pertinent to the distribution of *Lachesis*. The elevational limit of the species is about 1,000 m; thus it is confined within the tropical belt or zone both latitudinally and altitudinally. By definition, average annual temperatures (here equated with biotemperatures of Holdridge, 1964) are 24 C or more, corrected to sea level, for all tropical formations. Average annual precipitation in the Tropical Wet Forest is 4,000 mm or more and between 2,000 and 4,000 mm in the Tropical Moist Forest. Tropical Dry Forests are characterized by an annual average precipitation of between 1,000 and 2,000 mm. The Subtropical Moist Forest has a corrected average annual temperature of from 17.5 to 24 C and between 1,000 and 2,000 mm average annual precipitation. Readers seeking details as to the nature of life zones (vegetation formations) are referred to Holdridge (1964).

Present-day restriction of the bushmaster to certain habitats within the neotropics is reflected in evidence of its ecogeographic history. Modern neotropical crotalines are apparently derived from temperate zone ancestors which included a *Crotalus-Lachesis* prototype in the early Cenozoic of North America (Darlington, 1957; Brattstrom, 1964). There is no evidence to suggest that *Lachesis* has ever extended its range beyond the lowland tropics since it first appeared in Central America, probably in the Oligocene.

The relationships of body size and conditions of meeting thermal requirements among ectotherms are well known. Available heat from solar radiation gradually diminishes with increasing latitude and elevation. In the absence of any significant compensating mechanism, the capacity to attain minimum thermal demands is primarily influenced by body size. Thus, no large reptiles are found in the more extreme latitudes or altitudes. It follows that the bushmaster, largest of the vipers, should be confined to the warmest tropical habitats. We can offer no support for Brattstrom's (1964) hypothesis that present limitations in the distribution of *Lachesis* are related to competition with large, terrestrial *Bothrops*. In Central America we have observed that *B. nummifer, B. picadoi* and *B. atrox,* among the largest of the genus, not only occur sympatrically with *Lachesis* throughout much of its range in the tropical humid forests, but also are found in cooler subtropical formations.

The egg-laying habit of *Lachesis* is unique among New World pitvipers and could also be a factor in its limited distribution. The cooler subtropical regions may not maintain an adequate thermal level for incubation. It may be, too, that dry forest areas do not offer sufficiently sustained moisture conditions required by the permeable eggs.

Acknowledgments and Abbreviations.—We are indebted to James A. Peters, United States National Museum (USNM); Ernest E. Williams, Museum of Comparative Zoology (MCZ); William E. Duellman, University of Kansas Museum of Natural History (KUMNH); and Jaime Villa R. of Managua, Nicaragua, (private collection — JVR) for information and the loan of material. Our own acquisitions are catalogued in the University of Southern California Costa Rican Series (USC-CR). W. Leslie Burger generously provided information regarding the validity of certain museum records. Field work incidental to this study was carried out during the tenure of a grant to the senior author from the Penrose Fund of the American Philosophical Society.

REFERENCES

ALLEN, R. AND W. T. NEILL. 1959. Doubtful locality records in British Honduras. *Herpetologica,* **15**:227-233.

BRATTSTROM, B. H. 1964. Evolution of the pit-vipers. *Trans. San Diego Soc. Natur. Hist.,* **13**:185-268.

COCHRAN, D. L. 1943. Poisonous reptiles of the world. *Smithsonian Inst. Publ. 3727, War Background Studies No. 10.* Washington, D. C. 37 p.

DARLINGTON, P. J., JR. 1957. Zoogeography: The Geographic Distribution of Animals. John Wiley & Sons, New York. 675 p.

DITMARS, R. L. 1937. Snakes of the World. Macmillan, New York. 207 p.

HOLDRIDGE, L. R. 1947. Determination of world plant formations from simple climatic data. *Science,* **105**:367-368.

———. 1959a. Mapa Ecologico de Costa Rica. Insto. Interamericano de Ciencias Agricolas. San Jose, Costa Rica.

———. 1959b. Mapa Ecologico de Nicaragua, A. C. Agencia de Desarrollo Internacional. Managua, Nicaragua.

———. 1964. Life Zone Ecology (*Provisional Ed.*). Tropical Science Center. San Jose, Costa Rica. 124 p.

——— AND G. BUDOWSKI. 1962. Mapa Ecologico de Panama. Insto. Interamericano de Ciencias Agricolas. San Jose, Costa Rica.

RICHARDS, P. W. 1957. The Tropical Rain Forest. University Press, Cambridge, England. 450 p.

VILLA R., J. 1962. Las Serpientes Venenosas de Nicaragua. Managua Nicaragua. 82 p.

SUBMITTED 15 JUNE 1966 ACCEPTED 9 NOVEMBER 1966